



# The impact of Allee effect on a predator–prey system with Holling type II functional response

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## ABSTRACT

In this paper, the Allee effect is incorporated into a predator–prey model with Holling type II functional response. Compared with the predator–prey model without Allee effect, we find that the Allee effect of prey species increases the extinction risk of both predators and prey. When the handling time of predators is relatively short and the Allee effect of prey species becomes strong, both predators and prey may become extinct. Moreover, it is shown that the model with Allee effect undergoes the Hopf bifurcation and heteroclinic bifurcation. The Allee effect of prey species can lead to unstable periodical oscillation. It is also found that the positive equilibrium of the model could change from stable to unstable, and then to stable when the strength of Allee effect or the handling time of predators increases continuously from zero, that is, the model admits stability switches as a parameter changes. When the Allee effect of prey species becomes strong, longer handling time of predators may stabilize the coexistent steady state.

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## 1. Introduction

Both positive and negative interactions among species are common in communities [1,2]. For example, synchronous breeding is an important mechanism by which colonial guillemots (*Uria aalge*) increase reproductive success. Many carnivore species are better able to capture large prey by cooperative hunting and group living may thus be favored in areas with abundant large prey [3]. Historically, attention has focused on negative interactions, such as competition. However, for the last decade, the importance of positive interactions such as the Allee effect [4] has recently been recognized [1,5]. The Allee effect [4], and more recently as depensation [6] or inverse density dependence [7], refers to a decrease in per capita fertility rate at low population densities. Allee effect may occur under several mechanisms, such as difficulties in finding mates when population density is low [8,9], social dysfunction at small population sizes and increased predation risk due to failing flocking or schooling behavior [10,11]. When such mechanisms operate, the per capita fertility rate of a species increases with density, that is, positive interactions among species occur. The primary consequence of the Allee effect is that it creates a threshold density below which a population cannot survive. For example, this might correspond to the density below which it is so difficult to find a mate that reproduction does not compensate mortality. Each population whose density stochastically goes below this threshold is fated to extinction and species experiencing Allee effect are therefore more extinction prone [11]. The phenomenon has received considerable attention from ecologists [12,13]. The importance of this dynamic process in ecology has been under-appreciated and recent evidence [14] now suggests that it might have an important influence on the population dynamics of many plants and animal species. Therefore, the investigation of Allee effects is important for conservation biology [15].

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Interactions among species in a food web are multiform. Among these, the interactions between predators and prey are important. Predator–prey interactions are ubiquitous in nature and the dynamical behaviors of predator–prey system are very complex. Many forces may influence the dynamical behaviors of the predator–prey system [11,12]. It has been shown that a predator–prey model can lead to oscillatory behavior because of a nonlinear functional response. Interest in the stability of predator–prey system has continued unabated since the theoretical work of Lotka [16], Volterra [17] and the experimental work of Gause [18]. Theoreticians and experimentalists have proceeded to investigate the processes that affect the stability of predator–prey system [19,20]. Among the many processes that the Lotka–Volterra model ignores, the Allee effect may be the most important [21]. The Allee effect increases the likelihood of local and global extinction. But there have been few papers discussing its stabilizing or destabilizing effects on the predator–prey system (except for [21,22,33]). Kent et al. [22] conclude that the predator–prey system is stabilized by an influx of prey in the form of a rescue effect, and destabilized by an out flux of Allee effect. By combining mathematical analysis with numerical simulation, Zhou et al. [21] have shown that the Allee effect may be a destabilizing force in predator–prey system. However, the Lotka–Volterra model they considered does not consider the density-dependent effect of prey and the functional response is linear. Functional response is a double rate: it is the average number of prey killed by per individual predator per unit of time. In general, the functional response can be classified into two types: prey-dependent and predator-dependent. Prey-dependent means that the functional response is only a function of the prey’s density, while predator-dependent means that the functional response is a function of both densities of the prey and predators. Functional response that is strictly prey-dependent, such as the Holling family, is predominant in the literature. For example, since 1959, Holling’s prey-dependent type II functional response has served as the basis for many literatures on predator–prey theory. Therefore, the predator–prey model with Holling type II functional response is more realistic. However, the impact of the Allee effect on the stability of a predator–prey system with Holling type II functional response is poorly understood both empirically and theoretically.

The purpose of this paper is to show that the Allee effect of prey species has significant effects on the dynamics of predator–prey model with Holling type II functional response. We will investigate how predator and prey species are threatened by extinction when the population density of prey becomes low. Moreover, we will show that the predator–prey model with Allee effect and Holling type II functional response undergoes a sequence of bifurcations including supercritical Hopf bifurcation, subcritical Hopf bifurcation and heteroclinic bifurcation. We will also present a global analysis of the model by means of numerical simulations.

The organization of this paper is as follows. In the next section, we present the formulations of mathematical model with Allee effect. In Section 3, we present a qualitative analysis of the model. In Section 4, we use numerical simulations to reveal the global bifurcation structures and the influence of Allee effect on the dynamical behaviors of the model. A brief discussion is given in Section 5.

## 2. Model formulations

In this section, we first introduce the Rosenzweig–MacArthur predator–prey model with Holling type II functional response. Based on this model, we will construct a predator–prey model with Allee effect on prey species.

### 2.1. Rosenzweig–MacArthur predator–prey model

The objective of this subsection is to introduce the predator–prey model with Holling type II functional response and summarize its dynamical behaviors.

The classical Lotka–Volterra predator–prey model did not contain saturating effect. More realistically, the functional response of predator population is nonlinear. The Rosenzweig–MacArthur predator–prey model with Holling type II functional response is as follows:

$$\begin{cases} \frac{dN}{dt} = N(b - d_1 - \alpha N) - \frac{sNP}{1 + sh_1N}, \\ \frac{dP}{dt} = \frac{c_1sNP}{1 + sh_1N} - d_2P, \end{cases} \tag{1}$$

where  $N$  and  $P$  denote the population densities of prey and predators at time  $t$ , respectively,  $b$  is the per capita maximum fertility rate of prey population,  $d_i$  ( $i = 1, 2$ ) are the per capita death rates of prey and predators respectively,  $\alpha$  denotes the strength of intra-competition of prey population,  $s$  denotes the effective search rate,  $h_1$  denotes the handling time of predators, and  $c_1$  denotes the conversion efficiency of ingested prey into new predators. The product,  $sN/(1 + sh_1N)$ , represents the predator’s functional response, i.e. the relationship between prey density,  $N$ , and the amount ingested by an average predator. All the parameters are positive constants. Further, we assume that the growth rate of prey must exceed its death rate, i.e.,  $b > d_1$ , otherwise, both prey and predators will become extinct. In addition, the maximum growth rate of predator population must exceed its death rate, i.e.,  $c_1/h_1 > d_2$ . If not, prey population will never be able to sustain predators, which will go to extinction. In model (1), if the carrying capacity of prey  $(b - d_1)/\alpha$  is low, i.e.,

$$0 < \frac{b - d_1}{\alpha} < \frac{d_2}{s(c_1 - h_1d_2)}, \tag{2}$$

then the attractor is the trivial equilibrium  $((b - d_1)/\alpha, 0)$ , i.e., predator population goes extinct. By contrast, for intermediate value of the carrying capacity

$$\frac{d_2}{s(c_1 - h_1 d_2)} < \frac{b - d_1}{\alpha} \leq \frac{d_2 + c_1/h_1}{s(c_1 - h_1 d_2)},$$

stationary stable coexistence occurs at the strictly positive equilibrium

$$(N_1^*, P_1^*) = \left( \frac{d_2}{s(c_1 - h_1 d_2)}, \frac{(1 + sh_1 N_1^*)(b - d_1 - \alpha N_1^*)}{s} \right), \quad (3)$$

while for high value of the carrying capacity of prey, i.e.,

$$\frac{b - d_1}{\alpha} > \frac{d_2 + c_1/h_1}{s(c_1 - h_1 d_2)},$$

predator and prey populations coexist on a limit cycle and the limit cycle is globally stable. Moreover, the trivial equilibrium  $(0, 0)$  is always a saddle point in model (1). Therefore, the equilibrium  $(N_1^*, P_1^*)$  given by (3) is critically stable and the populations are balanced between stationary and cyclic coexistence.

Next, based on the predator–prey model (1), we construct a predator–prey model with Allee effect on prey species and study its impact on the stability of predator–prey system.

