

NONEXISTENCE OF PERIODIC ORBITS FOR PREDATOR-PREY SYSTEM WITH STRONG ALLEE EFFECT IN PREY POPULATIONS

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ABSTRACT. We use Dulac criterion to prove the nonexistence of periodic orbits for a class of general predator-prey system with strong Allee effect in the prey population growth. This completes the global bifurcation analysis of typical predator-prey systems with strong Allee effect for all possible parameters.

1. INTRODUCTION

The importance of limit cycles in predator-prey systems has been recognized by ecologists since the observation of Rosenzweig [26] and May [23]. The existence and uniqueness of the limit cycle in planar systems is mathematically quite non-trivial, and there are many important work on that direction in the last 30 years, see for example [4, 19, 34, 35]. On the other hand, the nonexistence of limit cycles of some planar systems is also useful for excluding oscillatory behavior, and it often implies the global stability of an equilibrium point.

It is well known that the Dulac criterion [8] is an efficient method for proving the nonexistence of closed orbits. However, in general it is difficult to find a suitable Dulac function for specific systems. Many work on the existence (nonexistence) and uniqueness of limit cycles are carried out, for example in [4, 19, 34, 35], by translating a planar system into a Liénard system. But the conditions for the nonexistence of limit cycles are usually difficult to verify ([32, 34]). In this paper, we prove the nonexistence of limit cycles for a class of general predator-prey systems with strong Allee effect, as well as a Rosenzweig-MacArthur predator-prey model [6, 14] (or Gause type predator-prey model [13, 27]) by constructing a suitable Dulac function.

A differential equation model of predator-prey interaction was first formulated by Lotka [21] and Volterra [31] in 1920s, hence it is called Lotka-Volterra equation:

$$\begin{aligned}\frac{du}{dt} &= au - buv, \\ \frac{dv}{dt} &= cuv - dv,\end{aligned}\tag{1.1}$$

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where $a, b, c, d > 0$. A more realistic predator-prey model assumes that the prey grows following a logistic law, and the interaction rate between the prey and predator species saturates to a finite limit when the prey population tends to infinity (Holling type II functional response). This was the basis of the Rosenzweig-MacArthur predator-prey model [26, 27]:

$$\begin{aligned}\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{muv}{a+u}, \\ \frac{dv}{dt} &= \frac{cmuv}{a+u} - dv,\end{aligned}\tag{1.2}$$

where $a, c, d, r, K > 0$. For some biological growth, a minimal threshold value for the growth exists then instead of the logistic type growth, one may assume a growth pattern of Allee effect [1], in which the growth rate per capita is initially increasing for the low density. Moreover it is called a strong Allee effect if the per capita growth rate of low density is negative, and a weak Allee effect means that the per capita growth rate is positive at low density. A predator-prey model under the assumption of strong Allee effect and Holling type II functional response is in form ([6, 32]):

$$\begin{aligned}\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right)\left(\frac{u}{M} - 1\right) - \frac{muv}{a+u}, \\ \frac{dv}{dt} &= \frac{cmuv}{a+u} - dv,\end{aligned}\tag{1.3}$$

where $a, c, d, r, K > 0$ and $0 < M < K$.

In this article we consider the following predator-prey system with strong Allee effect under very general conditions, following [32]:

$$\frac{du}{dt} = g(u)(f(u) - v), \quad \frac{dv}{dt} = v(g(u) - d),\tag{1.4}$$

where f, g satisfy the following assumptions:

- (A1) $f \in C^2(\mathbb{R}^+)$, $f(A) = f(K) = 0$, where $0 < A < K$; $f(u)$ is positive for $A < u < K$, and $f(u)$ is negative otherwise; there exists $\bar{\lambda} \in (A, K)$ such that $f'(u) > 0$ on $[A, \bar{\lambda}]$, $f'(u) < 0$ on $(\bar{\lambda}, K]$;
- (A2) $g \in C^1(\mathbb{R}^+)$, $g(0) = 0$; $g(u) > 0$ for $u > 0$ and $g'(u) > 0$ for $u \geq 0$, and there exists $\lambda > 0$ such that $g(\lambda) = d$.
- (A3) $f(u)$ and $g(u)$ are C^3 near $\lambda = \bar{\lambda}$, and $f''(\bar{\lambda}) < 0$.

Here the function $g(u)$ is the predator functional response, and $g(u)f(u)$ is the net growth rate of the prey. The graph of $v = f(u)$ is the prey isocline on the phase portrait. In the absence of the predator, the prey u has a strong Allee effect growth which can be seen from the assumptions (A1). The carrying capacity of the prey is K , while A is the survival threshold of the prey. The predator isocline is a vertical line $u = \lambda$ solved from $g(\lambda) = d$. The condition (A2) on the functional response $g(u)$ includes the commonly used Holling types II and III as well as the linear Lotka-Volterra one. When the functional response $g(u) = u$, then $f(u)$ is the growth rate per capita. The parameter d is the mortality rate of predator; the number λ can also be thought as a measure of the predator mortality as λ increases with d , and λ is also the stationary prey population density coexisting with predator. The C^3 conditions in (A3) is only to fulfill the standard condition for a Hopf bifurcation [33]. It is known that $\lambda = \bar{\lambda}$ is the Hopf bifurcation point, and the bifurcation is supercritical if $f'''(\bar{\lambda}) \leq 0$ and $g''(\bar{\lambda}) \leq 0$. We note that system (1.3) satisfies the

assumptions (A1)-(A3), and more examples satisfying (A1)-(A3) can be found in Section 3 where applications of our main results are given. On the other hand, we will also consider predator-prey systems of Rosenzweig-MacArthur type in Section 4, where we define a parallel set of assumptions (A1')-(A2') which are satisfied by (1.1) and (1.2).

