

ON A TWO-PATCH PREDATOR-PREY MODEL WITH ADAPTIVE HABITANCY OF PREDATORS

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ABSTRACT. A two-patch predator-prey model with the Holling type II functional response is studied, in which predators are assumed to adopt adaptive dispersal to inhabit the better patch in order to gain more fitness. Analytical conditions for the persistence and extinction of predators are obtained under different scenarios of the model. Numerical simulations are conducted which show that adaptive dispersal can stabilize the system with either weak or strong adaptation, when prey and predators tend to a globally stable equilibrium in one isolated patch and tend to limit cycles in the other. Furthermore, it is observed that the adaptive dispersal may cause torus bifurcation for the model when the prey and predators population tend to limit cycles in each isolated patch.

1. Introduction. Foraging behaviour is a common phenomenon in nature. As indicated in [19], foraging behaviour varies from ambush to active, in response to changes in environment and other circumstances. Although the foraging mode for a certain individual may change from time to time, many species have adopted the most advantageous foraging strategy through long-term evolution, either ambush or active, to maximize their survival probability. Species like spiders, or snakes, as indicated in [25], are classified as ambush predators because they “sit and wait” and then pounce when the opportunity arises. In contrast, other species, like wild dogs, as described in [6], move actively to forage prey.

Active foragers move back and forth searching for prey. Foraging behaviour of predators does not depend only on intra-species competition, but also depends on spatial abundance of resources and interspecies interaction in different patches. It has been widely observed in nature that many species migrate between different patches to search for resources because of apparent differences of resources, landscapes, or other environmental factors that affect the predators’ survival probability in different patches. Consequently, patch models have been introduced to simulate predator-prey dynamics with active foraging behaviour and dispersal of predators, as indicated in [3], [4], [16], and [17].

Patch models with dispersal of certain species have been studied extensively, see, e.g., [3], [4], [16], [17], [24] and the references therein. The common point in [16] and [17] is the assumption of density-independent dispersal rates. However, more and more experimental results and field observations in nature seem to suggest that

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predators have the ability to choose a better patch in which they can gain more fitness. Predators are more likely to move between different patches adaptively.

In behavioural ecology, an adaptive behaviour is a behaviour which contributes directly or indirectly to an individual's survival or reproductive success and is thus subject to the forces of natural selection ([22]). Adaptations are commonly defined as evolved solutions to recurrent environmental problems of survival and reproduction ([2]). Ecological species have the ability to adapt through learning ([21]). An individual will adjust its behaviour or strategy by learning in response to a change of the environment in order to survive and acquire the highest payoff. In evolutionary biology, analyzing an evolutionary stable strategy (ESS) under adaptation is one of the central topics. Another important concern is how species distribute themselves among different patches under adaptive dispersal. Based on the assumption that each individual has the ability to assess the condition of different patches and can move freely to maximize the individual fitness, the ideal free distribution (IFD) is proposed to illustrate the ecological equilibrium under adaptive dynamics ([10], [3]). It is natural to analyze the relationship between the ecological equilibrium and the evolutionary stable strategy. Several papers of [9], [7], [3], [14], [4] studied a variety of models including a single-species model, a two-patch competition model, a two-patch predator-prey model and an interacting-species model within finitely-many patches. They conclude that under certain conditions and assumptions, the evolutionary stable strategies are those which lead to the ideal free distribution.

In addition to the evolutionary and ecological aspects, predation behaviour can also produce a significant effect on predator-prey systems. As indicated in [1], different behaviour mechanisms can result in surprisingly different outcomes. Behavioural dynamics exerts significant effect on ecological and evolutionary dynamics. Functional responses are used to connect different behavioural dynamics of prey and predators. One important functional response which connects prey density and prey catch-per-predator is the Holling type II functional response, which was proposed by Holling ([13]). In contrast to the classical linear functional response, the Holling type II functional response assumes that the encounter rate of prey by predators is density-dependent. This matches experimental data for many species very well, as indicated in [20], [5]. Seitz *et al.* ([20]) conducted a series of experiments to study predator-prey dynamics of thin-shelled clams and their predators, the blue crabs, which inhabit the Chesapeake Bay. As indicated in [20], the predation on *Mya arenaria* (soft-shell clam) in mud and *M. mercenaria* (hard clam) in sand by their major predators, the blue crabs, obeys the Holling type II functional response. Clark *et al.* ([5]) conducted another experiment about foraging behaviour of the blue crabs in the Chesapeake Bay, but focused on studying the mechanism of foraging behaviour of the blue crabs between patches. In addition to predation of clams by the blue crabs in the Chesapeake Bay, there are other species in the ecological system which have similar predation mode, such as predation behaviour of rotifers on sessile planktonic species, and grazing behaviour of large herbivores. The above biological instances share one feature in common: all predators are mobile and migrate between different patches to forage prey or resources while prey or resources are sessile. In addition, as mentioned above, foraging behaviour of predators is adaptive because predators try to maximize individual fitness.

Křivan and Cressman ([15]) studied fast behaviour of predators moving between patches and showed that there exists a complicated relationship involving behavioural, population and evolutionary dynamics by studying three different

predator-prey models. Their study is based on the assumption that the behavioural dynamics runs on a much faster time scale than the demographical time scale and thus simplifies the original system. Krivan and Cressman ([15]) also explored the effect of adaptive dispersal exerting on population dynamics by using computer simulations. Based on [15], we consider a two-patch predator-prey model where predators move between two patches foraging on prey freely but each individual of the prey resides only within one patch. We combine population dynamics and behavioural dynamics together and investigate detailed dynamics of the whole system under the effect of adaptive dispersal.

The rest of the paper is organized as follows. In Section 2, we present the two-patch predator-prey model with the Holling type II functional response and adaptive dispersal of predators. In Section 3, mathematical analysis of the model is carried out to provide analytical conditions for persistence and extinction of the predators. Section 4 contains some numerical simulations. One interesting observation from these simulations is that if under isolation, the populations of the prey and predators in one patch tend to an equilibrium but those in the other patch tend to a limit cycle, then either weak or strong adaptation of the predators may stabilize the system in the sense that populations in both patches will tend to an equilibrium. Moreover, the strength of adaption has influences on the average biomass of predators. When the populations of the prey and predators tend to limit cycles in both patches under isolation, adaptive dispersal of predators may results in torus bifurcation. In Section 5, we summarize our findings and discuss some possible future projects along this line.

2. Model formulation. Our model will be built upon a two-patch predator-prey model with the Holling type II functional response, which is also known as the Rosenzweig-MacArthur model. This model is based on the assumptions that (i) prey and predators inhabit two patches which are totally separated; (ii) an individual of the prey does not disperse between the two patches and only predators move between two patches to forage on prey; (iii) the predators, they have the complete knowledge on the patch qualities and always tend to move to the better patch to gain more payoff which is measured by the per capita growth rate of predators. Under these assumptions, the two-patch Rosenzweig-MacArthur model is given by the following system of ordinary differential equations

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 (r_1 - a_1 x_1) - \frac{s_1 x_1 v y}{1 + h_1 s_1 x_1}, \\ \frac{dx_2}{dt} &= x_2 (r_2 - a_2 x_2) - \frac{s_2 x_2 (1 - v) y}{1 + h_2 s_2 x_2}, \\ \frac{dy}{dt} &= y \left(-m_1 v - m_2 (1 - v) + \frac{s_1 x_1 e_1 v}{1 + h_1 s_1 x_1} + \frac{s_2 x_2 e_2 (1 - v)}{1 + h_2 s_2 x_2} \right),\end{aligned}\tag{1}$$

where x_1 denotes the density of prey in patch 1, x_2 denotes the density of prey in patch 2, y represents the density of predators, v is the proportion of time that predators stay in patch 1 on average, r_i for $i = 1, 2$, is the intrinsic growth rate of prey in patch i , r_i/a_i is the carrying capacity of prey in patch i , s_i is the attacking rate of the predators in patch i , e_i is the expected biomass of prey converted to predators in patch i , m_i is the per capita mortality rate of predators in patch i , and h_i is the handling time of the predation in patch i respectively.

In model (1), the proportional time v that predators spend in patch 1 is assumed to be constant. However, predators seem to choose their habitat intelligently according to resource abundance in patches. In other words, they migrate between patches adaptively with the change of surrounding environment. If v increases, prey in patch 1 will be reduced due to the high predation risk and meanwhile, intra-specific competition of predators will be increased. As a consequence, predators tend to migrate to the second patch in order to maximize energy intake. Consequently, aggregation of predators in the second patch will again cause prey reduction in this patch, and this in turn impels predators to migrate to the first patch. Through adaptation of predators, v in model (1) should change with time rather than remain as a constant. Thus v can be viewed as the strategy of predators.