## 2.2. Predator–prey model with Allee effect on prey species

Because of difficulties in finding mates when prey population density becomes low, Allee effect may occur in prey species [9]. For example, this might correspond to the density below which it is so difficult to find a mate that reproduction does not compensate for mortality. Let  $f(N)$  be the fertility rate of a species that has  $N$  adults in an isolated patch, then the fertility rate increases with population density, which is described by

$$f(N) = \frac{bN}{A_1 + N},$$

where  $b$  is the per capita maximum fertility rate of the species,  $A_1$  is the Allee effect constant of the species [23]. If  $A_1 > 0$ , the fertility of the species is therefore zero when  $N$  is zero and approaches to  $b$  when  $N$  becomes very large. How fast  $f(N)$  increases with  $N$  depends on the parameter  $A_1$ . The bigger  $A_1$  is, the stronger the Allee effect will be. Biologically,  $A_1$  is the population density at which a species reaches half its maximum fertility (i.e.,  $f(A_1) = b/2$ ). When  $A_1 = 0$ , the fertility rate is density independent, with  $f(N) = b$ .

When prey population is subject to Allee effect, the predator–prey model becomes

$$\begin{cases} \frac{dN}{dt} = N \left( \frac{bN}{A_1 + N} - d_1 - \alpha N \right) - \frac{sNP}{1 + sh_1 N}, \\ \frac{dP}{dt} = \frac{c_1 sNP}{1 + sh_1 N} - d_2 P, \end{cases} \quad (4)$$

where  $A_1$  is a positive parameter denoting Allee effect imposed on prey population. If

$$b > d_1, c_1 > h_1 d_2, \frac{b - d_1}{\alpha} > \frac{d_2}{s(c_1 - h_1 d_2)},$$

$$0 < A_1 < \frac{d_2(s(b - d_1)(c_1 - h_1 d_2) - \alpha d_2)}{s(c_1 - h_1 d_2)(d_1 s(c_1 - h_1 d_2) + \alpha d_2)},$$

then model (4) yields one non-trivial equilibrium

$$(N_2^*, P_2^*) = \left( \frac{d_2}{s(c_1 - h_1 d_2)}, \frac{(1 + sh_1 N_2^*)(bN_2^*/(A_1 + N_2^*) - d_1 - \alpha N_2^*)}{s} \right). \quad (5)$$

It is obvious that now the equilibrium density of prey population is the same as that obtained from Eq. (1), however, the equilibrium density of predator population is smaller than that obtained from Eq. (1). That is to say, a decrease of predator population density at the equilibrium is caused by the Allee effect of prey population. Next, we investigate model (4) by way of mathematical analysis and numerical simulations. First, we perform a global qualitative analysis of system (4).

## 3. Qualitative analysis

In order to reduce parameters, we perform the following transformations:

$$X = \frac{\alpha N}{b}, \quad Y = \frac{sP}{b}, \quad \tau = bt.$$

For simplicity, we still use variables  $N, P, t$  instead of  $X, Y, \tau$ . Then we obtain

$$\begin{cases} \frac{dN}{dt} = N \left( \frac{N}{A+N} - m_1 - N - \frac{P}{1+hN} \right), \\ \frac{dP}{dt} = P \left( \frac{cN}{1+hN} - m_2 \right), \end{cases} \tag{6}$$

where

$$A = \frac{A_1 \alpha}{b}, \quad m_1 = \frac{d_1}{b}, \quad h = \frac{sh_1 b}{\alpha}, \quad c = \frac{c_1 s}{\alpha}, \quad m_2 = \frac{d_2}{b},$$

$A$  corresponds to the re-scaled strength of the Allee effect and  $m_1$  is a re-scaled death rate of prey population. All the parameters are positive constants. Note that  $b > d_1$ , so  $0 < m_1 = d_1/b < 1$  and we shall assume that this is the case in this paper.

For simplicity of computation, we consider the above system (6), which is equivalent to (4). Henceforth, we perform a qualitative analysis of system (6). We start by studying the local stability of equilibriums of system (6).

### 3.1. Extinction equilibrium

First, we consider the stability of trivial equilibrium  $E_0 = (0, 0)$ . Because the stability of  $E_0 = (0, 0)$  is important to understand the qualitative behavior of model (6) influenced by the Allee effect of prey population. The Jacobian matrix of system (6) at  $E_0$  is

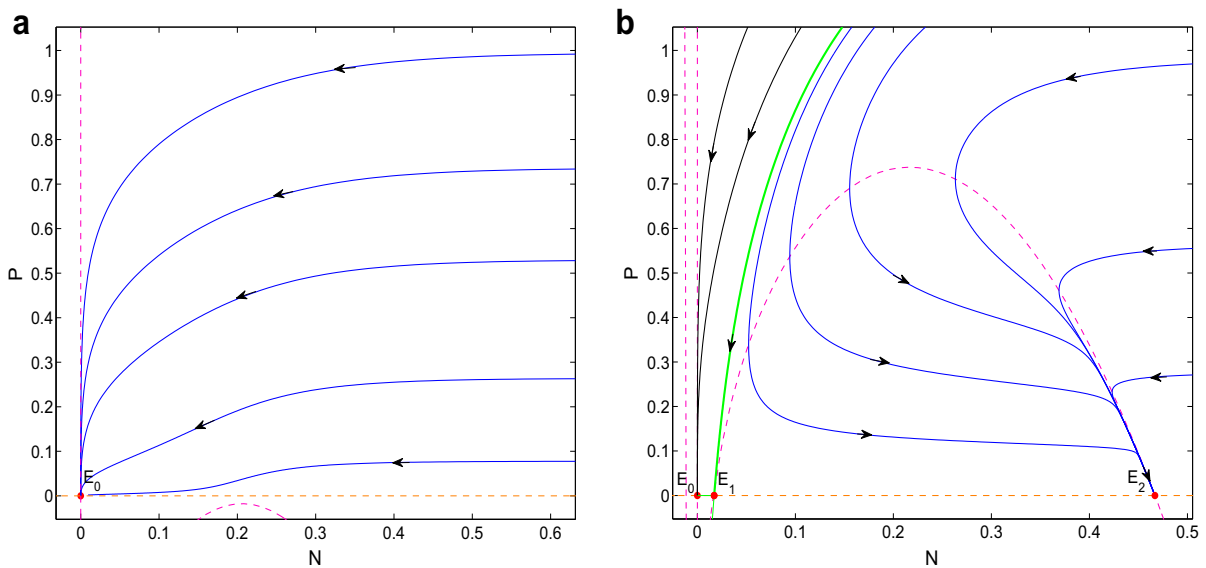
$$M_1 = \begin{bmatrix} -m_1 & 0 \\ 0 & -m_2 \end{bmatrix}.$$

It can be seen that  $E_0$  is always a locally stable node, which implies that both prey and predators will become extinct when their population densities lie in the attraction region of  $E_0$ . In particular, if the population density of prey becomes low, then both predators and prey will go extinct (see Fig. 1). Compared with the predator–prey model without Allee effect, we can see that the Allee effect of prey population increases the extinction risk of both predators and prey. Further, if model (6) does not have interior equilibrium and other boundary equilibriums, i.e., the Allee effect of prey population is very strong, then  $E_0$  is globally asymptotically stable. Any positive orbit converges to  $E_0$  as  $t$  tends to infinity, i.e., prey and predators cannot coexist even if the initial population density of prey is abundant. A typical phase portrait is shown in Fig. 1a.

### 3.2. Boundary equilibriums

In order to find positive equilibriums for prey population, set

$$\Delta_1 = (1 - A - m_1)^2 - 4Am_1 = A^2 - 2A(m_1 + 1) + (m_1 - 1)^2.$$



**Fig. 1.** Phase portraits of model (6). Isoclines are shown as dashed lines. (a)  $E_0$  is a global attractor when  $A = 0.0880$ . (b) Both  $E_0$  and  $E_2$  are attractors when  $A = 0.0160$ . Other parameter values:  $h = 11.2500, m_1 = 0.5000, c = 2.5000, m_2 = 0.2000$ .