The dynamical properties of some special cases of system (1.4) have been obtained by numerical simulation in recent studies [3, 22, 30]. The rigorous global dynamics and bifurcation of (1.4) has been thoroughly investigated in our previous paper [32], by utilizing phase portrait analysis and performing global bifurcation analysis, the existence/uniqueness of point-to-point heteroclinic orbit and limit cycle are obtained. One of the main results in [32] is as follows (see [32, Theorem 5.2], and we use the same numbering of assumptions in [32]).

Theorem 1.1. *Suppose that $f(u)$ satisfies (A1), (A3) and*

$$(A6) \quad uf'''(u) + 2f''(u) \leq 0 \text{ for all } u \in (A, K);$$

and $g(u)$ is one of the following:

$$g(u) = u, \quad \text{or} \quad g(u) = \frac{mu}{a+u}, \quad a, m > 0. \quad (1.5)$$

Then with a bifurcation parameter λ defined by

$$\lambda = d \text{ if } g(u) = u, \quad \text{or} \quad \lambda = \frac{ad}{m-d} \text{ if } g(u) = \frac{mu}{a+u}, \quad (1.6)$$

there exist two bifurcation points λ^\sharp and $\bar{\lambda}$ such that the dynamics of (1.4) can be classified as follows:

- (1) *If $0 < \lambda < \lambda^\sharp$, then the equilibrium $(0, 0)$ is globally asymptotically stable;*
- (2) *If $\lambda^\sharp < \lambda < \bar{\lambda}$, then there exists a unique limit cycle, and the system is globally bistable with respect to the limit cycle and $(0, 0)$;*
- (3) *If $\bar{\lambda} < \lambda < K$, and if there is no periodic orbit, then the system is globally bistable with respect to the coexistence equilibrium (λ, v_λ) and $(0, 0)$;*
- (4) *If $\lambda > K$, then the system is globally bistable with respect to $(K, 0)$ and $(0, 0)$.*

For more general results on the dynamics of (1.4), see [32]. However one can see that when $\bar{\lambda} < \lambda < K$, the nonexistence of periodic orbit is assumed rather than proved in Theorem 1.1. For several special cases, the nonexistence of periodic orbit is established by applying a general result on Liénard equation [34].

In this article we provide this missing link in our studies in [32] by proving a general nonexistence result of limit cycles for (1.4) with direct application of the Dulac criterion, and we will prove that under the conditions of Theorem 1.1, indeed there are no periodic orbits for (1.4). Hence the nonexistence of periodic orbits in the part 3 in Theorem 1.1 can be *proved* instead of *assumed*. Our result is proved under the conditions (A1)-(A2) on f and g , as well as one of two additional but natural conditions, see Theorem 2.3. Our result is motivated by earlier ones in [12, 13] for Rosenzweig-MacArthur model with logistic type growth.

The rest of the paper is structured in the following way. In Section 2, we prove our main result of the nonexistence of limit cycles of (1.4) by constructing a suitable Dulac function. In Section 3 we apply the main results to some typical predator-prey systems with strong Allee effect, following the same line as [32]. We discuss the

corresponding result for Rosenzweig-MacArthur model without strong Allee effect in Section 4, which includes the cases of logistic or weak Allee effect growth.

2. NONEXISTENCE OF PERIODIC ORBITS

Recalling from [32], there are four possible equilibrium points of (1.4):

$$(0, 0), \quad (K, 0), \quad (A, 0), \quad (\lambda, v_\lambda) = (\lambda, f(\lambda)),$$

where λ is defined in (A2). The coexistence equilibrium point (λ, v_λ) is the intersection of the prey isocline $v = f(u)$ and the predator isocline $g(u) = d$ (or $u = \lambda$), and it is a positive equilibrium only when $A < \lambda < K$ (see Figure 1 left). Otherwise there are only three equilibrium points in the positive quadrant or boundary.

We construct a bounded region that contains the limit cycle.

Lemma 2.1. *Suppose that f, g satisfy (A1)-(A2), and*

$$(A7) \quad f''(u) \leq 0 \text{ for all } u \in (A, K),$$

then all the closed orbits of (1.4) in the first quadrant lie in $\Omega = \Omega_1 \cup \Omega_2$ (see Figure 1 right), where Ω_1 and Ω_2 are defined by

$$\begin{aligned} \Omega_1 &= \{(u, v) : A \leq u \leq \lambda, 0 \leq v \leq (1 - f'(K))(K - \lambda)\}, \\ \Omega_2 &= \{(u, v) : \lambda \leq u \leq K, 0 \leq v \leq (1 - f'(K))(K - u)\}. \end{aligned} \quad (2.1)$$