We now derive the strategy equation based on [10] and the idea of the replicator dynamics. As indicated in [10], the assumption that predators have the complete knowledge about patch qualities and always tend to move to a better patch to gain more fitness is valid. Let

$$f_1 = -m_1 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1}, \quad f_2 = -m_2 + \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2},$$

which measures the fitness of predators in patches 1 and 2 respectively. Because the proportion of time that predators forage in patch 1 is v and the corresponding proportion of time that predators stay in patch 2 is $1 - v$, the *average fitness* of predators switching over the two patches is

$$\bar{f} = v f_1 + (1 - v) f_2. \quad (2)$$

By the theory of adaptive dynamics ([12]), we have

$$\frac{dv}{dt} = k v (f_1 - \bar{f}). \quad (3)$$

By plain language, this means that the relative change rate of v is proportional to the difference of the fitness in patch 1 and the mean fitness over the two patches. In equation (3), k is a positive constant, with large k accounting for strong (fast) adaptation of predators in response to a change of prey abundance in the local patch, while small k explaining weak (slow) adaptation of predators.

Plugging (2) into (3), we obtain

$$\begin{aligned} \frac{dv}{dt} &= k v (1 - v) (f_1 - f_2) \\ &= k v (1 - v) \left(-m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right). \end{aligned} \quad (4)$$

Combining (1) and (4), we obtain our model system which describes both population dynamics and adaptive dynamics:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 (r_1 - a_1 x_1) - \frac{s_1 x_1 v y}{1 + h_1 s_1 x_1}, \\ \frac{dx_2}{dt} &= x_2 (r_2 - a_2 x_2) - \frac{s_2 x_2 (1 - v) y}{1 + h_2 s_2 x_2}, \\ \frac{dy}{dt} &= y \left(-m_1 v - m_2 (1 - v) + \frac{s_1 x_1 e_1 v}{1 + h_1 s_1 x_1} + \frac{s_2 x_2 e_2 (1 - v)}{1 + h_2 s_2 x_2} \right), \\ \frac{dv}{dt} &= k v (1 - v) \left(-m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right). \end{aligned} \quad (5)$$

In the next section, we will analyze this model system.

3. Mathematical analysis. We first address the well-posedness of the model (5), including non-negativity and boundedness of solutions. Since (5) is of Gauss type, the solution with any set of non-negative initial values for the four unknowns will remain non-negative for all t at which the solution exists. Moreover, if $x_1(0) = 0$, then $x_1(t) = 0$ for all $t \geq 0$. The same conclusion also holds for all other unknowns. For the strategy variable $v(t)$, writing the last equation in (5) as the following integral form

$$v(t) = 1 - 1 / \left(1 + v(0) / (1 - v(0)) \exp \left\{ \int_0^t \psi(\xi) d\xi \right\} \right), \tag{6}$$

where

$$\begin{aligned} \psi(\xi) = k \left(-m_1 + m_2 + (e_1 s_1 x_1(\xi)) / (1 + h_1 s_1 x_1(\xi)) \right. \\ \left. - (e_2 s_2 x_2(\xi)) / (1 + h_2 s_2 x_2(\xi)) \right). \end{aligned} \tag{7}$$

From (6), we know that $v(t) \in [0, 1]$ for $t \geq 0$, as long as $v(0) \in [0, 1]$; if the case $v(0) = 0$ then $v(t) = 0$ for all $t \geq 0$; if $v(0) = 1$ then $v(t) = 1$ for $t \geq 0$; and if $v(0) \in (0, 1)$ then so is $v(t)$ for all $t \geq 0$. Although the dedicated cases $v(0) = 0$ and $v(0) = 1$ will be addressed for mathematical purpose, we are mainly interested in the case of $v(0) \in (0, 1)$. This can be justified by assuming that initially there are predators in both patches. Next, we address boundedness of solutions. To this end, let $(x_1(t), x_2(t), y(t), v(t))$ be any non-negative solution with $x_1(0) \geq 0, x_2(0) \geq 0, y(0) \geq 0$ and $v(0) \in [0, 1]$. We have seen from the above that $v(t) \in [0, 1]$ for all $t \geq 0$ where the solution exists. We only need to confirm the boundedness of $x_1(t), x_2(t)$ and $y(t)$. To this end, let $G = e_1 x_1 + e_2 x_2 + y$. By direct calculation, we obtain

$$\begin{aligned} \frac{dG}{dt} &= -m_1 v G - m_2 (1 - v) G + [e_1 r_1 + m_1 v e_1 + m_2 (1 - v) e_1] x_1 \\ &\quad + [e_2 r_2 + m_1 v e_2 + m_2 (1 - v) e_2] x_2 - e_1 a_1 x_1^2 - e_2 a_2 x_2^2 \\ &\leq -m_1 v G - m_2 (1 - v) G + \frac{[e_1 r_1 + m_1 v e_1 + m_2 (1 - v) e_1]^2}{4 e_1 a_1} \\ &\quad + \frac{[e_2 r_2 + m_1 v e_2 + m_2 (1 - v) e_2]^2}{4 e_2 a_2}. \end{aligned} \tag{8}$$

Because we have shown that v is bounded between 0 and 1, we obtain

$$\frac{dG}{dt} \leq -m_0 G + \eta_0, \tag{9}$$

where $m_0 = \min\{m_1, m_2\}$ and η_0 is a positive constant. By the comparison principle, we conclude that

$$\limsup_{t \rightarrow \infty} G(t) = \frac{\eta_0}{m_0},$$

implying that G is bounded. This also indicates that $\eta_0/m_0 e_1, \eta_0/m_0 e_2$ and η_0/m_0 are also *a priori* bounds of $x_1(t), x_2(t)$ and $y(t)$ respectively. The boundedness of the solution also implies that it exists globally, that it, it exists for all $t \in (0, \infty)$.

The above analysis also show that the set

$$X = \mathcal{R}_+^4 = \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y \geq 0, 0 \leq v \leq 1\},$$

is positively invariant, and we will only need to consider the dynamics of the model in this set.

In order to analyze the long-term behaviour of system (5), we first discuss the structure of all possible equilibria for this system. For convenience of notations, we let

$$\begin{aligned} A_1 &= \frac{e_1 s_1 r_1}{a_1 + h_1 s_1 r_1} - m_1, & A_2 &= \frac{e_2 s_2 r_2}{a_2 + h_2 s_2 r_2} - m_2, \\ A_3 &= e_2, & A_4 &= e_2 - m_2 h_2, & A_5 &= r_2 s_2, & A_6 &= a_2 m_2, \\ A_7 &= e_1, & A_8 &= e_1 - m_1 h_1, & A_9 &= r_1 s_1, & A_{10} &= a_1 m_1. \end{aligned} \quad (10)$$

Denote

$$\begin{aligned} x_1^* &= \frac{m_1}{s_1(e_1 - m_1 h_1)}, & y_1^* &= \frac{e_1(r_1 s_1 e_1 - r_1 s_1 h_1 m_1 - a_1 m_1)}{s_1^2(e_1 - m_1 h_1)^2}, \\ x_2^* &= \frac{m_2}{s_2(e_2 - m_2 h_2)}, & y_2^* &= \frac{e_2(r_2 s_2 e_2 - r_2 s_2 h_2 m_2 - a_2 m_2)}{s_2^2(e_2 - m_2 h_2)^2}. \end{aligned} \quad (11)$$

Then, direct calculations show that there are always eight equilibria for the biologically meaningful parameters:

$$\begin{aligned} E_0^2 &= (0, 0, 0, 0), & E_1^2 &= \left(\frac{r_1}{a_1}, 0, 0, 0\right), & E_2^2 &= \left(0, \frac{r_2}{a_2}, 0, 0\right), & E_3^2 &= \left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 0\right), \\ E_0^1 &= (0, 0, 0, 1), & E_1^1 &= \left(\frac{r_1}{a_1}, 0, 0, 1\right), & E_2^1 &= \left(0, \frac{r_2}{a_2}, 0, 1\right), & E_3^1 &= \left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 1\right). \end{aligned}$$

In addition, five other equilibria including a unique positive equilibrium may come into existence under certain conditions on the model parameters:

$$\begin{aligned} E_4^1 &= (x_1^*, 0, y_1^*, 1), & E_5^1 &= \left(x_1^*, \frac{r_2}{a_2}, y_1^*, 1\right), \\ E_4^2 &= (0, x_2^*, y_2^*, 0), & E_5^2 &= \left(\frac{r_1}{a_1}, x_2^*, y_2^*, 0\right), \\ E^* &= (\tilde{x}_1^*, \tilde{x}_2^*, \tilde{y}^*, \tilde{v}^*) \text{ with } \tilde{x}_1^* > 0, \tilde{x}_2^* > 0, \tilde{y}^* > 0, \tilde{v}^* \in (0, 1). \end{aligned}$$

Obviously, $y_1^* > 0$ if and only if $A_1 > 0$ which implies $A_8 > 0$ (hence $x_1^* > 0$). Similarly, $y_2^* > 0$ if and only if $A_2 > 0$ which implies $A_4 > 0$ (hence $x_2^* > 0$). Here, all equilibria, except for E^* , have explicit formulas and each represents one situation of the specialist strategies ($v = 0$ or $v = 1$) meaning that all predators choose to inhabit in one patch. However, E^* with $\tilde{v}^* \in (0, 1)$ represents a generalist strategy, which can not be obtained explicitly; indeed, its existence will be established by an argument using abstract persistence theory.