Then we can see that there exist two boundary equilibriums  $E_1 = (N_1, 0)$  and  $E_2 = (N_2, 0)$  if  $\Delta_1 > 0$  and  $A < 1 - m_1$ , where

$$N_1 = \frac{1}{2} \left( 1 - A - m_1 - \sqrt{(1 - A - m_1)^2 - 4Am_1} \right),$$

$$N_2 = \frac{1}{2} \left( 1 - A - m_1 + \sqrt{(1 - A - m_1)^2 - 4Am_1} \right).$$

We first determine the local stability of  $E_1$ . Note that  $N_1/(A + N_1) - m_1 - N_1 = 0$ , then the Jacobian matrix of system (6) at  $E_1$  is

$$M_2 = \begin{bmatrix} \frac{1 - A - m_1 - 2N_1}{A + N_1} & -\frac{N_1}{1 + hN_1} \\ 0 & \frac{cN_1}{1 + hN_1} - m_2 \end{bmatrix}.$$

The determinant of Jacobian matrix  $M_2$  is given by

$$\det(M_2) = \frac{\sqrt{(1 - A - m_1)^2 - 4Am_1}((c - m_2h)N_1 - m_2)}{(A + N_1)(1 + hN_1)}.$$

It can be seen that the determinant of the Jacobian matrix  $M_2$  may be positive or negative. The trace of Jacobian matrix  $M_2$  is

$$\begin{aligned} \text{tr}(M_2) &= \frac{1 - A - m_1 - 2N_1}{A + N_1} + \left( \frac{cN_1}{1 + hN_1} - m_2 \right), \\ &= \frac{\sqrt{(1 - A - m_1)^2 - 4Am_1}}{A + N_1} + \frac{(c - m_2h)N_1 - m_2}{1 + hN_1}. \end{aligned}$$

When  $\det(M_2) > 0$ , the trace of Jacobian matrix  $M_2$  is always positive. Therefore, we obtain the following results on the stability of  $E_1$ .

**Theorem 1.** Assume that  $0 < m_1 < 1$  and  $0 < A < (1 - \sqrt{m_1})^2$ . Then

(i)  $E_1$  is a saddle point if

$$h > c/m_2 - 2 / \left( 1 - A - m_1 - \sqrt{(1 - A - m_1)^2 - 4Am_1} \right).$$

(ii)  $E_1$  is unstable if

$$0 < h < c/m_2 - 2 / \left( 1 - A - m_1 - \sqrt{(1 - A - m_1)^2 - 4Am_1} \right). \quad (7)$$

Next, we analyze the stability of  $E_2$ . The Jacobian matrix of system (6) at  $E_2$  is

$$M_3 = \begin{bmatrix} \frac{1 - A - m_1 - 2N_2}{A + N_2} & -\frac{N_2}{1 + hN_2} \\ 0 & \frac{cN_2}{1 + hN_2} - m_2 \end{bmatrix}.$$

By a similar argument as above, we have the following results on the stability of  $E_2$ .

**Theorem 2.** Assume that  $0 < m_1 < 1$  and  $0 < A < (1 - \sqrt{m_1})^2$ . Then

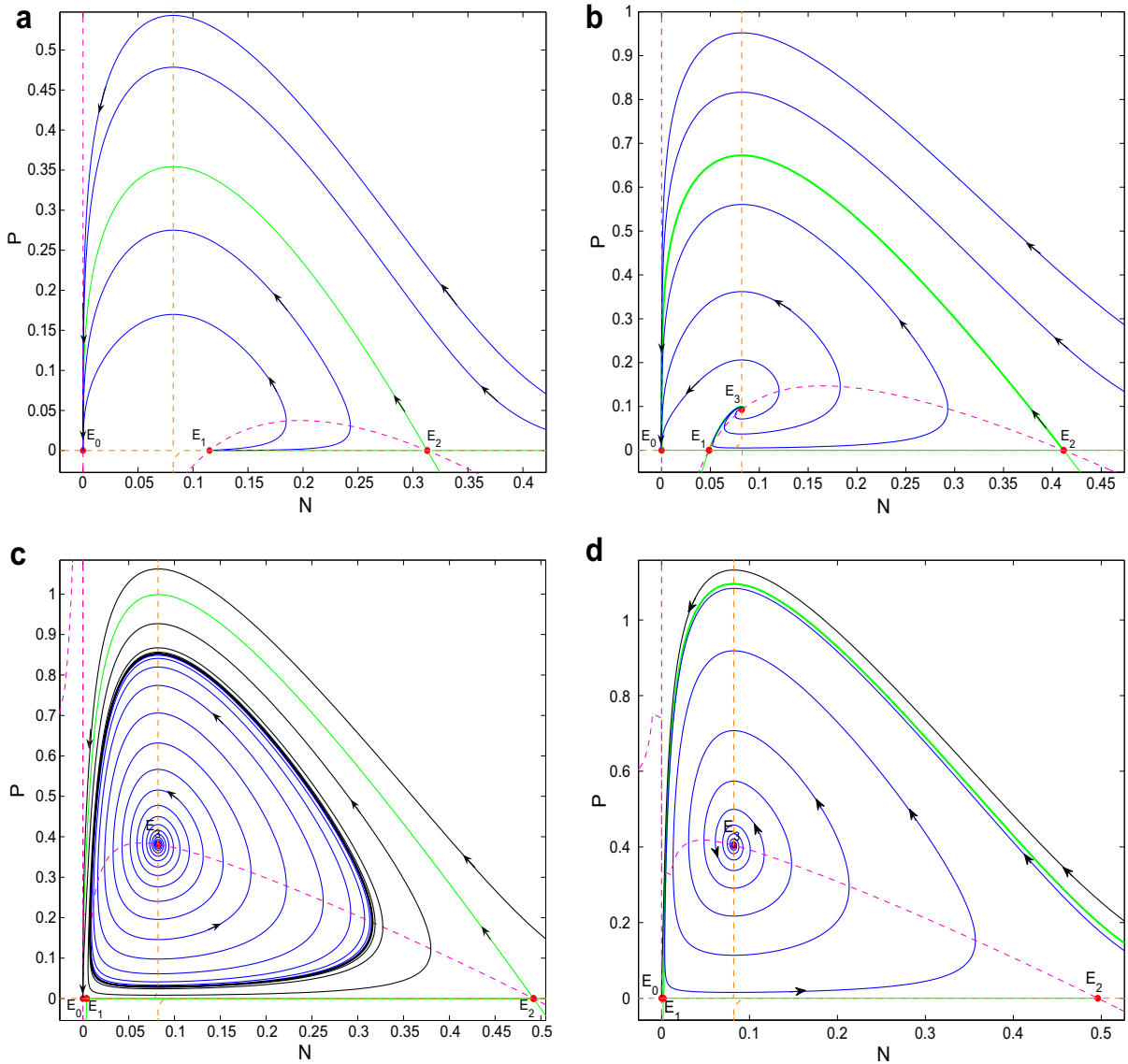
(i)  $E_2$  is a saddle point if

$$0 < h < c/m_2 - 2 / \left( 1 - A - m_1 + \sqrt{(1 - A - m_1)^2 - 4Am_1} \right). \quad (8)$$

(ii)  $E_2$  is locally asymptotically stable if

$$h > c/m_2 - 2 / \left( 1 - A - m_1 + \sqrt{(1 - A - m_1)^2 - 4Am_1} \right).$$

If model (6) does not have interior equilibrium, i.e., the carrying capacity of prey is low, then its asymptotic behavior is determined by the local stability of  $E_0$ ,  $E_1$  and  $E_2$ . Note that  $A$  corresponds to a re-scaled strength of the Allee effect and  $h$  corresponds to a re-scaled handling time of predator population. From Theorems 1 and 2, it can be seen that if the Allee effect of prey is relatively weak and the handling time of predators is relatively long, then  $E_1$  is a saddle point and  $E_2$  is asymptotically stable. The stable manifold of  $E_1$ , which is the threshold induced by the Allee effect of prey population, divides the first quadrant into two parts, one is the attraction region of  $E_0$ , the other is the attraction region of  $E_2$  (see Fig. 1b). From Fig. 1b, it can be seen that if the population density of prey becomes low, then both predators and prey will become extinct. This



**Fig. 2.** Phase portraits of model (6). Isoclines are shown as dashed lines. (a)  $E_0$  is a global attractor when  $A = 0.0720$ . (b)  $E_0$  is a global attractor when  $A = 0.0400$ ,  $E_3$  is unstable. (c) An unstable limit cycle when  $A = 0.0040$ . (d) Both  $E_0$  and  $E_3$  are attractors when  $A = 0.0020$ . Other parameter values are the same as in Fig. 1 except  $h = 0.3125$ .

dependence on the initial population densities is very important. A slight difference in the initial population densities makes the asymptotic state very different [24]. On the contrary, if the Allee effect of prey is relatively strong and the handling time of predators is relatively short, then  $E_1$  is unstable and  $E_2$  is a saddle point, any positive orbit converges to  $E_0$  as  $t$  tends to infinity, i.e.,  $E_0$  is globally asymptotically stable, both predators and prey will go extinct independent of the initial population densities (see Fig. 2 a). Therefore, if model (6) does not have interior equilibrium, then depending on the strength of Allee effect, the handling time of predators and the initial population densities, either predator population becomes extinct or both predators and prey go extinct.