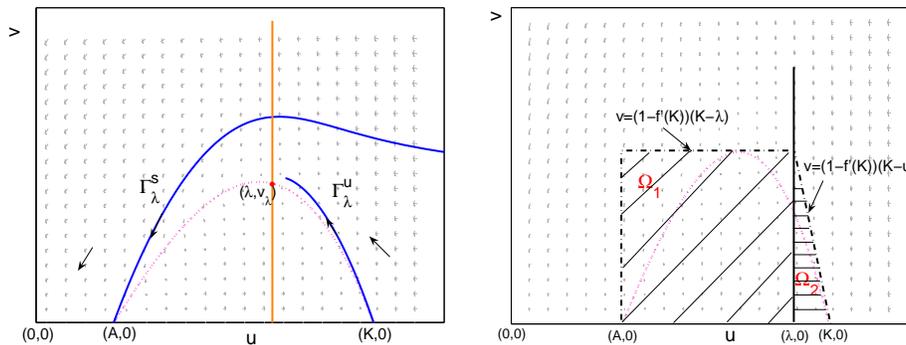


FIGURE 1. (Left): The phase portrait of (1.4); (Right): The bound of closed orbits. The horizontal axis is the prey population u , and the vertical axis is the predator population v . The dotted curve is the u -isocline $v = f(u)$, and the solid vertical line is the v -isocline $g(u) = d$ or $u = \lambda$

Proof. Define

$$f_1(u, v) = g(u)(f(u) - v), \quad f_2(u, v) = v(g(u) - d).$$

Since the positive equilibrium (λ, v_λ) only exists when $A < \lambda < K$, then (1.4) can only have a periodic orbit in the first quadrant when $A < \lambda < K$. Hence we always assume that $A < \lambda < K$ in the following. In this case, the boundary equilibria $(A, 0)$ and $(K, 0)$ are both saddle points. Thus the stable manifold of $(A, 0)$ (denoted by Γ_λ^s) and the unstable manifold of $(K, 0)$ (denoted by Γ_λ^u) are

the separatrices to the dynamical behavior of (1.4). From [32, Propositions 2.2 and 2.4], if there exists a periodic orbit, it must be below both Γ_λ^s and Γ_λ^u , and it is in the region $\{(u, v) : A < u < K, v > 0\}$.

We denote the portion of Γ_λ^u between $u = \lambda$ and $u = K$ by $(u, v_1(u))$. We claim that $v_1(u) \leq (1 - f'(K))(K - u)$. Define $v_2(u) = (1 - f'(K))(K - u)$, we notice that the tangent line of the unstable manifold is

$$v = \left(1 - f'(K) - \frac{d}{g(K)}\right)(K - u),$$

which is below $v = v_2(u)$. Hence we only need to show that the vector field $(f_1(u, v), f_2(u, v))$ points towards the region below the line $v = v_2(u)$ when $(u, v) = (u, v_2(u))$ and $\lambda < u < K$. Then the claim is equivalent to

$$\left|\frac{dv}{du}\right| \leq 1 - f'(K), \quad (u, v) = (u, v_2(u)).$$

Let $M = 1 - f'(K)$, then for $(u, v) = (u, v_2(u))$, $\lambda \leq u < K$,

$$\left|\frac{dv}{du}\right| = \frac{M(K - u)(g(u) - d)}{|f(u) - M(K - u)g(u)|} \leq \frac{M(K - u)}{|f(u) - M(K - u)|}.$$

The condition (A7) implies that $f'(u)$ is non-increasing for $u \in [\lambda, K]$. Then from the mean-value theorem, we have

$$f(u) - f(k) = f'(\xi)(u - K) \leq f'(K)(u - K) = (1 - M)(u - K)$$

for some $\xi \in (u, K)$. Hence $f(u) - M(K - u) \leq (1 - M)(u - K) - M(K - u) = u - K$. Therefore $|f(u) - M(K - u)| \geq K - u$ and

$$\left|\frac{dv}{du}\right| \leq \frac{M(K - u)}{|(1 - M)(u - K) + M(u - K)|} = M,$$

which proves that $v_1(u) \leq v_2(u) = (1 - f'(K))(K - u)$. It is easy to see that the other sides of the boundary of Ω are invariant for the vector field (f_1, f_2) , hence Ω is invariant for (1.4), and the periodic must lie inside Ω . \square

We recall the following well-known Dulac criterion [8], see for example, [14, Theorems 6.1.2, 6.1.3] and [33, Theorem 1.1.5].

Lemma 2.2. *Consider a planer system*

$$\frac{du}{dt} = f(u, v), \quad \frac{dv}{dt} = g(u, v), \tag{2.2}$$

where f, g are continuously differentiable functions defined on a simply-connected region $D \subset \mathbb{R}^2$. Let $h(u, v)$ be another continuously differentiable function on D . For the system (2.2), if $\frac{\partial(fh)}{\partial u} + \frac{\partial(gh)}{\partial v}$ is of one sign in D , then (2.2) has no closed orbits in D .

Our main result on the nonexistence of periodic orbits is as follows (here we continue the numbering of assumptions in [32]).

Theorem 2.3. *Suppose that f, g satisfy (A1)–(A3), and one of the following holds:*

- (A8) $f \in C^3(\mathbb{R}^+)$ and $g \in C^2(\mathbb{R}^+)$, $(uf'(u))'' \leq 0$ and $(u/g(u))'' \geq 0$ for $u \in [A, K]$, and $(uf'(u))' \leq 0$ for $u \in (\lambda, K)$; or
- (A9) $f \in C^3(\mathbb{R}^+)$ and $g \in C^2(\mathbb{R}^+)$, $f'''(u) \leq 0$, $g''(u) \leq 0$ for $u \in [A, K]$, and $f''(u) \leq 0$ for $u \in (\lambda, K)$,

then (1.4) has no closed orbits in the first quadrant for $\bar{\lambda} < \lambda < K$.

