A host–parasitoid interaction with Allee effects on the host

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Abstract

We explore the addition of Allee effects to single-species discrete-time models with overcompensatory density dependence. When the intrinsic growth rate of the population, $r$, is large, the population bifurcates into chaos. The population goes extinct if $r$ is either below a threshold level or very large. The model is then used to study host–parasitoid interactions with and without Allee effects in the host. The coexistence of the host and parasitoid populations both depends on threshold levels of $r$, threshold levels of the host population size, and the parasitoid potential, which is the product of the searching efficiency of the parasitoid for the host, and the fecundity of the parasitoid. The addition of Allee effects has a negative impact on the coexistence of both populations.

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1. Introduction

The Allee effect, or the decrease in population growth rates at low population densities, was first described in the 1930s [1,2]. Allee effects may be caused by a variety of mechanisms operating in small populations, including an inability to find mates, reduced foraging efficiency in social animals, lessened defenses against predators, reduced reproductive success in cooperative breeders, and reduced fertilization success in broadcast spawners. The presence of Allee effects indicates that there is a minimal population size necessary for a population to maintain itself in nature. Allee effects have been reported in many natural populations, including plants [3], marine invertebrates (e.g. [4]), insects (e.g. [5]), birds, and mammals (see [6]). Interest in the dynamics of small populations, including Allee effects, has increased in recent years [7–15] due to the increasing number of rare and endangered species, invasions of exotic species, depletions of species due to overharvest or disease, and the presence of metapopulations due to the fragmentation of habitats.

Interest has also increased in how small populations interact with other populations, including predator–prey and host–parasitoid systems. In these instances, Allee effects can occur at either the higher trophic level (predator, parasite), the lower level (prey, host), or in the interaction between them. Recent work has shown that adding Allee effects to a predator–prey system can be destabilizing, depending on the formulation of the equations, and where
Allee effects are added [15]. In host–parasitoid systems, Allee effects may change the dynamics of the host–parasitoid system in unexpected ways. For example, in a recent field study on an endangered plant and its seed-eating parasite, Allee effects in the parasite population due to low densities of the host plant enabled small populations of the host plant to have higher net seed production than larger populations. The Allee effect in the interaction therefore reversed some of the negative effects of habitat fragmentation on the host plant [16].

Without Allee effects, density dependence in the host is thought to stabilize the interaction between host and parasitoid [17]. However, the timing of density dependence relative to the timing of the parasitoid attack has been found to be important in determining the dynamics of the system [18–20]. Given this, it is likely that the functional form of density dependence is also important in determining the stability of the host–parasite interaction, but the effects of differences in the functional form of the density dependence have not been explicitly explored. The most common forms of density dependence are compensatory dynamics (the Beverton–Holt-type functions), where the population reaches an asymptote even at high population sizes, and overcompensatory dynamics (Ricker-type functions), where the population reaches a maximum at intermediate population sizes, then declines at high population sizes due to intra-specific scramble competition. When density dependence is compensatory, Allee effects in predatory–prey systems have been investigated previously in [11,12]. In [11], a predator–prey model with Allee effects occurring in the prey is studied, and an age-structured predator–prey model with Allee effects in the prey is investigated in [12]. The single population dynamics of the prey in both of these models are governed by Beverton–Holt-type functions and the derivation of the age-structured model given in [12] is motivated by the egg, larvae and adult stages consideration in the host.

In this paper, we explore the dynamics of a host–parasitoid model system when the host population is subject to Allee effects and the prey population is governed by the Ricker-type functions. It is well known that Beverton–Holt-type functions generate very simple dynamics while Ricker-type functions possess complex dynamical behavior including chaos. It is demonstrated in [12] that similar biological conclusions as the model without age structure are obtained [11], that is, the initial prey population must exceed a minimum level in order for both populations to survive. However, the prey population can drive the parasitoid population to extinction if prey is synchronizing initially. We shall not consider the stage-structured prey model in this work. Nor do we consider a delay model. Our main purpose is to understand the impact of Allee effects in overcompensatory dynamics. Adding delay in the model will very likely complicate the system even further.