### 3.3. Coexistent equilibrium

To obtain the positive equilibrium  $E_3 = (N^*, P^*)$  of system (6), we propose the following assumption:

$$\begin{aligned}
 &0 < m_1 < 1, \quad c > \frac{m_2(1 + (1 - m_1)h)}{1 - m_1}, \\
 &0 < A < \frac{m_2((c - m_2h)(1 - m_1) - m_2)}{(c - m_2h)(m_2 + m_1(c - m_2h))}.
 \end{aligned}
 \tag{9}$$

Then set

$$\begin{cases} \frac{cN}{1+hN} - m_2 = 0, \\ \frac{N}{A+N} - m_1 - N - \frac{P}{1+hN} = 0, \end{cases}$$

which yields

$$\begin{cases} N^* = \frac{m_2}{c - m_2 h}, \\ P^* = \frac{c}{c - m_2 h} \left( \frac{m_2}{m_2 + A(c - m_2 h)} - \frac{m_2}{c - m_2 h} - m_1 \right). \end{cases}$$

The Jacobian matrix of system (6) at  $(N^*, P^*)$  is

$$M_4 = \begin{bmatrix} N^* \left( \frac{A}{(A+N^*)^2} + \frac{hP^*}{(1+hN^*)^2} - 1 \right) & -\frac{N^*}{1+hN^*} \\ \frac{cP^*}{(1+hN^*)^2} & 0 \end{bmatrix}.$$

Thus, we have

$$\begin{aligned} \text{tr}(M_4) &= N^* \left( \frac{A}{(A+N^*)^2} + \frac{hP^*}{(1+hN^*)^2} - 1 \right), \\ \det(M_4) &= \frac{cN^*P^*}{(1+hN^*)^3}. \end{aligned}$$

When condition (9) is valid, it can be seen that  $\det(M_4)$  is always positive, but  $\text{tr}(M_4)$  may be positive or negative. Therefore, the locally asymptotic stability of  $E_3$  is decided by the sign of  $\text{tr}(M_4)$ . Substitute  $N^*$  and  $P^*$  into  $\text{tr}(M_4)$ , we obtain

$$\text{tr}(M_4) = \frac{m_2(a_1 A^2 + a_2 A + a_3)}{c(c - m_2 h)(Ahm_2 - Ac - m_2)^2}, \quad (10)$$

where

$$\begin{aligned} a_1 &= -(m_1 h(c - m_2 h) + c + m_2 h)(c - m_2 h)^2, \\ a_2 &= (c - m_2 h)(-2m_1 m_2 h(c - m_2 h) + (c^2 - m_2^2 h^2) - 2m_2(c + m_2 h)), \\ a_3 &= (-m_1 h(c - m_2 h) + h(c - m_2 h) - (c + m_2 h))m_2^2. \end{aligned} \quad (11)$$

Note that  $c > m_2 h$ , so the sign of  $\text{tr}(M_4)$  is determined by the sign of  $F(A)$ , where  $F(A)$  is a quadratic function of  $A$ , i.e.,

$$F(A) = a_1 A^2 + a_2 A + a_3.$$

Because  $a_1 < 0$ , in order to determine the sign of  $F(A)$ , we further assume that  $a_2 > 0$  and  $a_3 < 0$ , i.e.,

$$\begin{aligned} c &> m_2(2 + h), \\ \frac{h(c - m_2 h) - (c + m_2 h)}{h(c - m_2 h)} &< m_1 < \frac{(c^2 - m_2^2 h^2) - 2m_2(c + m_2 h)}{2m_2 h(c - m_2 h)}, \end{aligned} \quad (12)$$

and set

$$\Delta_2 = a_2^2 - 4a_1 a_3 = -(c - m_2 h)^3 (4cm_1 m_2 h(c - m_2 h) + (c + m_2 h)(4cm_2 + m_2^2 h^2 - c^2)). \quad (13)$$

When conditions (12) hold and  $\Delta_2 > 0$ , then  $F(A) = 0$  admits two positive solutions  $A^*$  and  $A^{**}$ , where

$$A^* = -\frac{a_2 - \sqrt{\Delta_2}}{2a_1}, \quad A^{**} = -\frac{a_2 + \sqrt{\Delta_2}}{2a_1}.$$

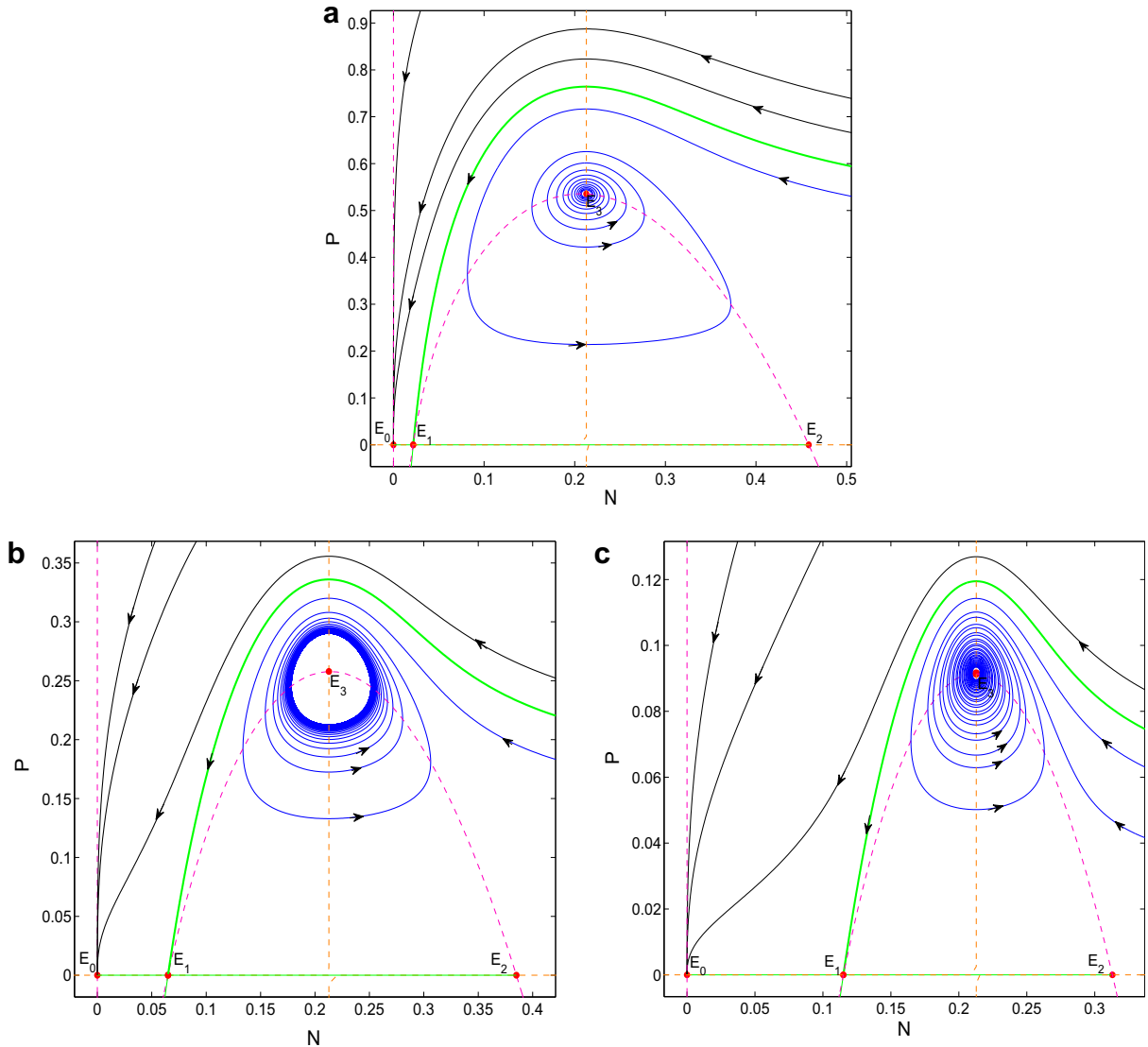
In this case, if  $0 < A < A^*$  or  $A > A^{**}$ , then  $F(A) < 0$ , i.e.,  $\text{tr}(M_4) < 0$ ,  $E_3$  is locally asymptotically stable. When conditions (12) hold and  $\Delta_2 < 0$ , then  $F(A) < 0$  for all  $A > 0$ , i.e.,  $E_3$  is always locally asymptotically stable. Set

$$\begin{aligned} m_1^* &= \frac{(c + m_2 h)(c^2 - 4cm_2 - m_2^2 h^2)}{4cm_2 h(c - m_2 h)}, \\ A_c &= \frac{m_2((c - m_2 h)(1 - m_1) - m_2)}{(c - m_2 h)(m_2 + m_1(c - m_2 h))}, \end{aligned}$$

then we have the following results on the local stability of  $E_3$  if (9) and (12) hold (see Table 1).