Proof. From Lemma 2.1, a periodic orbit of (1.4) must be inside Ω . In particular the orbit satisfies $A < u(t) < K$ (this does not require (A7)). Define $h(u, v) = [g(u)]^\alpha v^\beta$ for $u \geq 0, v \geq 0$ and some $\alpha, \beta \in \mathbb{R}$ to be determined later. Therefore, thanks to Dulac's criterion, we have

$$\begin{aligned} \frac{\partial(hf_1)}{\partial u} + \frac{\partial(hf_2)}{\partial v} &= h[(\alpha + 1)g'(u)(f(u) - v) + g(u)f'(u) + (\beta + 1)(g(u) - d)] \\ &= h[g(u)f'(u) + (\beta + 1)(g(u) - d)], \end{aligned}$$

if $\alpha = -1$.

First we assume (A8) holds. Then

$$\frac{\partial(hf_1)}{\partial u} + \frac{\partial(hf_2)}{\partial v} = \frac{h(u, v)g(u)}{u} F_1(u), \quad (2.3)$$

where

$$F_1(u) = uf'(u) + \eta\left(u - \frac{du}{g(u)}\right), \quad (2.4)$$

with $\eta = \beta + 1$. It is clear that $F_1(\lambda) = \lambda f'(\lambda) < 0$ for $\lambda \in (\bar{\lambda}, K)$ and any choice of β . We prove that $F_1(u) < 0$ for all $u \in [A, K]$ for a selected β . With direct calculation, we have

$$F_1'(u) = (uf'(u))' + \eta\left(1 - d\left(\frac{u}{g(u)}\right)'\right), \quad F_1''(u) = (uf'(u))'' - \eta d\left(\frac{u}{g(u)}\right)''.$$

From (A1), (A2) and (A8), if we choose $\eta = -\frac{(\lambda f''(\lambda) + f'(\lambda))g(\lambda)}{\lambda g'(\lambda)}$, then

$$F_1'(\lambda) = \lambda f''(\lambda) + f'(\lambda) + \eta \frac{\lambda g'(\lambda)}{g(\lambda)} = 0,$$

and $\eta \geq 0$ from (A8). From (A8) and $\eta \geq 0$, $F_1''(u) \leq 0$ for all $u \in [A, K]$, so $F_1(u)$ is concave on $u \in [A, K]$. Hence $u = \lambda$ is the unique critical point of $F_1(u)$ for $u \in (A, K)$, $F_1(\lambda) < 0$, and $u = \lambda$ is local maximum of F_1 for all $\lambda \in (\bar{\lambda}, K)$. Then $F_1(u) < 0$ for all $u \in [A, K]$. Therefore by choosing $\alpha = -1$ and $\beta = -\frac{(\lambda f''(\lambda) + f'(\lambda))g(\lambda)}{\lambda g'(\lambda)} - 1$, we have shown that $\frac{\partial(hf_1)}{\partial u} + \frac{\partial(hf_2)}{\partial v} < 0$ for $u \in (A, K)$ and $v > 0$. By the Dulac criterion (Lemma 2.2), (1.4) has no closed orbits in the first quadrant if $\bar{\lambda} < \lambda < K$.

Secondly if (A9) is satisfied, we rewrite (2.3) into

$$\frac{\partial(hf_1)}{\partial u} + \frac{\partial(hf_2)}{\partial v} = h(u, v)g(u)F_2(u),$$

where

$$F_2(u) = f'(u) + \eta\left(1 - \frac{d}{g(u)}\right), \quad (2.5)$$

again with $\eta = \beta + 1$. It is clear that $F_2(\lambda) = f'(\lambda) < 0$ for $\lambda \in (\bar{\lambda}, K)$ and any choice of β . Similarly we have

$$\begin{aligned} F_2'(u) &= f''(u) + \eta d \frac{g'(u)}{[g(u)]^2}, \\ F_2''(u) &= f'''(u) + \eta d \frac{[g(u)]^2 g''(u) - 2g(u)[g'(u)]^2}{[g(u)]^4}. \end{aligned}$$

If we choose $\eta = -f''(\lambda)g(\lambda)/g'(\lambda)$, then $F_2'(\lambda) = 0$ and $\eta \geq 0$ since $f''(\lambda) \leq 0$ from (A9). Then from (A1), (A2) and (A9), $F_2''(u) \leq 0$ for all $u \in [A, K]$, so $F_2(u)$ is concave on $u \in [A, K]$. Hence $u = \lambda$ is the unique critical point of $F_2(u)$ for $u \in (A, K)$, $F_2(\lambda) < 0$, and $u = \lambda$ is local maximum of F_2 for all $\lambda \in (\bar{\lambda}, K)$. Then the same conclusion holds. \square

Note that Theorem 2.3 improves the result in [32] (Theorem 1.1) in the following way.