The stability/instability of these equilibria can be analyzed by the standard method of investigating the characteristic equation at each of them, except for E^* . Below, we showcase the analysis on E_5^2 .

Theorem 3.1. *Assume that $A_2 > 0$ so that E_5^2 exists. Then, it is locally asymptotically stable if and only if*

$$A_1 < 0 \text{ and } A_4 A_5 (A_3 - A_4) < A_6 (2 A_3 - A_4). \quad (12)$$

Proof. The Jacobian matrix of (5) is

$$\begin{bmatrix} J_{11} & 0 & -\frac{s_1 x_1 v}{1 + h_1 s_1 x_1} & -\frac{s_1 x_1 y}{1 + h_1 s_1 x_1} \\ 0 & J_{22} & -\frac{s_2 x_2 (1 - v)}{1 + h_2 s_2 x_2} & \frac{s_2 x_2 y}{1 + h_2 s_2 x_2} \\ \frac{e_1 v s_1 y}{(1 + h_1 s_1 x_1)^2} & \frac{e_2 (1 - v) s_2 y}{(1 + h_2 s_2 x_2)^2} & J_{33} & J_{34} \\ \frac{k v (1 - v) e_1 s_1}{(1 + h_1 s_1 x_1)^2} & -\frac{k v (1 - v) e_2 s_2}{(1 + h_2 s_2 x_2)^2} & 0 & J_{44} \end{bmatrix}, \tag{13}$$

where

$$\begin{aligned} J_{11} &= r_1 - 2 a_1 x_1 - \frac{s_1 v y}{(1 + h_1 s_1 x_1)^2}, \\ J_{22} &= r_2 - 2 a_2 x_2 - \frac{s_2 (1 - v) y}{(1 + h_2 s_2 x_2)^2}, \\ J_{33} &= -m_1 v - m_2 (1 - v) + e_1 v \frac{s_1 x_1}{1 + h_1 s_1 x_1} + e_2 (1 - v) \frac{s_2 x_2}{1 + h_2 s_2 x_2}, \\ J_{34} &= y \left(-m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right), \\ J_{44} &= k (1 - 2 v) \left(-m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right). \end{aligned}$$

Substituting equilibrium E_5^2 into the Jacobian matrix (13) gives the characteristic equation at E_5^2 :

$$(\lambda + r_1) (\lambda - \bar{J}_{44}) (\lambda^2 - \bar{J}_{22} \lambda - \bar{J}_{23} \bar{J}_{32}) = 0, \tag{14}$$

where

$$\begin{aligned} \bar{J}_{44} &= k \left(-m_1 + m_2 + \frac{e_1 s_1 r_1}{a_1 + h_1 s_1 r_1} - \frac{e_2 s_2 x_2^*}{1 + h_2 s_2 x_2^*} \right), \\ \bar{J}_{22} &= r_2 - \frac{2 a_2 m_2}{s_2 (-m_2 h_2 + e_2)} - \frac{s_2 y_2^*}{(1 + h_2 s_2 x_2^*)^2}, \\ \bar{J}_{23} &= -\frac{s_2 x_2^*}{1 + h_2 s_2 x_2^*}, \quad \bar{J}_{32} = \frac{e_2 s_2 y_2^*}{(1 + h_2 s_2 x_2^*)^2}. \end{aligned}$$

Obviously, $\lambda_1 = -r$ and $\lambda_2 = \bar{J}_{44}$ are real roots of (14), and the other two roots of (14) are determined by the quadratic equation:

$$\lambda^2 - \bar{J}_{22} \lambda - \bar{J}_{23} \bar{J}_{32} = 0. \tag{15}$$

Note that $\bar{J}_{23} \bar{J}_{32} < 0$. Thus, the two roots of (15) have negative real parts if and only if $\bar{J}_{22} < 0$. Therefore, all roots of (14) have negative real parts if and only if

$$\bar{J}_{22} < 0 \quad \text{and} \quad \bar{J}_{44} < 0,$$

which are, by the notations defined in (11), equivalent to the two conditions in (12). This completes the proof. \square

The analysis of stability/instability of other equilibria, except for E^* , can be similarly done and will be omitted here since it would cost too much space. Table 1 summarizes such results.

As mentioned before, the existence of E^* can not established through solving the equations for equilibria. Instead it is established as a result of uniform persistence

Equilibrium	Existence	Stability	Condition for stability
$E_0^2(0, 0, 0, 0)$	always exists	unstable	
$E_1^2\left(\frac{r_1}{a_1}, 0, 0, 0\right)$	always exists	unstable	
$E_2^2\left(0, \frac{r_2}{a_2}, 0, 0\right)$	always exists	unstable	
$E_3^2\left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 0\right)$	always exists	Locally Stable	$A_2 < 0, A_1 < A_2$
$E_4^2(0, x_0^*, y_0^*, 0)$	$0 < A_2$	unstable	
$E_5^2\left(\frac{r_1}{a_1}, x_0^*, y_0^*, 0\right)$	$0 < A_2$	Locally Stable	$A_1 < 0, A_4 A_5(A_3 - A_4) < A_6(2A_3 - A_4)$
$E_0^1(0, 0, 0, 1)$	always exists	unstable	
$E_1^1\left(\frac{r_1}{a_1}, 0, 0, 1\right)$	always exists	unstable	
$E_2^1\left(0, \frac{r_2}{a_2}, 0, 1\right)$	always exists	unstable	
$E_3^1\left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 1\right)$	always exists	Locally Stable	$A_1 < 0, A_2 < A_1$
$E_4^1(x_1^*, 0, y_1^*, 1)$	$0 < A_1$	unstable	
$E_5^1\left(x_1^*, \frac{r_2}{a_2}, y_1^*, 1\right)$	$0 < A_1$	Locally Stable	$A_2 < 0, A_8 A_9(A_7 - A_8) < A_{10}(2A_7 - A_8)$
$E(\tilde{x}_1^*, \tilde{x}_2^*, \tilde{y}^*, \tilde{v}^*)$	$0 < A_1, 0 < A_2$		

TABLE 1. The upper index i ($i = 1, 2$) indicates that predators forage only in patch i without migrating to the other patch. $E(\tilde{x}_1^*, \tilde{x}_2^*, \tilde{y}^*, \tilde{v}^*)$ is the unique positive equilibrium.

of the model. To this end, we will first establish the uniform persistence of the population with a generalist strategy ($v \in (0, 1)$) under the conditions $A_1 > 0$ and $A_2 > 0$. For this purpose, we need to obtain some information about the patch-wise dynamics, that is, the population dynamics when the predator only stays in one patch, by considering the following system (obtained by taking taking $v = 0$ or $v = 1$ in (5)):

$$\begin{cases} \frac{dx_i}{dt} = x_i(r_i - a_i x_i) - \frac{s_i x_i y}{1 + h_i s_i x_i}, \\ \frac{dy}{dt} = y\left(-m_i + e_i \frac{s_i x_i}{1 + h_i s_i x_i}\right). \end{cases} \quad (16)$$

For such a classic prey-predator model, generally, when the carrying capacity of the prey is not too large, the populations of prey and predator tend to a unique positive steady state; while when the carrying capacity of the prey is sufficiently large, oscillations will occur and the populations of prey and predators tend to a globally stable limit cycle. To state this more precisely, we first note that for $i = 1, 2$, $A_i > 0$ is equivalent to

$$\frac{m_i h_i}{s_i h_i(e_i - m_i h_i)} < \frac{r_i}{a_i},$$

which is also the condition for x_i^* and y_i^* to be positive (hence existence of positive equilibrium (x_i^*, y_i^*) for (16)). Thus, if both A_1 and A_2 are negative, regardless of whether choosing to stay in patch 1 ($v(t) = 1$) or patch 2 ($v(t) = 0$), the predator will go to extinction. Indeed, in such a case, this conclusion remains true for any general strategies in (5), as is confirmed in the following theorem.