**Table 1**  
The local stability of the positive equilibrium  $E_3$  of model (6).

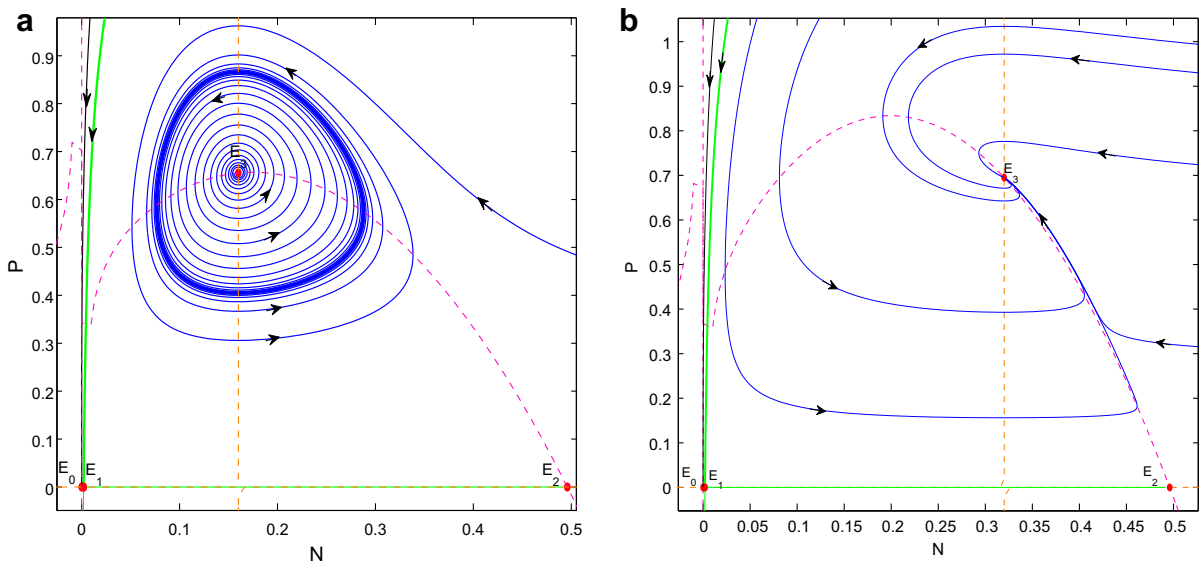
Range of parameter $m_1$	Range of Allee effect parameter $A$	The stability of $(N^*, P^*)$
$0 < m_1 < m_1^*$	$0 < A < A^*$ or $A^{**} < A < A_c$	Asymptotically stable
	$A^* < A < A^{**}$	Unstable
	$A = A^*$ or $A = A^{**}$	Center
$m_1 > m_1^*$	For all $0 < A < A_c$	Asymptotically stable
$m_1 = m_1^*$	$A = -\frac{a_2}{2a_1}$	Center
	$A \neq -\frac{a_2}{2a_1}$	Asymptotically stable



**Fig. 3.** Phase portraits of model (6). Isoclines are shown as dashed lines. (a)  $E_3$  is locally asymptotically stable when  $A = 0.0200$ . (b)  $E_3$  is unstable and there is stable limit cycle in model (6) when  $A = 0.0500$ . (c)  $E_3$  is locally asymptotically stable when  $A = 0.0720$ . Other parameter values are the same as in Fig. 1 except  $h = 7.8000$ .

From Table 1, we can conclude that the positive equilibrium of model (6) could change from asymptotically stable to unstable, and then to stable when the Allee effect parameter  $A$  varies continuously from zero and  $0 < m_1 < m_1^*$ . As an example, we fix  $m_1 = 0.5000$ ,  $h = 7.8000$ ,  $c = 2.5000$ ,  $m_2 = 0.2000$ . Then  $0 < m_1 < m_1^* = 0.5029$ , conditions (9) and (12) hold. In this case,  $A^* = 0.0362$ ,  $A^{**} = 0.0638$  and  $A_c = 0.0857$ . Thus, Table 1 shows that  $E_3$  is locally asymptotically stable when  $0 < A = 0.0200 < A^*$ , which is shown in Fig. 3a.  $E_3$  is unstable and there is a stable limit cycle when  $A^* < A = 0.0500 < A^{**}$ , which is shown in Fig. 3b.  $E_3$  is locally asymptotically stable when  $A^{**} < A = 0.0720 < A_c$ , which is shown in Fig. 3c. From Fig. 3, it can be





**Fig. 4.** Phase portraits of model (6). Isoclines are shown as dashed lines. (a) A stable limit cycle when  $h = 6.2500$ . (b) Both  $E_0$  and  $E_3$  are attractors when  $h = 9.3750$ . Other parameter values are the same as in Fig. 1 except  $A = 0.0020$ .

seen that when the handling time of predators is relatively long, larger  $A$  stabilizes the positive equilibrium. This is because the Allee effect of prey species and type II functional response creates a hump in the prey isocline, there appears positive density dependence in a part of the prey isocline and higher predator density becomes necessary for suppression of the prey growth. This phenomenon destabilizes the positive equilibrium and a limit cycle appears. However, increasing Allee effect decreases the equilibrium predator density. Larger  $A$  increases boundary equilibrium  $E_1$  and decreases  $E_2$ , two isoclines tend to cross in the right hand side of the hump for larger  $A$  and negative density dependence appears again. This is the mechanism why the positive equilibrium changes from stable to unstable, and again to stable as the strength of Allee effect changes.

If model (6) does not have a limit cycle, its asymptotic behavior is determined by the local stability of  $E_0, E_1, E_2$  and  $E_3$ . Specifically, if  $E_3$  is unstable and  $E_1$  and  $E_2$  are saddle points, i.e., the Allee effect of prey species is relatively strong, any positive orbit except the positive equilibrium and the stable manifolds of  $E_1$  and  $E_2$  converges to  $E_0$  as  $t$  tends to infinity, i.e., prey and predators cannot coexist even if the initial population density of prey is abundant (see Fig. 2b). If  $E_3$  is stable and  $E_1$  and  $E_2$  are saddle points, i.e., the Allee effect of prey population is weak, because the origin is always locally stable, then there exists a stable coexistent region divided by the stable manifold of  $E_1$ , which is the threshold induced by the Allee effect of prey species. If the initial position lies outside the region, positive orbits converge to  $E_0$  as  $t$  tends to infinity; if the initial position lies in the stable region, positive orbits converge to  $E_3$  as  $t$  tends to infinity (see Figs. 2d and 4b). In Fig. 2, it can be seen that the stable coexistent region of predators and prey will shrink when the strength of Allee effect increases. If the handling time of predator population is relatively short, the Allee effect of prey species is a destabilizing force in the predator–prey system. A slight difference in the initial population densities makes the asymptotic state very different [24]. Therefore, prey and predator populations can coexist only if the initial position lies in the stable region and will go to extinction if the initial position lies outside this region.

Let us now consider the nonexistence of limit cycle in model (6). Note that  $E_3$  is a node, a focus or a center. A limit cycle of (6) must include  $E_3$ . Take a Dulac function  $D = (A + N)(1 + hN)/(NP)$  and denote the right-hand sides of (6) by  $R$  and  $Q$ , respectively. We have

$$\frac{\partial(DR)}{\partial N} + \frac{\partial(DQ)}{\partial P} = -\frac{3hN^2 + 2(Ah + m_1h - h + 1)N + ((1 + m_1h)A + m_1 - 1) + P}{P}, \tag{14}$$

which is negative in the first quadrant if the following condition holds:

$$A > \max \left\{ \frac{1 - m_1}{1 + m_1h}, \frac{h(1 - m_1) - 1}{h} \right\}. \tag{15}$$

Hence, we obtain the following results.