Corollary 2.4. *Suppose that f, g satisfy all conditions in Theorem 1.1. Then part 3 of Theorem 1.1 can be changed to: if $\bar{\lambda} < \lambda < K$, then (1.4) has no periodic orbit in the first quadrant, and the system is globally bistable with respect to the coexistence equilibrium (λ, v_λ) and $(0, 0)$.*

Proof. We notice that if f satisfies (A6), and $g(u)$ satisfies (1.5), then the conditions on the $(uf'(u))'' \leq 0$ and $(u/g(u))'' \geq 0$ in (A8) hold. In fact, $(u/g(u))'' = 0$ for $g(u)$ in (1.5), thus the condition on $(uf'(u))'$ in (A8) is not needed as $F_1''(u) = (uf'(u))' \leq 0$. Hence the conclusion holds from Theorem 2.3. \square

The condition (A8) is sharp for the validity of Dulac criterion since in [32], we have shown that if $f'''(\bar{\lambda}) + 2\bar{\lambda}f''(\bar{\lambda}) > 0$ and $g(u)$ is one of the forms in (1.5), then the Hopf bifurcation at $\lambda = \bar{\lambda}$ is subcritical and (1.4) has two periodic orbits for $\lambda \in (\bar{\lambda}, \bar{\lambda} + \epsilon)$ for a small $\epsilon > 0$ (see [32] for examples). On the other hand, we only assume some concavity condition on $f(u)$ for $u \in (\bar{\lambda}, K)$ not for all $u \in (A, K)$.

3. EXAMPLES

In this section we apply our results to several examples of predator-prey system with strong Allee effect which have been studied in [32].

3.1. Bazykin-Conway-Smoller model. The predator-prey model with Lotka-Volterra interaction and Allee effect quadratic growth rate per capita (in dimensionless version) is:

$$\begin{aligned} \frac{du}{dt} &= u(1-u) \left(\frac{u}{b} - 1 \right) - muv, \\ \frac{dv}{dt} &= -dv + muv. \end{aligned} \quad (3.1)$$

Analysis of (3.1) can be found in [2, 6, 32], and we only consider the nonexistence of periodic orbits here. For (3.1), we define

$$f(u) = \frac{(1-u)(u-b)}{bm}, \quad g(u) = mu. \quad (3.2)$$

One can easily verify that

$$\bar{\lambda} = \frac{1+b}{2}, \quad f'(u) = \frac{-2u+(b+1)}{bm}, \quad f''(u) = \frac{-2}{bm} < 0, \quad f'''(u) = 0.$$

Then (A1), (A2) and (A8) (or (A9)) are satisfied for f, g in (3.2). Hence the result in Theorem 2.3 holds. In fact we have obtained the same result as in [32] due to [34, Theorem 2.5] (or [32, Theorem 4.2]), but Theorem 2.3 is much easier to apply. The corresponding phase portrait can be found in Figure 2(left).

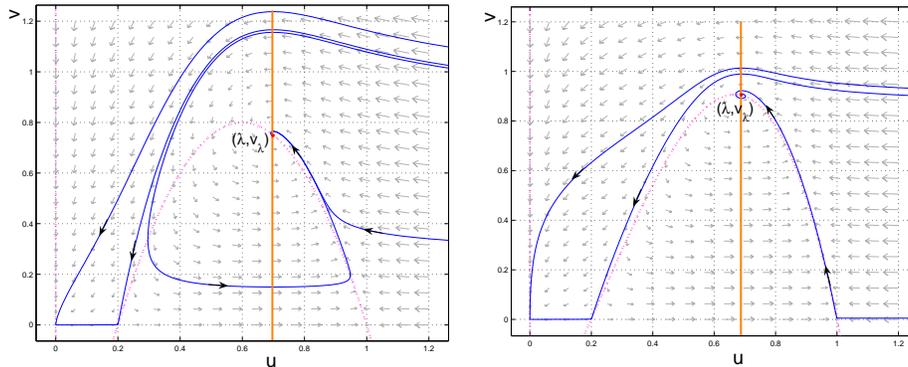


FIGURE 2. Phase portraits of (3.1)(Left) and (3.3)(Right). For either cases, there is no limit cycle, and there are two locally stable equilibrium points $(0, 0)$ and (λ, v_λ) . The horizontal axis is the prey population u , and the vertical axis is the predator population v . The dotted curve is the u -isocline $v = f(u)$, and the solid vertical line is the v -isocline $g(u) = d$ or $u = \lambda$. Parameters used are given: (Left) (3.1) with $m = 1$, $A = 0.2$, $K = 1$, $d = 0.7$; (Right) (3.3) with $m = 1$, $A = 0.2$, $K = 1$, $d = 0.58$, $a = 0.5$

3.2. Owen-Lewis model. A prototypical predator-prey model with Holling type II functional response and Allee effect on the prey was proposed by Owen and Lewis [25], and also Petrovskii et.al. [24], which in dimensionless version is

$$\begin{aligned} \frac{du}{dt} &= u(1-u) \left(\frac{u}{b} - 1 \right) - \frac{mu v}{a+u}, \\ \frac{dv}{dt} &= -dv + \frac{mu v}{a+u}. \end{aligned} \quad (3.3)$$

For (3.3),

$$f(u) = \frac{(a+u)(1-u)(u-b)}{bm}, \quad g(u) = \frac{mu}{a+u}. \quad (3.4)$$

The critical point $\bar{\lambda}$ of $f(u)$ in (b, λ) (which is also the Hopf bifurcation point) has the form

$$\bar{\lambda} = \frac{b+1-a + \sqrt{(b+1-a)^2 + 3(ab+a-b)}}{3}$$

which is the larger root of $f'(\lambda) = 0$. Here

$$\begin{aligned} f'(u) &= \frac{-3u^2 + 2(1+b-a)u + a(1+b) - b}{bm}, \\ f''(u) &= \frac{2(-3u+b+1-a)}{bm}, \quad f'''(u) = \frac{-6}{bm} < 0. \end{aligned}$$

Hence $f''(\bar{\lambda}) = \frac{2(-3\bar{\lambda}+b+1-a)}{bm} < 0$ implies that $f''(u) < 0$ for all $\bar{\lambda} \leq u < K$. Then (A1), (A2) and (A9) are all satisfied for f, g in (3.4). Again the result in Theorem 2.3 holds. The corresponding phase portrait can be found in Figure 2(right). Note that here $f'''(u)$ may be positive for $u \in (A, \bar{\lambda})$.