Theorem 3.2. *The predators go to extinction if $A_1 < 0$ and $A_2 < 0$.*

Proof. Applying the comparison principle to the first and the second equation in (5), we have the estimates:

$$\limsup_{t \rightarrow \infty} x_i(t) \leq \frac{r_i}{a_i}, \quad i = 1, 2.$$

Thus, for any $\epsilon > 0$, there exists $t^* > 0$ such that

$$x_i(t) \leq \frac{r_1}{a_1} + \epsilon \quad \text{for } t \geq t^*. \tag{17}$$

This together with the third equation in (5) lead to

$$\frac{dy}{dt} \leq By, \tag{18}$$

where

$$B = -m_1 v - m_2 (1 - v) + \frac{e_1 v s_1 (r_1 + a_1 \epsilon)}{a_1 + h_1 s_1 (r_1 + a_1 \epsilon)} + \frac{e_2 (1 - v) s_2 (r_2 + a_2 \epsilon)}{a_2 + h_2 s_2 (r_2 + a_2 \epsilon)}.$$

Noting that

$$\lim_{\epsilon \rightarrow 0} \left(-m_1 v - m_2 (1 - v) + \frac{e_1 v s_1 (r_1 + a_1 \epsilon)}{a_1 + h_1 s_1 (r_1 + a_1 \epsilon)} + \frac{e_2 (1 - v) s_2 (r_2 + a_2 \epsilon)}{a_2 + h_2 s_2 (r_2 + a_2 \epsilon)} \right) \tag{19}$$

$$= v(A_1 - A_2) + A_2 = vA_1 + (1 - v)A_2 < 0.$$

One can choose $\epsilon > 0$ sufficiently small such that $B < 0$. This together with (18) implies that $y(t) \rightarrow 0$ as $t \rightarrow \infty$, that is, the predator goes to extinction. \square

By this theorem, in order for the predators to be persistent, at least one of the two quantities A_1 and A_2 must be positive. To proceed further, we need the following lemma, which can be easily proved by standard methods (see, e.g., [18]), on the prey-predator model (16).

Lemma 3.3. *Assume that $A_i > 0$. If*

$$(H_i) \quad \frac{r_i}{a_i} < \frac{e_i + m_i h_i}{s_i h_i (e_i - m_i h_i)},$$

then, every positive solution of (16) approaches to a positive equilibrium; and if

$$(H_i^-) \quad \frac{e_i + m_i h_i}{s_i h_i (e_i - m_i h_i)} < \frac{r_i}{a_i},$$

then, every positive solution of (16) tends to a positive limit cycle, except for those solutions starting from unstable equilibria.

In the remainder of this section, we consider the case when both A_1 and A_2 are positive, and will leave the case that $A_1 A_2 < 0$ to the next section for discussion where we will present some numerical simulation results.

Now we are in the position to establish the persistence of the predators, as well as of the strategy functions $v(t)$ and $1 - v(t)$ for the case when both A_1 and A_2 are positive.

Theorem 3.4. *Assume that $A_1 > 0$ and $A_2 > 0$. Then the predator population in system (5) is uniformly persistent.*

Proof. We apply the theory in [11, 23] to complete the proof. To this end, we distinguish four cases:

- (I) (H_1) and (H_2) hold; (II) (H_1) and (H_2^-) hold;
- (III) (H_1^-) and (H_2) hold; (IV) (H_1^-) and (H_2^-) hold.

We only give the proof for Case (I), since the proofs for the other three cases are similar and are thus omitted to save space.

Define

$$\begin{aligned} X &= \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y \geq 0, 0 \leq v \leq 1\}, \\ X_0 &= \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y > 0, 0 \leq v \leq 1\}, \\ Y &= X/X_0 = \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y = 0, 0 \leq v \leq 1\}. \end{aligned} \quad (20)$$

There are eight equilibria in set Y :

$$\begin{aligned} E_0^2(0, 0, 0, 0), E_1^2\left(\frac{r_1}{a_1}, 0, 0, 0\right), E_2^2\left(0, \frac{r_2}{a_2}, 0, 0\right), E_3^2\left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 0\right), \\ E_0^1(0, 0, 0, 1), E_1^1\left(\frac{r_1}{a_1}, 0, 0, 1\right), E_2^1\left(0, \frac{r_2}{a_2}, 0, 1\right), E_3^1\left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 1\right). \end{aligned}$$

Following notations in [11], A_∂ being the global attractor in the boundary set Y , we have

$$\begin{aligned} \tilde{A}_\partial &= \bigcup_{x \in A_\partial} \omega(x) \\ &= \bigcup E_i^j, \quad i = 0, 1, 2, 3, \quad j = 1, 2. \end{aligned}$$

In order to show \tilde{A}_∂ is isolated and has an acyclic covering, first, we consider the system restricted on Y :

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - a_1 x_1), \\ \frac{dx_2}{dt} &= x_2(r_2 - a_2 x_2), \\ \frac{dv}{dt} &= kv(1-v) \left(-m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right). \end{aligned} \quad (21)$$

Note that among equilibria E_i^j for $i = 0, 1, 2, 3; j = 1, 2$, the sequence E_i^2 , $i = 0, 1, 2, 3$ correspond to $v = 0$ and the sequence E_i^1 , $i = 0, 1, 2, 3$ correspond to $v = 1$. First, we show the analysis for the former case. When $v = 0$, the three-dimensional system (21) reduces to a two-dimensional system. Because equilibrium E_3^2 is globally asymptotically stable for the two-dimensional system, it is clear that $E_0^2, E_1^2, E_2^2, E_3^2$ are isolated and acyclic in set Y . By checking eigenvalues of each equilibrium, it can be shown that $E_0^2, E_1^2, E_2^2, E_3^2$ are also isolated in set X .

Next, we show that $W^s(E_3^2) \cap X_0 = \emptyset$. Suppose this is not true. Then there exists a solution of (5) with $y(t)$ positive such that

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t), v(t)) = \left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 0 \right). \quad (22)$$

Denote

$$R(t) = -m_1 v - m_2(1-v) + \frac{e_1 v s_1 x_1}{1 + h_1 s_1 x_1} + \frac{e_2(1-v) s_2 x_2}{1 + h_2 s_2 x_2}.$$

Then (22) implies that $R(t) \rightarrow A_2 > 0$ as $t \rightarrow \infty$. Thus, for $\epsilon \in (0, A_2)$, there exists $T > 0$ such that $R(t) > A_2 - \epsilon > 0$ for $t \geq T$. Therefore,

$$\frac{dy}{dt} = R(t)y \geq (A_2 - \epsilon)y, \quad \text{for } t \geq T, \quad (23)$$

which implies that y grows unboundedly by the comparison principle. This contradicts the boundedness of $y(t)$. Therefore, $W^s(E_3^2) \cap X_0 = \emptyset$ if $A_2 > 0$. Similarly, we can prove $W^s(E_i^2) \cap X_0 = \emptyset$ for $i = 0, 1, 2$ when condition $A_2 > 0$ holds.

For the case corresponding to $v = 1$, we can prove that $A_1 > 0$ implies $W^s(E_i^1) \cap X_0 = \emptyset$ for $i = 0, 1, 2, 3$. The proof here is similar to the proof for the case $v = 0$ (it is actually a result of the conjugacy of v and $1 - v$) and is thus omitted.

Now, by the theoretical results in persistence theory (see, e.g., [11] or [23]), we have proved that the predator’s population in system (5) is uniformly persistent. \square

Next, we show that strategy variable $v(t)$ is also persistent if both A_1 and A_2 are positive. We also distinguish the local case (H_i) (convergence to equilibrium) from the local case (H_i^-) (convergence to limit cycle).

Theorem 3.5. *Assume that $A_1 > 0$ and $A_2 > 0$. Then the strategy functions $v(t)$ and $1 - v(t)$ are uniformly persistent in the sense that there exists a $\eta > 0$ such that*

$$\liminf_{t \rightarrow \infty} v(t) > \eta, \quad \text{and} \quad \liminf_{t \rightarrow \infty} [1 - v(t)] > \eta.$$

In order to prove the strategy’s persistence, we need to prove that $v = 0$ and $v = 1$ are both uniform repellers. To this end, we define the same set X as in the proof of Theorem 3.4 but define the interior set and the boundary set with respect to v and $1 - v$ by

$$\begin{aligned} \hat{X}_0 &= \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y \geq 0, 0 < v < 1\}, \\ \hat{Y} &= X/\hat{X}_0 = Y_1 \cup Y_2, \end{aligned}$$

where, $Y_1 = \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y \geq 0, v = 0\}$ and $Y_2 = \{(x_1, x_2, y, v) : x_1 \geq 0, x_2 \geq 0, y \geq 0, v = 1\}$.