**Theorem 3.** Let (15) hold. Then system (6) does not admit limit cycle in the first quadrant.

Condition (15) will be satisfied if the Allee effect of prey is relatively strong or the handling time of predator is relatively long. Therefore, Theorem 3 essentially means that there is no limit cycle in system (6) if the Allee effect of prey population is relatively strong or the handling time of predator is relatively long.

From Theorems 1–3 and Table 1, we can obtain the following results on the global stability of  $E_0$ . Three typical phase portraits are shown in Figs. 1a and 2a and b.

**Theorem 4.**  $E_0$  is a global attractor of system (6) in the first quadrant if any one of the following conditions holds:

- (i)  $A > 1 - m_1$  and one of the opposite inequalities of (9) holds;
- (ii)  $0 < A < (1 - \sqrt{m_1})^2$ , (7), (8) and one of the opposite inequalities of (9) hold;
- (iii)  $0 < A < (1 - \sqrt{m_1})^2$ ,  $0 < m_1 < m_1^*$ ,  $A^* < A < A^{**}$ , (7), (8), (9) and (15) hold.

### 3.4. Hopf bifurcation

From Table 1, it can be seen that when the Allee effect coefficient  $A$  increases continuously from zero and  $0 < m_1 < m_1^*$ , then  $E_3$  undergoes stable state, unstable state and stable state. This suggests a possibility that model (6) admits a Hopf bifurcation. If model (6) has limit cycles, the dynamical behavior of the model is determined by the stability of  $E_3$  and the number of limit cycles. We first verify the existence of a Hopf bifurcation in (6) and determine its direction. Set

$$\sigma = ((c^2 - m_2^2 h^2 + m_1 h c^2 - 2c m_1 m_2 h^2 + m_1 m_2^2 h^3) A^* - c^2 + m_2^2 h^2 + m_1 c^2 - m_1 m_2^2 h^2 + 2m_2 c + h m_2^2)((-2m_2 h^2 + 2ch)(A^*)^2 + (-2ch + 2m_2 h^2 - 2m_1 m_2 h^2 + 6m_2 h + 2c m_1 h + 2c) A^* + m_2 h - m_2 - m_2 m_1 h), \tag{16}$$

where  $A^* = (-a_2 + \sqrt{\Delta_2}) / (2a_1)$ ,  $a_1$ ,  $a_2$  and  $\Delta_2$  are described as in (11) and (13). Then we have the following results on the Hopf bifurcation of model (6).

**Theorem 5.** Let (9), (12) hold and  $0 < m_1 < m_1^*$ .

- (i) If  $\sigma < 0$ , then there is a family of stable limit cycles in (6) as  $A$  increases from  $A^*$ .
- (ii) If  $\sigma > 0$ , then there is a family of unstable limit cycles in (6) as  $A$  decreases from  $A^*$ .

**Proof.** Suppose  $A = A^*$ , then  $\text{tr}(M_4) = 0$ . Set  $\omega = \sqrt{\det(M_4)}$ , then the eigenvalues of  $M_4$  are  $\lambda_1 = \omega i$  and  $\lambda_2 = -\omega i$ .

For simplicity of computation, we consider the following system which is equivalent to (6):

$$\begin{cases} \frac{dN}{dt} = N(N(1 + hN) - (m_1 + N)(A + N)(1 + hN) - P(A + N)), \\ \frac{dP}{dt} = P(A + N)((c - m_2 h)N - m_2). \end{cases} \tag{17}$$

Make a transformation of  $x = N - N^*$ ,  $y = P - P^*$  to translate  $(N^*, P^*)$  to the origin. Then (17) becomes

$$\begin{cases} \frac{dx}{dt} = a_{11}x + a_{12}y + f_1(x, y), \\ \frac{dy}{dt} = a_{21}x + a_{22}y + f_2(x, y), \end{cases} \tag{18}$$

where  $f_i(x, y)$  ( $i = 1, 2$ ) represent the higher order terms and

$$\begin{aligned} a_{11} &= N^*(1 + 2hN^* - (m_1 + N^*)(A + N^*)h - (m_1 + A + 2N^*)(1 + hN^*) - P^*), \\ a_{12} &= -N^*(A + N^*), \\ a_{21} &= (c - m_2 h)(A + N^*)P^*, \\ a_{22} &= 0. \end{aligned}$$

Setting

$$\begin{aligned} u &= x, \\ v &= -\frac{a_{11}x}{\omega} - \frac{a_{12}y}{\omega}, \end{aligned} \tag{19}$$

and using

$$\text{tr}(M_4) = a_{11} + a_{22} = 0, \quad \omega^2 = \det(M_4) = -a_{12}a_{21},$$

we obtain

$$\begin{cases} \frac{du}{dt} = -\omega v + f(u, v), \\ \frac{dv}{dt} = \omega u + g(u, v), \end{cases} \tag{20}$$

where

$$f(u, v) = f_1 \left( u, -\frac{a_{11}u + \omega v}{a_{12}} \right),$$

$$g(u, v) = -\frac{a_{11}}{\omega} f_1 \left( u, -\frac{a_{11}u + \omega v}{a_{12}} \right) - \frac{a_{12}}{\omega} f_2 \left( u, -\frac{a_{11}u + \omega v}{a_{12}} \right),$$

which represent the higher order terms. Let

$$\mu = \frac{1}{16} (f_{uuu} + f_{uvv} + g_{uvv} + g_{vvv}) + \frac{1}{16\omega} (f_{uv}(f_{uu} + f_{vv}) - g_{uv}(g_{uu} + g_{vv}) - f_{uu}g_{uu} + f_{vv}g_{vv}),$$

where  $f_{uv}$  denotes  $(\partial^2 f / (\partial u \partial v))(0, 0)$ , etc. Using the fact that  $A = A^*$ , with the aid of software MAPLE13, we obtain

$$\mu = \frac{m_2((c - m_2h)A^* + m_2)\sigma}{8\omega^2(c - m_2h)^4}. \quad (21)$$

Since  $c > m_2h$ , we can see that the sign of  $\mu$  is determined by  $\sigma$ . The conclusion of this Theorem follows from Theorem 3.4.2 and formula (3.4.11) of Guckenheimer and Holmes [25].  $\square$

As an example, we fix  $m_1 = 0.5000$ ,  $h = 0.3125$ ,  $c = 2.5000$ ,  $m_2 = 0.2000$ . Then (9), (12) and  $0 < m_1 < m_1^*$  hold. By (16), we have  $\sigma = 0.2799 > 0$ . Theorem 5 shows that there is an unstable limit cycle when  $A$  decreases from  $A^* = 0.0071$ , which is shown in Fig. 2c when  $A = 0.0040$ . Therefore, we can see that the stable coexistent region of predators and prey collapses with the disappearance of the unstable limit cycle. In addition, if the handling time of predators is long, such as  $h = 7.8000$ , then we have  $\sigma = -0.2845 < 0$ . Thus, there is a stable limit cycle when  $A$  increases from  $A^* = 0.0362$ , which is shown in Fig. 3b when  $A = 0.0500$ . This analysis reveals that the unstable or stable periodical oscillation can be caused by the Allee effect of prey species.

If model (6) has a unique limit cycle, its asymptotic behavior is determined by the stability of  $E_0, E_1, E_2, E_3$  and the limit cycle. Specifically, if  $E_1$  and  $E_2$  are saddle points and  $E_3$  is unstable, then there exists a stable limit cycle. The stable manifold of  $E_1$ , which is the threshold induced by the Allee effect of prey, divides the first quadrant into two parts, any positive orbit between the stable limit cycle and the stable manifold of  $E_1$  converges to the limit cycle as  $t$  tends to infinity. Positive orbits outside the stable manifold of  $E_1$  converge to  $E_0$  as  $t$  tends to infinity, i.e., prey and predators cannot coexist if the initial population densities of prey and predators lies outside the stable manifold of  $E_1$  (see Fig. 3b). If  $E_1$  and  $E_2$  are saddle points and  $E_3$  is stable, there exists an unstable limit cycle. Any positive orbit outside the unstable limit cycle except the stable manifold of  $E_1$  converges to  $E_0$  as  $t$  tends to infinity (see Fig. 2c). Compared with model (1) which does not include Allee effect, we can say that the Allee effect of prey species may be a destabilizing force in the predator–prey system when the handling time of predators is relatively short.