3.3. Boukal-Sabelis-Berec model. Boukal, Sabelis and Berec [3] considered the equations

$$\begin{aligned}\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right)\left(1 - \frac{A+C}{u+C}\right) - \frac{Bu^n}{1+Bhu^n}v, \\ \frac{dv}{dt} &= -dv + \frac{Bu^n}{1+Bhu^n}v,\end{aligned}\tag{3.5}$$

where $K > A > 0$, $r, B, C, n > 0$ and $h \geq 0$. With $K > A > 0$, (3.5) exhibits a strong Allee effect in prey population density. If $n = 1$ and $h = 0$, then the functional response is linear, and we have

$$\begin{aligned}\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right)\left(1 - \frac{A+C}{u+C}\right) - Buv, \\ \frac{dv}{dt} &= -dv + Buv.\end{aligned}\tag{3.6}$$

If $n = 1$ and $h > 0$, then the functional response is Holling II, and we have

$$\begin{aligned}\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right)\left(1 - \frac{A+C}{u+C}\right) - \frac{muv}{a+u}, \\ \frac{dv}{dt} &= -dv + \frac{muv}{a+u},\end{aligned}\tag{3.7}$$

with $a = 1/(hB)$, $m = 1/h$.

For (3.6) with linear functional response,

$$f(u) = \frac{r(K-u)(u-A)}{BK(u+C)}, \quad g(u) = Bu.\tag{3.8}$$

The critical point $\bar{\lambda}$ of $f(u)$ in (A, K) (Hopf bifurcation point) has the form

$$\bar{\lambda} = -C + \sqrt{N}, \quad \text{where } N = (C+A)(C+K).$$

which is the larger root of $f'(\lambda) = 0$ with

$$\begin{aligned}f'(u) &= \frac{r}{BK} \left(-1 + \frac{N}{(u+C)^2} \right), \\ f''(u) &= \frac{-2rN}{BK(u+C)^3} < 0, \quad f'''(u) = \frac{6rN}{BK(u+C)^4} > 0.\end{aligned}$$

Here (A9) is not satisfied. But it is obvious that (A1)-(A2) and (A7) are satisfied, and if $C \geq K/2$, then for any $u \in [A, K]$,

$$uf'''(u) + 2f''(u) = \frac{2rN(u-2C)}{BK(u+C)^4} \leq 0.$$

Thus (A8) holds and the result in Theorem 2.3 holds for all $\bar{\lambda} < \lambda < K$. The corresponding phase portrait can be found in Figure 3(left).

For (3.7) with Holling II functional response,

$$f(u) = \frac{r(a+u)(K-u)(u-A)}{mK(u+C)}, \quad g(u) = \frac{mu}{a+u}.\tag{3.9}$$

The Hopf bifurcation point $\bar{\lambda}$ is the larger root of $f'(\lambda) = 0$ and

$$\begin{aligned}f'(u) &= \frac{r}{mK} \left(-2u + M_1 - \frac{M_2}{(u+C)^2} \right), \\ f''(u) &= \frac{r}{mK} \left(-2 + \frac{2M_2}{(u+C)^3} \right), \quad f'''(u) = \frac{-6rM_2}{mK(u+C)^4},\end{aligned}$$

where

$$M_1 = K + A + C - a,$$

$$M_2 = C^3 + (K - a + A)C^2 + (-Ka + KA - Aa)C - K A a.$$

Since

$$(\bar{\lambda} + C)^3 - M_2 = C^3 + (C + a - K - A)C^2 + (9C + a - K - A)\bar{\lambda} + 2(3C + a - K - A)C\bar{\lambda},$$

it follows that $f''(u) < 0$ for all $u > \bar{\lambda}$ if C is sufficiently large such that $C + a - K - A \geq 0$. Moreover when C is sufficiently large such that $M_2 > 0$, then (A1), (A2) and (A9) are satisfied. Hence the result in Theorem 2.3 holds. The corresponding phase portrait can be found in Figure 3(right). For both (3.6) and (3.7), subcritical Hopf bifurcation is possible when C is small, see [32] for details.

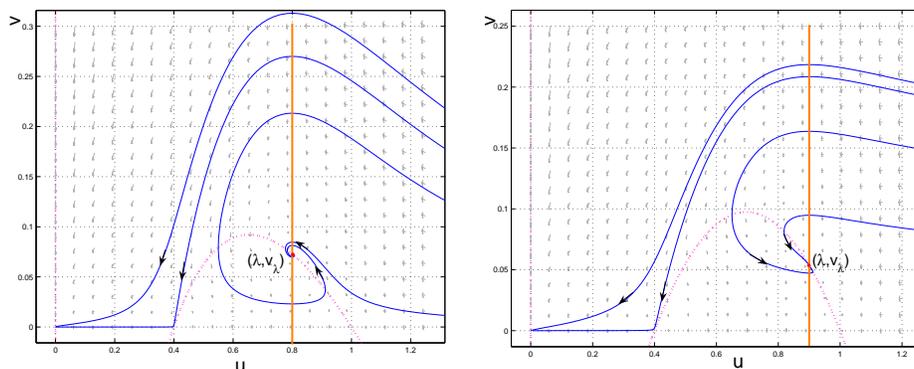


FIGURE 3. Phase portraits of (3.6)(Left) and (3.7)(Right). The horizontal axis is the prey population u , and the vertical axis is the predator population v . The dotted curve is the u -isocline $v = f(u)$, and the solid vertical line is the v -isocline $g(u) = d$ or $u = \lambda$. Parameters used are given: (Left)(3.6) with $r = B = 1$, $A = 0.4$, $K = 1$, $d = 0.8$, $C = 0.6$; (Right) (3.7) with $r = m = 1$, $A = 0.4$, $K = 1$, $d = 0.62$, $a = 0.5$, $C = 3$