As in the proof of Theorem 3.4, we also distinguish four local cases as in the proof of Theorem 3.5, depending on whether the local dynamics is convergence to equilibrium (i.e., under (H_i)), or convergence to limit cycle (i.e., under (H_i^-)).

Proof of Case (I). (H_1) and (H_2) hold. First, we prove that $v = 0$ (i.e. Y_1) is a uniform repeller. When $v = 0$, six equilibria, namely

$$\begin{aligned} &E_0^2(0, 0, 0, 0), E_1^2\left(\frac{r_1}{a_1}, 0, 0, 0\right), E_2^2\left(0, \frac{r_2}{a_2}, 0, 0\right), \\ &E_3^2\left(\frac{r_1}{a_1}, \frac{r_2}{a_2}, 0, 0\right), E_4^2(0, x_2^*, y_2^*, 0), E_5^2\left(\frac{r_1}{a_1}, x_2^*, y_2^*, 0\right), \end{aligned}$$

exist in set Y_1 . Let us consider the system restricted in Y_1 :

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - a_1 x_1), \\ \frac{dx_2}{dt} &= x_2(r_2 - a_2 x_2) - \frac{s_2 x_2 y}{1 + h_2 s_2 x_2}, \\ \frac{dy}{dt} &= y\left(-m_2 + \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2}\right). \end{aligned} \tag{24}$$

For system (24), equilibrium E_5^2 is globally asymptotically stable when $A_2 > 0$, i.e. when equilibrium E_5^2 exists. Therefore, equilibria $E_0^2, E_1^2, E_2^2, E_3^2, E_4^2, E_5^2$ are isolated and acyclic in the set Y . By checking the eigenvalues of each equilibrium, we can see that E_i^2 for $i = 0, 1, 2, 3, 4, 5$ are also isolated in set X .

Next, we prove that $W^s(E_5^2) \cap X_0 = \emptyset$. Suppose that is not the case. Then there exists a solution of (5) in X_0 , such that

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t), v(t)) = \left(\frac{r_1}{a_1}, x_2^*, y_2^*, 0 \right). \tag{25}$$

Denote

$$r(t) = -m_1 + m_2 + \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} - \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2}.$$

Then (25) implies that $r(t) \rightarrow A_1 > 0$ as $t \rightarrow \infty$. Thus for any $\epsilon \in (0, A_1)$, there exists $T > 0$ such that $r(t) > A_1 - \epsilon$ for $t \geq T$. Therefore,

$$\frac{dv}{dt} = kv(1-v)r(t) \geq kv(1-v)(A_1 - \epsilon), \quad \text{for } t \geq T, \tag{26}$$

which implies that v is increasing in t . This contradicts the fact that $v \rightarrow 0$ when $t \rightarrow \infty$. Therefore, $W^s(E_5^2) \cap X_0 = \emptyset$ if condition $A_1 > 0$ is satisfied. Similarly, we can prove that $W^s(E_i^2) \cap X_0 = \emptyset$, for $i = 0, 1, 2, 3, 4$.

For the case where $v = 1$, we can prove that $W^s(E_i^1) \cap X_0 = \emptyset$ for $i = 0, 1, 2, 3, 4, 5$ if $A_2 > 0$ by the conjugacy of v and $1 - v$.

Based on persistence theory (e.g., [11] or [23]), we have proved that the strategy is uniformly persistent. \square

Proof of Case (II). (H_1^-) and (H_2^-) hold. We assume the period in patch 1 is T_1 and the period in patch 2 is T_2 , and $T_2 > T_1$ for convenience. First, we show that $v = 0$, i.e. Y_1 is a uniform repeller. Let $(\bar{x}_2(t), \bar{y}(t))$ denote points of the limit cycle. It is sufficient to prove $W^s\left(\frac{r_1}{a_1}, \bar{x}_2, \bar{y}, 0\right) \cap X_0 = \emptyset$ in order to prove that $v = 0$ is a uniform repeller. Suppose this is not the case. Then there exists a solution of (5) such that

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t), v(t)) = \left(\frac{r_1}{a_1}, \bar{x}_2, \bar{y}, 0 \right). \tag{27}$$

As indicated in (6), we have obtained the solution of v as

$$v(t) = 1 - 1 / \left(1 + v(0)/(1 - v(0)) \exp \left\{ \int_0^t \psi(\xi) d\xi \right\} \right).$$

We rewrite $\exp \left\{ \int_0^t \psi(\xi) d\xi \right\}$ as

$$\exp \left\{ \int_0^t \psi(\xi) d\xi \right\} = \exp \left\{ \frac{\left(\int_0^t \psi(\xi) d\xi \right)}{t} t \right\}. \tag{28}$$

Substituting (7) into $\int_0^t \psi(\xi) d\xi / t$, we obtain

$$\begin{aligned} & -k(m_2 + \epsilon e_2 s_2 L_1) + \frac{k e_1 s_1 (r_1/a_1 - \epsilon)}{1 + h_1 s_1 (r_1/a_1 - \epsilon)} \\ & \leq \frac{k \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) ds}{n T_2} - \frac{k \int_0^{nT_2} (e_2 s_2 x_2) / (1 + h_2 s_2 x_2) ds}{n T_2} \\ & \leq \frac{k e_1 s_1 (r_1/a_1 + \epsilon)}{1 + h_1 s_1 (r_1/a_1 + \epsilon)} - k(m_2 - \epsilon e_2 s_2 L_2). \end{aligned} \tag{29}$$

Substituting $t = n T_2$ into (29), we obtain

$$\begin{aligned} & \frac{\int_0^{nT_2} k ((e_1 s_1 x_1)/(1 + h_1 s_1 x_1) - (e_2 s_2 x_2)/(1 + h_2 s_2 x_2)) d\xi}{n T_2} \\ &= \frac{k \int_0^{nT_2} (e_1 s_1 x_1)/(1 + h_1 s_1 x_1) d\xi}{n T_2} - \frac{k \int_0^{nT_2} (e_2 s_2 x_2)/(1 + h_2 s_2 x_2) d\xi}{n T_2}. \end{aligned} \tag{30}$$

The predator’s equation in system (5) shows

$$\frac{dy}{y} = \left(-m_2 + \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \right) dt. \tag{31}$$

Substituting (\bar{x}_2, \bar{y}) into (31) and integrating both sides of (31) from 0 to $n T_2$ gives

$$\int_0^{nT_2} \frac{d\bar{y}}{\bar{y}} = \int_0^{nT_2} \left(-m_2 + \frac{e_2 s_2 \bar{x}_2}{1 + h_2 s_2 \bar{x}_2} \right) dt. \tag{32}$$

Direct calculations indicate that $\int_0^{nT_2} \frac{d\bar{y}}{\bar{y}} = 0$. Further calculations show that the right-hand side of (32) equals $-m_2 n T_2 + \int_0^{nT_2} (e_2 s_2 \bar{x}_2)/(1 + h_2 s_2 \bar{x}_2) dt$. Therefore, we obtain

$$\int_0^{nT_2} \frac{e_2 s_2 \bar{x}_2}{1 + h_2 s_2 \bar{x}_2} dt = n m_2 T_2. \tag{33}$$

Let

$$f(x) = \frac{e_2 s_2 x}{1 + h_2 s_2 x}.$$

The function $f(x)$ is increasing. In addition, from (27), for ϵ small enough, there exists $n^* > 0$ such that $\bar{x}_2 - \epsilon < x_2 < \bar{x}_2 + \epsilon$. Using the above two properties, when $n > n^*$, we obtain,

$$\begin{aligned} \frac{e_2 s_2 (\bar{x}_2 - \epsilon)}{1 + h_2 s_2 \bar{x}_2} &< \frac{e_2 s_2 (\bar{x}_2 - \epsilon)}{1 + h_2 s_2 (\bar{x}_2 - \epsilon)} < \frac{e_2 s_2 x_2}{1 + h_2 s_2 x_2} \\ &< \frac{e_2 s_2 (\bar{x}_2 + \epsilon)}{1 + h_2 s_2 (\bar{x}_2 + \epsilon)} < \frac{e_2 s_2 (\bar{x}_2 + \epsilon)}{1 + h_2 s_2 \bar{x}_2}. \end{aligned}$$