Next, we investigate the global bifurcation of system (4) by means of numerical simulations.

#### 4. Global bifurcation analysis

In this section, we provide the global bifurcation analysis of model (4) by means of the software packages PPLANE8 and MATCONT [26]. We will depict and discuss the heteroclinic cycles occurring in this model.

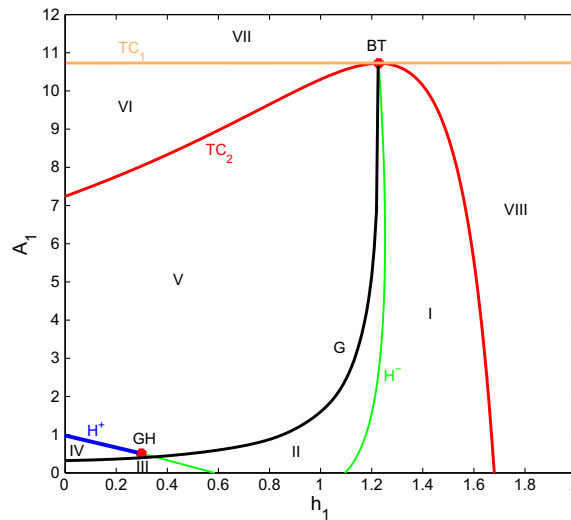
##### 4.1. Local bifurcation analysis

Previous calculations show that the handling time of predators  $h_1$  and the Allee effect of prey species  $A_1$  have an important impact on the dynamical behaviors of model (4), so we concentrate on the effect caused by the changes of  $A_1$  and  $h_1$ . Corresponding to parameter values in Figs. 1–4, we fix  $b = 0.5000$ ,  $d_1 = 0.2500$ ,  $d_2 = 0.1000$ ,  $\alpha = 0.0040$ ,  $s = 0.0500$ ,  $c_1 = 0.2000$  in model (4) (we always keep four decimal places for a real number in this paper). When  $A_1$  and  $h_1$  vary continuously from zero, we obtain two-parameter bifurcation diagram of model (4), which is shown in Fig. 5). It can be seen that there exists a Bogdanov–Takens (or double-zero) point  $BT$  and a generalized Hopf bifurcation point  $GH$  (also called Bautin point). At the generalized Hopf point  $GH$ , an equilibrium with an unstable limit cycle  $H^+$  turns into an equilibrium with a stable limit cycle  $H^-$ .

When

$$A_1 > (\sqrt{b} - \sqrt{d_1})^2 / \alpha = 10.7233,$$

i.e., in region VII, the Allee effect of prey species is very strong, then only the trivial equilibrium  $E_0 = (0, 0)$  is biologically relevant equilibrium, which is globally asymptotically stable. All positive orbits converge to this equilibrium  $E_0$  as  $t$  tends to infinity, that is to say, both predators and prey cannot exist in this region. A typical phase portrait in this region is qualita-



**Fig. 5.** Two-parameter bifurcation diagram of model (4). *BT* indicates a Bogdanov–Takens point; *GH* indicates a generalized Hopf bifurcation point; *TC<sub>1</sub>* indicates an extinction threshold for prey; *TC<sub>2</sub>* indicates a predator invasion boundary; *H<sup>+</sup>* indicates a subcritical Hopf bifurcation curve; *H<sup>-</sup>* indicates a supercritical Hopf bifurcation curve and *G* indicates the heteroclinic cycle curve. Parameter values:  $b = 0.5000$ ,  $d_1 = 0.2500$ ,  $d_2 = 0.1000$ ,  $\alpha = 0.0040$ ,  $s = 0.0500$ ,  $c_1 = 0.2000$ .

tively similar to Fig. 1a. When  $A_1 = 10.7233$ , there is a transcritical bifurcation  $TC_1$  occurring. This bifurcation is also called ‘an extinction threshold for prey’.

Further, when

$$\frac{0.5}{0.25/(0.1/(0.01 - 0.005h_1)) + 0.004} - \frac{0.1}{0.01 - 0.005h_1} < A_1 < 10.7233,$$

boundary equilibria  $E_1$  and  $E_2$  are also biologically relevant. If  $0 < h_1 < 1.2275$ , that is, the handling time of predator is relatively short, i.e., in region VI, then  $E_0$  is the globally stable equilibrium,  $E_1$  is unstable and  $E_2$  is a saddle point. A typical phase portrait in this region is qualitatively similar to Fig. 2a. However, if  $h_1 > 1.2275$ , that is, the handling time of predator is relatively long, i.e., in region VIII, then both equilibria  $E_0$  and  $E_2$  are asymptotically stable,  $E_1$  is a saddle point. The stable manifold of  $E_1$ , which is the threshold induced by the Allee effect of prey population, divides the first quadrant into two parts, one is the attraction region of  $E_0$ , the other is the attraction region of  $E_2$ . A typical phase portrait in region VIII is qualitatively similar to Fig. 1b. Therefore, if the Allee effect of prey is relatively strong and the handling time of predator is relatively short, then prey population will become extinct even if the initial population density of prey is abundant.

When

$$A_1 = \frac{0.5}{0.25/(0.1/(0.01 - 0.005h_1)) + 0.004} - \frac{0.1}{0.01 - 0.005h_1},$$

there is another transcritical bifurcation  $TC_2$  occurring. This bifurcation is also called ‘a predator invasion boundary’. When

$$0 < A_1 < \frac{0.5}{0.25/(0.1/(0.01 - 0.005h_1)) + 0.004} - \frac{0.1}{0.01 - 0.005h_1},$$

equilibria  $E_1$ ,  $E_2$  and  $E_3$  are biologically relevant. Thus, predators and prey may coexist in this region. In this region, there is a supercritical Hopf bifurcation curve  $H^-$  and a subcritical Hopf bifurcation curve  $H^+$ , which is separated by the generalized Hopf point  $GH$ . On the right of the supercritical Hopf bifurcation curve  $H^-$ , i.e., in region I, limit cycles cannot occur, the equilibrium  $E_3$  is asymptotically stable. That is to say, if the handling time of predator population is relatively long, then prey and predators can coexist. A typical phase portrait in region I is qualitatively similar to Fig. 4b. However, when the handling time of predators is relatively short, limit cycles appear. In order to find the extinction boundary in  $(h_1, A_1)$ -plane where the system collapses after predator invasion, we need to proceed the global bifurcation analysis of model (4).

#### 4.2. Global bifurcation analysis

If a limit cycle is continued in two parameters  $h_1$  and *Period*, where *Period* is the cycle period, this results in *Period* tending to infinity at, for example,  $A_1 = 2.0000$ ,  $h_1 = 1.0566$  (see Fig. 6). At this point the non-trivial orbit connects the saddle  $E_2$  to the saddle  $E_1$ , going around the non-trivial equilibrium  $E_3$ . That is, a heteroclinic cycle occurs at  $A = 2.0000$ ,  $h = 1.0566$  (see Fig. 7), which is broken into two heteroclinic connections between the two saddle points  $E_1$  and  $E_2$ . Outside the heteroclinic cycle

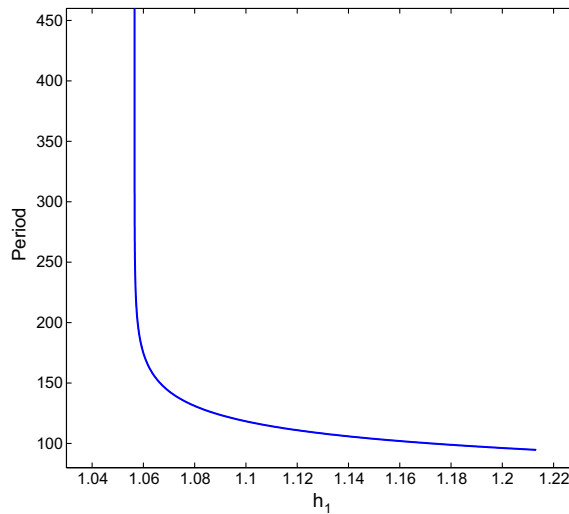


Fig. 6. Bifurcation curve of period of cycles versus  $h_1$  in model (4) when  $A_1 = 2.0000$ . Other parameter values are the same as in Fig. 5.