4. ROSENZWEIG-MACARTHUR MODEL

Most of these work are for predator-prey model with positive prey isocline without Allee effect, namely the Rosenzweig-MacArthur (or Gause type) predator-prey model, which takes a similar form as (1.4):

$$\begin{aligned} \frac{du}{dt} &= g(u)(f(u) - v), \\ \frac{dv}{dt} &= v(g(u) - d(u)). \end{aligned} \tag{4.1}$$

Here we assume that f, g, d satisfy

- (A1') $f \in C^3(\mathbb{R}^+)$, $f(0) > 0$, there exists $K > 0$, such that for any $u > 0$, $u \neq K$, $f(u)(u - K) < 0$ and $f(K) = 0$; there exists $\bar{\lambda} \in (0, K)$ such that $f'(u) > 0$ on $[0, \bar{\lambda})$, $f'(u) < 0$ on $(\bar{\lambda}, K]$;

- (A2') $g, d \in C^2(\mathbb{R}^+)$, $g(0) = 0$; $g(u) > 0$ for $u > 0$ and $g'(u) > 0$ for $u \geq 0$; $d(0) > 0$, $d'(u) \leq 0$ for $u \geq 0$ and $\lim_{u \rightarrow \infty} d(u) = d_\infty > 0$; there exists a unique $\lambda \in (0, K)$ such that $g(\lambda) = d(\lambda)$.

The function $g(u)f(u)$ is the net growth rate of the prey in the absence of predators, $g(u)$ is the predator functional response, and $d(u)$ is the mortality rate of the predator which depends on the prey density.

The method of constructing a Dulac function to prove the nonexistence of periodic orbits in predator-prey systems was first used in Hsu [13], and it was modified and improved in Hofbauer and so [12], Kuang [18], Liu [20], Ruan and Xiao [28]. In this case, the nonexistence of periodic orbits here and the local stability of the coexistence equilibrium point together imply the global stability of the coexistence equilibrium in the first quadrant. Another way of proving global stability of coexistence equilibrium is to use appropriate Lyapunov functional, see [13, 28, 34]. Other studies of the limit cycle of (4.1) can be found in [4, 9, 10, 11, 15, 17, 19]

Here we revisit the nonexistence of periodic orbits of (4.1), and we modify the method in Section 2 to obtain the following global stability result. Similar construction has been used in [12, 20, 28], but the results are not completely same.

Theorem 4.1. *Suppose that f, g, d satisfies (A1'), (A2') and one of the followings:*

- (A8') $(uf'(u))'' \leq 0$, $(ud(u)/g(u))'' \geq 0$ for all $u \in [0, K]$, and $(uf'(u))' \leq 0$ for $u \in (\bar{\lambda}, K)$; or
 (A9') $f'''(u) \leq 0$ and $(d(u)/g(u))'' \geq 0$ for all $u \in [0, K]$, and $f''(u) \leq 0$ for $u \in (\bar{\lambda}, K)$,

then (4.1) has no closed orbits in the first quadrant for $\bar{\lambda} < \lambda < K$ and the positive equilibrium $(\lambda, v_\lambda) = (\lambda, f(\lambda))$ is globally asymptotically stable in the first quadrant.

Proof. The proof is similar to that of Theorem 2.3. First it is clear that a periodic orbit must satisfy $0 < u(t) < K$, see for example [12]. Hence we only need to show that there is no periodic orbits in $\{(u, v) : 0 < u < K\}$. We still use the same $h(u, v)$ and choose $\alpha = -1$.

If (A8') is satisfied, then

$$\begin{aligned} F_1(u) &= uf'(u) + \eta \left(u - \frac{ud(u)}{g(u)} \right), \\ F_1'(u) &= uf''(u) + f'(u) + \eta \left[1 - \left(\frac{ud(u)}{g(u)} \right)' \right], \\ F_1''(u) &= uf'''(u) + 2f''(u) - \eta \left[\left(\frac{ud(u)}{g(u)} \right)'' \right]. \end{aligned}$$

From (A1'), (A2') and (A8'), we choose

$$\eta = - \frac{(\lambda f''(\lambda) + f'(\lambda))g(\lambda)}{\lambda(g'(\lambda) - d'(\lambda))} > 0.$$

Then $F_1'(\lambda) = 0$, $F_1(\lambda) = \lambda f'(\lambda) < 0$. Again (A8') and $\eta > 0$ imply that $F_1''(u) \leq 0$ for all $u \in [0, K]$, so $F_1(u)$ is concave on $u \in [0, K]$. Therefore $F_1(u) < 0$ for all $u \geq 0$. The Dulac criterion implies that (4.1) has no closed orbits in first quadrant for $\bar{\lambda} < \lambda < K$.