By using (33), when $n > n^*$, we have

$$\begin{aligned} & \frac{\int_0^{nT_2} (e_2 s_2 (\bar{x}_2 + \epsilon)) / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2} \\ &= \frac{\int_0^{nT_2} (e_2 s_2 \bar{x}_2) / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2} + \frac{\int_0^{nT_2} (e_2 s_2 \epsilon) / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2} \\ &= \frac{n m_2 T_2}{n T_2} + \frac{\int_0^{nT_2} (e_2 s_2 \epsilon) / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2} \\ &= m_2 + \frac{\epsilon e_2 s_2 \int_0^{nT_2} 1 / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2}. \end{aligned} \tag{34}$$

Because \bar{x}_2 is bounded, we assume

$$L_2 \leq 1 / (1 + h_2 s_2 \bar{x}_2) \leq L_1, \tag{35}$$

where L_1 and L_2 are positive constants. By using (35), we obtain

$$\epsilon e_2 s_2 L_2 \leq \frac{\epsilon e_2 s_2 \int_0^{nT_2} 1 / (1 + h_2 s_2 \bar{x}_2) d\xi}{n T_2} \leq \epsilon e_2 s_2 L_1, \text{ when } n > n^*.$$

From the above analysis, when $n > n^*$, we have

$$\begin{aligned} m_2 - \epsilon e_2 s_2 L_2 &\leq \frac{\int_0^{nT_2} (e_2 s_2 (\bar{x}_2 - \epsilon)) / (1 + h_2 s_2 \bar{x}_2) d\xi}{nT_2} \\ &\leq \frac{\int_0^{nT_2} (e_2 s_2 x_2) / (1 + h_2 s_2 x_2) d\xi}{nT_2} \\ &\leq \frac{\int_0^{nT_2} (e_2 s_2 (\bar{x}_2 + \epsilon)) / (1 + h_2 s_2 \bar{x}_2) d\xi}{nT_2} \leq m_2 + \epsilon e_2 s_2 L_1. \end{aligned} \quad (36)$$

Again from (27), when $n > n^*$, we have

$$\frac{r_1}{a_1} - \epsilon < x_1(t) < \frac{r_1}{a_1} + \epsilon.$$

By using the above inequality, we obtain

$$\frac{e_1 s_1 (r_1/a_1 - \epsilon)}{1 + h_1 s_1 (r_1/a_1 - \epsilon)} < \frac{e_1 s_1 x_1}{1 + h_1 s_1 x_1} < \frac{e_1 s_1 (r_1/a_1 + \epsilon)}{1 + h_1 s_1 (r_1/a_1 + \epsilon)}. \quad (37)$$

Integrating (37) from 0 to nT_2 , we obtain

$$\begin{aligned} \frac{nT_2 e_1 s_1 (r_1/a_1 - \epsilon)}{1 + h_1 s_1 (r_1/a_1 - \epsilon)} &< \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) d\xi \\ &< \frac{nT_2 e_1 s_1 (r_1/a_1 + \epsilon)}{1 + h_1 s_1 (r_1/a_1 + \epsilon)}. \end{aligned} \quad (38)$$

It is obvious that (38) is equivalent to

$$\begin{aligned} \frac{k e_1 s_1 (r_1/a_1 - \epsilon)}{1 + h_1 s_1 (r_1/a_1 - \epsilon)} &< \frac{k \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) d\xi}{nT_2} \\ &< \frac{k e_1 s_1 (r_1/a_1 + \epsilon)}{1 + h_1 s_1 (r_1/a_1 + \epsilon)}. \end{aligned} \quad (39)$$

Comparing (36), (39) with (30), when $n > n^*$, we obtain

$$\begin{aligned} &-k(m_2 + \epsilon e_2 s_2 L_1) + \frac{k e_1 s_1 (r_1/a_1 - \epsilon)}{1 + h_1 s_1 (r_1/a_1 - \epsilon)} \\ &\leq \frac{k \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) ds}{nT_2} - \frac{k \int_0^{nT_2} (e_2 s_2 x_2) / (1 + h_2 s_2 x_2) ds}{nT_2} \\ &\leq \frac{k e_1 s_1 (r_1/a_1 + \epsilon)}{1 + h_1 s_1 (r_1/a_1 + \epsilon)} - k(m_2 - \epsilon e_2 s_2 L_2). \end{aligned} \quad (40)$$

From (40), we have

$$\begin{aligned} &\limsup_{n \rightarrow \infty} \frac{k \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) ds}{nT_2} - \frac{k \int_0^{nT_2} (e_2 s_2 x_2) / (1 + h_2 s_2 x_2) ds}{nT_2} \\ &= \frac{k e_1 s_1 r_1}{a_1 + h_1 s_1 r_1} - k m_2, \\ &\liminf_{n \rightarrow \infty} \frac{k \int_0^{nT_2} (e_1 s_1 x_1) / (1 + h_1 s_1 x_1) ds}{nT_2} - \frac{k \int_0^{nT_2} (e_2 s_2 x_2) / (1 + h_2 s_2 x_2) ds}{nT_2} \\ &= \frac{k e_1 s_1 r_1}{a_1 + h_1 s_1 r_1} - k m_2. \end{aligned} \quad (41)$$

By comparing (41) and (29), we obtain

$$\frac{\int_0^t \psi(\xi) d\xi}{t} \rightarrow -k m_1 + \frac{w e_1 s_1 r_1}{a_1 + h_1 s_1 r_1}, \quad \text{when } t \rightarrow \infty. \tag{42}$$

Let $\alpha = k((e_1 s_1 r_1)/(a_1 + h_1 s_1 r_1) - m_1) = k A_1$. From (6) and (42), we obtain

$$\begin{aligned} v(t) &= 1 - 1/\left(1 + (v(0)/(1 - v(0))) \exp\left\{\int_0^t \psi(\xi) d\xi\right\}\right) \\ &\rightarrow 1, \quad \text{when } t \rightarrow \infty. \end{aligned} \tag{43}$$

This contradicts the fact that $v \rightarrow 0$, when $t \rightarrow \infty$. Therefore, we can conclude that $v = 0$ is a uniform repeller.

The proof of $v = 1$ being a uniform repeller is similar to the proof above. The only difference lies in choosing $t = nT_1$ instead of $t = nT_2$. Here we omit this part.

When $t \neq nT_1$ or $t \neq nT_2$, from (41), we see that

$$\int_0^{nT_2} (e_i s_i x_i)/(1 + h_i s_i x_i) ds, \quad i = 1, 2$$

are bounded because x_1, x_2 are bounded. When n is sufficiently large, (41) is still valid. Taking all the above into consideration, we can conclude that if $A_1 > 0, A_2 > 0$, the strategies $v(t)$ and $1 - v(t)$ are uniformly persistent. \square

Proof of Case (III). (H_1) and (H_2^-) hold. When (H_1) and (H_2^-) hold, we assume the period of the limit cycle of (5) in patch 2 is T . First, we prove that $v = 0$ is a uniform repeller. When $v = 0$, predators forage only in patch 2. Let $(\bar{x}_{20}(t), \bar{y}_0(t))$ denote points of the limit cycle in patch 2. It is sufficient to prove $W^s\left(\frac{r_1}{a_1}, \bar{x}_{20}, \bar{y}_0, 0\right) \cap X_0 = \emptyset$ in order to prove that v is a uniform repeller. The remaining proof is similar to the proof of Case (II) except that we choose $t = nT$ here instead of $t = nT_1$ or $t = nT_2$. Following the same procedure as in the proof of Case (II), we can prove that $v = 0$ is a uniform repeller when conditions $A_1 > 0, A_2 > 0$ are satisfied. The proof of $v = 1$ being a uniform repeller is similar to the proof of $v = 0$ being a uniform repeller of Case (II), and is thus omitted.

The proof of the theorem is completed. \square

4. Numerical simulations. We now discuss the mixed scenario of either “ $A_1 > 0$ and $A_2 < 0$ ” or “ $A_1 < 0$ and $A_2 > 0$ ”. In such a case, if the two patches are fully isolated, then the results on the dynamics of the patch-wise model (16) show that the predators will persist in the advantageous patch (i.e., with $A_i > 0$) but go to extinction in the disadvantageous patch (i.e., with $A_i < 0$). When the two patches are not isolated, $v(t)$ evolves in $(0, 1)$. Unfortunately we are unable to obtain any theoretical results at this moment for such a case. However, our numerical explorations seem to suggest that the above conclusion remains true. For example, if we take the parameter values $r_1 = 2.0, r_2 = 0.3, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2, k = 1.0$, we have $A_1 > 0$ and $A_2 < 0$. Numerical simulation shows that $v(t) \rightarrow 1$ as $t \rightarrow \infty$ (see Fig. 1(a)), implying that the predators will eventually stay in patch 1 (the advantageous patch). Then by the theory of asymptotically autonomous systems, we obtain the above conclusion. Similarly, by choosing the parameter values $r_1 = 0.8, r_2 = 2.0, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 =$

0.3, $h_2 = 0.2$, $k = 1.0$, we have $A_1 < 0$ and $A_2 > 0$, and simulation shows that $v(t) \rightarrow 0$ as $t \rightarrow \infty$ (see Fig. 1(b)), leading to the above conclusion again.