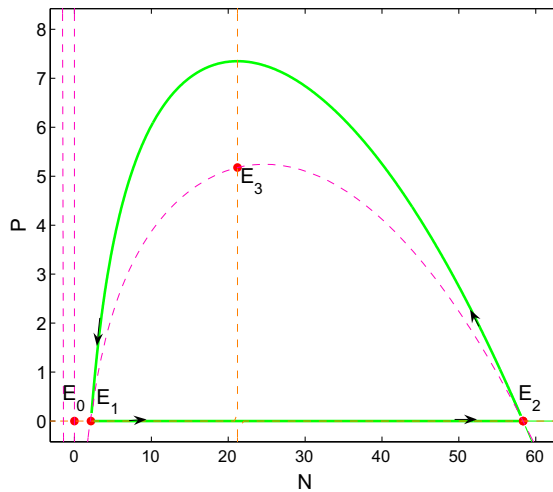


Fig. 7. A heteroclinic cycle occurs at  $h_1 = 1.0566$ . Other parameter values are the same as in Fig. 5 except  $A_1 = 2.0000$ .

the solution goes asymptotically to the stable zero state  $E_0$ , while inside the heteroclinic cycle there is convergence towards the heteroclinic cycle. When  $1.0566 < h < 1.2131$ , there exists a stable limit cycle. The limit cycle shrinks to the positive equilibrium  $E_3$  at 1.2131 and becomes larger and larger when  $h_1$  decreases in this interval. The disappearance of the limit cycles is associated with the occurrence of these heteroclinic connections. If  $0 < h < 1.0566$ , the heteroclinic orbit is broken, all positive orbits except  $E_3$  and the stable manifold of  $E_1$  converge to  $E_0$  as  $t$  tends to infinity. The typical phase portraits are qualitatively similar to Figs. 3b and 2b.

In Fig. 5, the continuation curve of the heteroclinic connecting orbit in the  $(h_1, A_1)$ -plane is depicted as  $G$ . It can readily be seen that this curve is very close to the supercritical Hopf bifurcation curve  $H^-$  when  $A_1$  is relatively large. Limit cycles are therefore almost immediately destroyed. On the left of the supercritical Hopf bifurcation curve  $H^-$ , limit cycles can occur, the heteroclinic cycle curve  $G$  together with the Hopf bifurcation curves  $H^-$  and  $H^+$  separate the  $(h_1, A_1)$ -plane into four parts. In region II, there exist stable limit cycles in model (4), stable periodic oscillation behaviors occur. A typical phase portrait in region II is qualitatively similar to Figs. 3b and 4a. It can be seen that when the Allee effect of prey becomes strong, longer handling time of predators can maintain the cyclic coexistence. Region III is qualitatively similar to region I. That is to say, if the Allee effect of prey is relatively weak, then the positive equilibrium  $E_3$  could change from stable, to unstable, and then stable when the handling time coefficient  $h_1$  varies continuously from zero (see Figs. 2d and 4a and b). In region IV, there exist unstable limit cycles in model (4),  $E_3$  is locally asymptotically stable. Inside the unstable limit cycle, any positive orbits converge to  $E_3$  as  $t$  tends to infinity; outside the unstable limit cycle, any positive orbit converges to  $E_0$  as  $t$  tends to infinity. A

**Table 2**  
The existence and local stability of equilibriums in different regions of Fig. 5.

Region	Equilibriums		
I	$E_1$ saddle,	$E_2$ saddle,	$E_3$ stable
II	$E_1$ saddle,	$E_2$ saddle,	$E_3$ unstable
III	$E_1$ saddle,	$E_2$ saddle,	$E_3$ stable
IV	$E_1$ saddle,	$E_2$ saddle,	$E_3$ stable
V	$E_1$ saddle,	$E_2$ saddle,	$E_3$ unstable
VI	$E_1$ unstable,	$E_2$ saddle,	–
VII	–	–	–
VIII	$E_1$ saddle,	$E_2$ stable,	–

Note: The equilibrium  $E_0$  exists and is asymptotically stable in all regions.

typical phase portrait in region IV is qualitatively similar to Fig. 2c. In region V,  $E_3$  is unstable, prey and predators cannot coexist. All positive orbits except  $E_3$  and the stable manifold of  $E_1$  converge to  $E_0$  as  $t$  tends to infinity. A typical phase portrait in region V is qualitatively similar to Fig. 2b. Therefore, if the Allee effect of prey is relatively strong and the handling time of predator is relatively short, then prey and predators cannot coexist. From Fig. 5, it is clear that only in region I, II, III and IV, prey and predators may coexist, and whether prey and predators can coexist or not also depends on the initial population densities of them. When the Allee effect becomes stronger, larger  $h_1$  may stabilize the coexistent steady state.

The existence and stability of equilibriums in different regions of Fig. 5 are presented in Table 2. In all regions the equilibrium  $E_0$  is locally stable. This implies that in all cases the solutions of system (4) can converge to the state with the extinction of both prey and predators, as long as the initial position lies in the attraction region of  $E_0$ .

### 4.3. Implications of global bifurcation

The occurrence of a heteroclinic cycle in model (4) has important implications. According to the global bifurcation structure in Fig. 5, we can clearly get four different kinds of dynamical behaviors in model (4).

First, in regions I, II, III and IV, depending on the initial states of the system, predators and prey can coexist after predator invasion. Especially, in region II, predators and prey coexist on a stable limit cycle. Because in region II, there exists a supercritical Hopf bifurcation curve, where a stable limit cycle is born, which is also bounded on the other side by the global bifurcation curve G. In region IV, the coexistent region of predators and prey is bounded by the unstable limit cycle. It also can be seen that longer handling time of predators may stabilize the coexistent steady state when the Allee effect of prey species becomes strong.

Second, in region V,  $E_3$  is unstable, any predator invasion is unsuccessful. Both prey and predators will go extinct if the initial position of them does not lie in the stable manifold of  $E_1$ . That is, if the Allee effect of prey is strong and the handling time of predators is relatively short, prey and predators cannot coexist.

Third, in region VIII, predator population cannot survive, prey population is either at carrying capacity ( $E_2$ ) or absent ( $E_0$ ), depending on the initial states of the system.

Fourth, in regions VI and VII, only the trivial equilibrium  $E_0$  is asymptotically stable and the system collapses for all positive initial states. Both prey and predators will go extinct if the Allee effect of prey species becomes strong.

## 5. Discussion

In recent years, the Allee effect has drawn considerable attention in almost every aspect of ecology and conservation. The consequences of Allee effect become more and more significant. In this paper, based on a predator–prey model with Holling type II functional response, we investigate the impact of Allee effect on the stability of a predator–prey system when prey population is subject to Allee effect. We show that the predator–prey model with Allee effect may admit Hopf bifurcation and heteroclinic bifurcation. Compared with model (1) that does not include Allee effect, we can say that the Allee effect of prey species may be a destabilizing force in predator–prey system when the handling time of predators is short. The extinction of prey and predators occurs through the destruction of a stable limit cycle by a global bifurcation. This phenomenon does not occur in the standard food chain model (1) which does not include Allee effect. The global bifurcations found in the model are heteroclinic cycles that consist of two heteroclinic connections between two saddle equilibriums in the zero biomass plane of predators. The disappearance of the limit cycles is associated with the occurrence of these heteroclinic connections. When we get the global bifurcation, it is clear for us to distinguish the stable region with unstable region in the  $(h_1, A_1)$ -plane. In addition, we find that longer handling time of predators may stabilize the coexistent steady state when the Allee effect of prey becomes strong. The positive equilibrium of model (4) could change from stable to unstable, and then to stable when the Allee effect coefficient  $A_1$  or the handling time coefficient  $h_1$  varies continuously from zero. However, whether the prey and predators can coexist or not also depends on the initial population densities of them when prey population is subject to Allee effect.

In nature, the dynamical behaviors of predator–prey system are very complex [12,27–30]. Many forces may influence the dynamics of prey or predator populations. A model can lead to oscillatory behavior either because of a nonlinear functional

response or because of Allee effect [31–33]. It gives insight when we may expect oscillations to occur in real predator–prey system. Sometimes the Allee effect should not be neglected, as we have shown clearly in this paper. Conclusions in this paper also remind us of the importance of the Allee effect. The Allee effect is probably an unstable factor in the food web [21], which cautions us that, in nature preservation, if the prey or predators to be protected is subject to Allee effect, the measures taken should take this into account. If the number of prey or predators is lower than a certain value range, they will become extinct. However, a slight difference in the initial population density can make the asymptotic state very different. In addition, the Allee effect of different species, due to their different mechanisms, may affect the dynamics of populations differently [21].

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