If (A9') is satisfied, then

$$F_2(u) = f'(u) + \eta \left(1 - \frac{d(u)}{g(u)} \right),$$

$$F_2'(u) = f''(u) + \eta \left(\frac{d(u)g'(u) - d'(u)g(u)}{g^2(u)} \right),$$

$$F_2''(u) = f'''(u) - \eta \left(\frac{d(u)}{g(u)} \right)''.$$

From (A1'), (A2') and (A9'), we choose

$$\eta = \frac{-f''(\bar{\lambda})g(\bar{\lambda})}{g'(\bar{\lambda}) - d'(\bar{\lambda})} > 0.$$

Then $F_2'(\bar{\lambda}) = 0$, $F_2(\bar{\lambda}) = f'(\bar{\lambda}) < 0$. Again (A9') and $\eta > 0$ imply that $F_2(u)$ is concave for $0 \leq u \leq K$. Therefore $F_2(u) < 0$ for all $u \geq 0$, the same conclusion holds.

Moreover, (A1') shows that the unique nonnegative equilibrium (λ, v_λ) is locally stable for $\bar{\lambda} < \lambda < K$; (A8') implies that (4.1) undergoes a supercritical Hopf bifurcation at $\lambda = \bar{\lambda}$ and has a unique limit cycle for $0 < \lambda < \bar{\lambda}$. [13, Lemma 3.1] shows that all solutions are bounded and Poincaré-Bendixson Theorem (see [33, Theorem 1.1.19]) implies that (λ, v_λ) is globally stable in the first quadrant for $\bar{\lambda} < \lambda < K$. \square

The applications of Theorem 4.1 to ecological models are discussed in the following two subsections.

4.1. Logistic type. Examples of f , g and d which satisfy conditions (A8') or (A9') can be found in [5, 13, 18, 20, 28, 34], and two prominent examples are (1.1) and (1.2) shown in the introduction. A result like Theorem 4.1 was first proved by Hsu [13]. He claimed that there is no limit cycle for $\lambda \in (\bar{\lambda}, K)$ if $f(u)$ is concave and it has a hump at $u = \bar{\lambda}$. But there was a gap in the proof and counterexamples have been found [5, 12], and results similar to Theorem 4.1 have been proved in [18, 20, 28, 34] and others. Theorem 4.1 shows that the concavity of $f(u)$ on $[0, K]$ is neither sufficient nor necessary for the nonexistence of periodic orbits.

4.2. Weak Allee effect case. Here we point out that the growth rate per capita corresponding to f satisfying (A1') could be of weak Allee effect type, that is, a positive function on $[0, K)$ which is increasing in $[0, \bar{\lambda})$ and decreasing on $(\bar{\lambda}, K)$ (see [7, 16, 29]). In fact, when $g(u) = u$ and $d(u) = d > 0$, then the growth rate per capita $f(u)$ must be of weak Allee effect type from (A1').

An example with weak Allee effect growth rate on the prey is given by (3.6) when $A < 0$ and $C > -A$. It has been shown in [32] that at the Hopf bifurcation point $(\bar{\lambda}, v_{\bar{\lambda}})$, the sign of bifurcation stability is determined by

$$a(\bar{\lambda}) = \bar{\lambda}f'''(\bar{\lambda}) + 2f''(\bar{\lambda}) = \frac{2rN(\bar{\lambda} - 2C)}{BK(\bar{\lambda} + C)^4}.$$

If we choose the parameters so that $KA + (K + A)C > 8C^2$ to make $a(\bar{\lambda}) > 0$, then the Hopf bifurcation is subcritical, and there are two periodic orbits for $\lambda \in (\bar{\lambda}, \bar{\lambda} + \epsilon)$ (see Figure 4). This again shows the condition (A8') is optimal.

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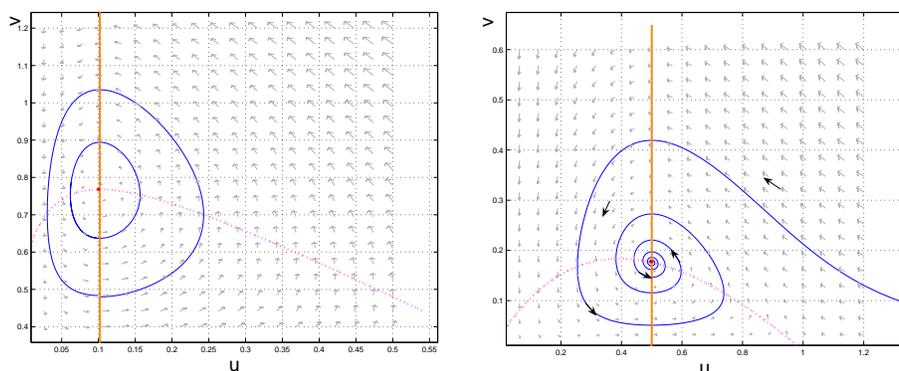


FIGURE 4. Phase portraits of (3.6) with weak Allee effect. (Left): The Hopf bifurcation at $\bar{\lambda}$ is subcritical with parameters $r = B = 1$, $A = -0.028$, $K = 1$, $d = 0.10199$, $C = 0.05$; (Right) The Hopf bifurcation at $\bar{\lambda}$ is supercritical with parameters $r = B = 1$, $A = -0.028$, $K = 1$, $d = 0.6$, $C = 2$

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