Mathematical results in Section 3 show that the dispersal rate of predators or the strength of adaptation (i.e., k) does not affect the persistence or extinction of the predators. However, numerical simulations indicate that k may induce rich patterns and have an effect on average biomass of the predators. Figures 2, 3, 4 are obtained under the case where the carrying capacity of prey in patch 1 is small and the carrying capacity of prey in patch 2 is large enough to support oscillations, reflected by the conditions " $A_1 > 0$ and $A_2 > 0$ " together with " (H_1) and (H_2^-) ".

Figure 2 indicates that when k is large or small, i.e. when the adaptation strength of predators is strong or weak, the dispersal of predators stabilizes the system; while when the adaptation strength is mediate, there will be Hopf bifurcation. Figures 3 and 4 show that in the interval of Hopf bifurcation, prey, predators and the strategy behave periodically. Figure 5 shows that there is a complicated relationship between predator's average biomass and the dispersal rate k in the interval of Hopf bifurcation.

When the carrying capacity of prey in each isolated patch is large enough to support oscillations, i.e. conditions (H_1^-) and (H_2^-) in Lemma 3.3 are satisfied, a torus bifurcation may occur. Figures 6(a) and 6(b) are produced under conditions (H_1^-) and (H_2^-) in Lemma 3.3. Figure 6(a) shows modulated oscillation. Figure 6(b) shows a torus surface. As indicated in [8], a torus bifurcation may be due to the aperiodic behavior of predators. Making use of the simulations in Figures 3, 4, or 5, we increase the local recruitment rate of prey in patch 1 such that prey and predators in both patches exhibit periodic behaviour. Because the amplitude of the periodic solutions in two patches are different, the aperiodic behaviour of the predators occurs, which leads to the torus bifurcation.

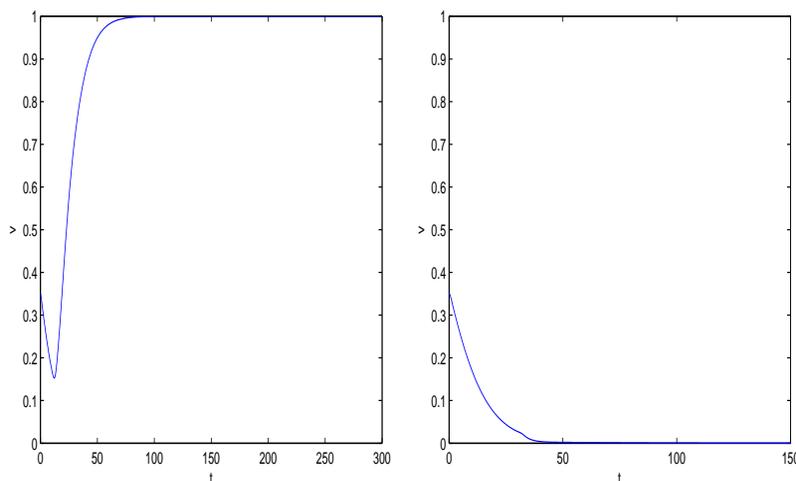
5. Conclusion and discussions. In this paper, we have studied the dynamics of a two-patch predator-prey model with the Holling type II functional response and allowing the predators to move adaptively between the two patches to gain fitness. We have analyzed the persistence and extinction of predators and the corresponding mixed strategy, in terms of the combined parameters A_i , $i = 1, 2$ which determine whether patch i is advantageous or disadvantageous to the predators. When patches are isolated, in an advantageous patch, by Lemma 3.3, prey and predators can persist in two different modes: (i) convergence to a positive equilibrium; (ii) convergence to a positive periodic solution, depending on whether (H_i) or its opposite (H_i^-) holds.

With the adaptive dispersal, we have proved that predators will go to extinction on both patches when $A_1 < 0$ and $A_2 < 0$; and when $A_1 > 0$, $A_2 > 0$, the predators will persist in both patches, and so will be the dispersion strategy function $v(t)$. Interestingly, the strength of adaptation (i.e. k) does not affect the above conclusion. However, numerical simulations indicate that it does have an impact on the patterns of persistence and affect the average population of the predators. When prey and predators tend to an equilibrium in one patch and tend to a limit cycle in the other patch, numerical simulations show that the adaptive movement of predators can stabilize the system when the adaptation of predators is either weak or strong, and there is an intermediate window for the adaptation strength in which Hopf bifurcation occurs, causing periodic fluctuations for prey and predator populations in both patches. Also found by numerical simulations is that the average biomass

of predators has a complicated relationship with the dispersal rate of the predators. Moreover when prey and predators tend to limit cycles in each isolated patch, a torus bifurcation is numerically observed.

For the case of $A_1A_2 < 0$ (i.e., one patch is advantageous and the other is disadvantageous), we are unable to obtain theoretical results. In such situation, our numerical investigations seem to show that adaptive dispersal also does not affect the global outcome in the sense that the predators will persist in the advantageous patch and go extinct in the disadvantageous patch. In plain language, the adaptive dispersal is always in favor of the advantageous patch, if any.

We point out that recently Cressman and Křivan ([8]) studied a two-patch predator-prey model focusing on adaptive dispersals of both prey and predators. In contrast to their work, we consider a system including both population dynamics and adaptive dynamics. By studying the combined system, we can gain more biological and mathematical insights.



(a) Adaptive dispersion is in favor of patch 1 (b) Adaptive dispersion is in favor of patch 2

FIGURE 1. Adaptive dispersion. (a) The initial values are $(0.2, 0.1, 12, 0.35)$, and the parameter values are $r_1 = 2.0, r_2 = 0.3, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2, k = 1.0$ leading to $A_1 > 0$ and $A_2 < 0$; (b) The initial values are $(0.5, 0.2, 12, 0.35)$, and the parameter values are $r_1 = 0.8, r_2 = 2.0, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2, k = 1.0$ leading to $A_1 < 0$ and $A_2 > 0$.

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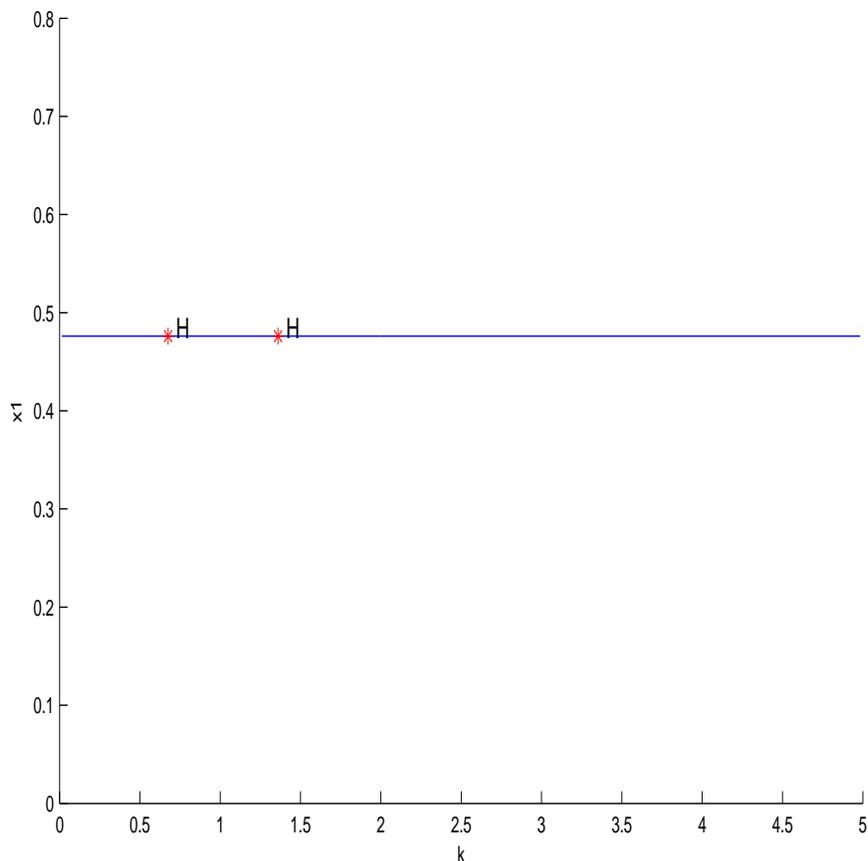


FIGURE 2. There exists Hopf bifurcation for the case where $A_1 > 0, A_2 > 0, H_1, H_2^-$. Between the two Hopf bifurcation point, periodic solutions exist. Parameters are $r_1 = 5, r_2 = 8, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2$.

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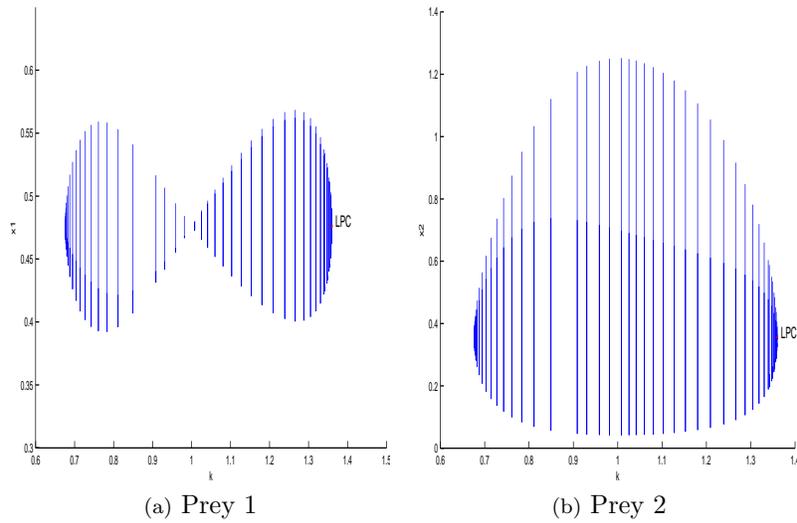


FIGURE 3. Prey populations in both patches oscillate periodically with varying k in the interval of Hopf bifurcation, when $A_1 > 0, A_2 > 0, H_1, H_2^-$. Parameters are $r_1 = 5, r_2 = 8, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2$.

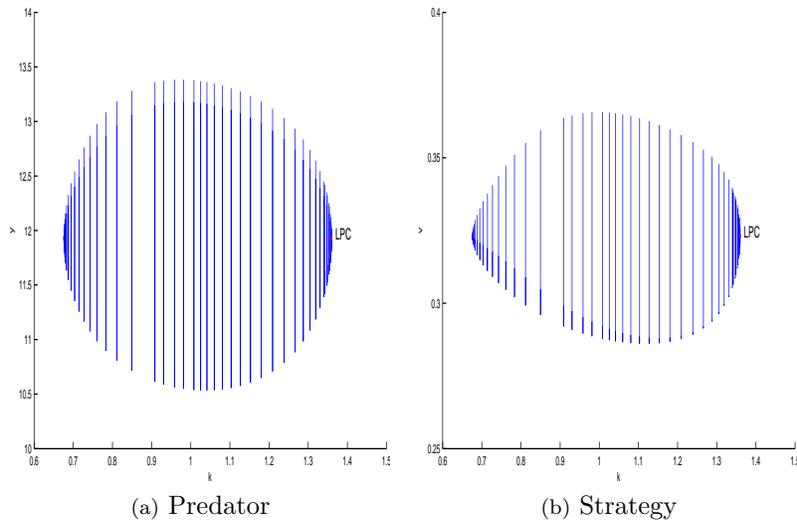


FIGURE 4. Predators population and strategy oscillate periodically with varying k in the interval of Hopf bifurcation, when $A_1 > 0, A_2 > 0, H_1, H_2^-$. Parameters are $r_1 = 5, r_2 = 8, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2$.

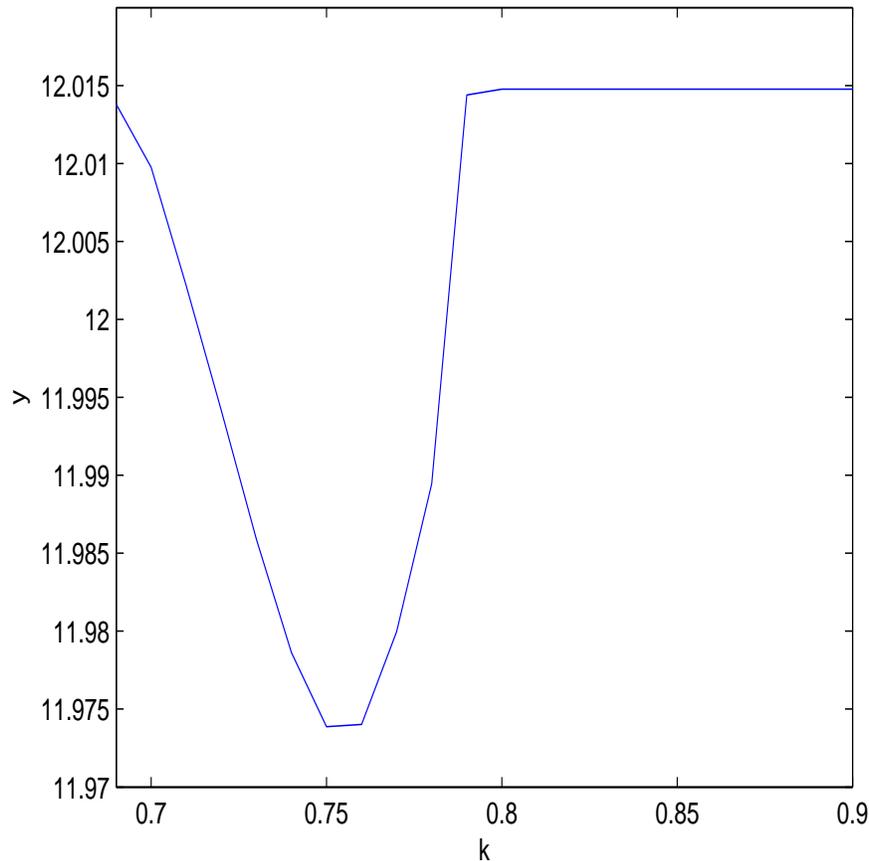


FIGURE 5. The average biomass of predators has a complicated relationship with the strength of adaptation of predators in the interval of Hopf bifurcation, when $A_1 > 0, A_2 > 0, H_1, H_2^-$. Parameters are $r_1 = 5, r_2 = 8, a_1 = 2, a_2 = 1.3, s_1 = 1.2, s_2 = 1, m_1 = 0.2, m_2 = 0.1, e_1 = 0.4, e_2 = 0.3, h_1 = 0.3, h_2 = 0.2$.

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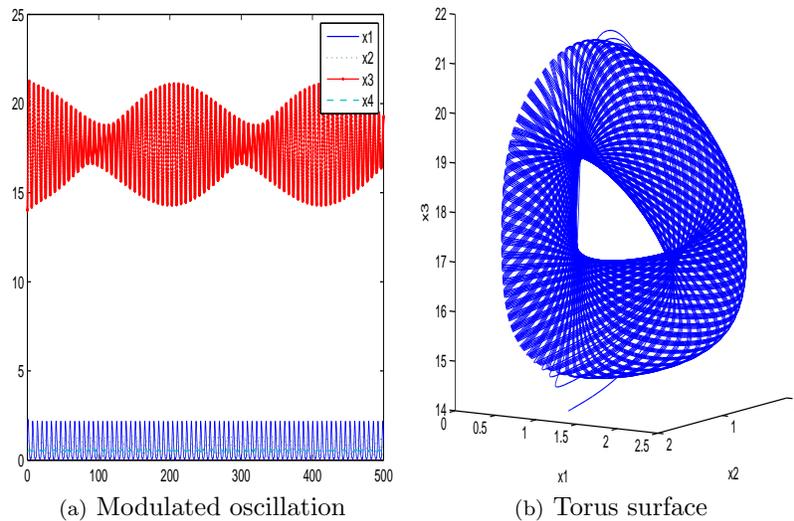


FIGURE 6. A torus surface exists when $A_1 > 0, A_2 > 0, H_1^-, H_2^-$, which indicates a torus bifurcation. Parameters are $r_1 = 9, r_2 = 8, a_1 = 2, a_2 = 2, s_1 = 1, s_2 = 1, m_1 = 0.2, m_2 = 0.2, e_1 = 0.4, e_2 = 0.4, h_1 = 0.4, h_2 = 0.4, w = 1.0$.

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