In [21], a general class of two-dimensional difference equations motivated by the host–parasitoid interaction is considered. In addition to some imposed conditions, it is assumed in [21] that the map induced by the equations is a diffeomorphism in the positive quadrant of $R^2$. It is shown in [21] that there exists no nontrivial periodic solutions if the intrinsic growth rate $\lambda$ of the host is greater than 1 but close to 1, where $\lambda = 1$ is a bifurcation point of the model. However, global strict oscillations do occur for both forward and backward bifurcations when $\lambda$ is large. Their results are then applied to the classical Nicholson–Bailey model. Our model of host–parasitoid interaction given in (3.1) is not a one-to-one map and thus the model (3.1) does not fall into the class of models investigated by Hsu et al. [21]. In particular, system (3.1) is not the classical Nicholson–Bailey model [22] and our system does possess a periodic solution when the growth rate of the host $r$ is a little bit greater than 2, where $r = 2$ is a bifurcation point in our model.

In the following, we first present a single-species discrete-time model with overcompensatory density dependence, and compare the model behavior with and without Allee effects. Next, we will present a basic host–parasitoid model with overcompensatory dynamics in the host population, and then assume that the host population undergoes Allee effects. Asymptotic dynamics of host–parasitoid models with and without the Allee effects will be investigated. Numerical simulations will also be performed to illustrate theoretical results.

2. Allee effects in a single-species population model

Let $x_t$ be the population size of a species at time $t$, $t = 0, 1, 2, \ldots$. Under the biological assumptions of the classical Ricker stock recruitment model, the population size from generation $t$ to generation $t + 1$ is governed by the following difference equation:

$$
\begin{align*}
    x_{t+1} &= x_t e^{r - \lambda_t} \\
    x_0 &> 0,
\end{align*}
$$

(2.1)
where parameter $r$ is positive. The equation possesses similar complex dynamical behavior as the discrete logistic model. It has two steady states: 0 and $r$, where 0 is always unstable and $r$ is locally asymptotically stable if $0 < r < 2$. It is well known that the positive steady state $r$ is globally asymptotically stable for (2.1) if $0 < r < 2$. Moreover, period-doubling bifurcation occurs when $r = 2$, and as we increase $r$, the equation undergoes period-doubling bifurcation cascade to chaos [23]. Qualitative behavior of (2.1) is summarized below.

**Proposition 2.1.** Solutions of (2.1) satisfy $x_t \leq e^{r-1}$ for all $t$ large and steady state $r$ is globally asymptotically stable for (2.1) in $\mathbb{R}_+ \setminus \{0\}$ if $0 < r < 2$. Moreover, Eq. (2.1) is uniformly persistent, i.e., there exists $c > 0$ such that $\liminf_{t \to \infty} x_t \geq c$ for all solutions of (2.1) with $x_0 > 0$.

**Proof.** Let $\hat{f}(x) = xe^{r-x}$ for $x \geq 0$. Then $\hat{f}$ attains its maximum at $x = 1$. As a result, $x_t \leq e^{r-1}$ for all large $t$. It is clear that $r$ is globally asymptotically stable when $0 < r < 2$ [23]. To prove uniform persistence of (2.1), we apply Theorem 4.1 of [24] (cf. Theorem 3.1 below). If there exists a solution $x_t$ with $x_0 > 0$ such that $\lim_{t \to \infty} x_t = 0$, then for any $\epsilon > 0$ there exists $t_0 > 0$ such that $x_t < \epsilon$ for $t \geq t_0$. We choose $\epsilon < r$. But then $x_{t+1} > x_te^{r-\epsilon} > x_t$ for $t \geq t_0$ implies $\lim_{t \to \infty} x_t = x^\circ > 0$. We obtain a contradiction and conclude that (2.1) is uniformly persistent. □

It follows from Proposition 2.1 that populations with positive initial population size will always survive indefinitely. We remark that if $0 < r < 2$, then since $\lim_{t \to \infty} x_t = r$ if $x_0 > 0$, we may choose $c = r$ or any positive number less than $r$. On the other hand $c < r$ if $r > 2$. To see this, notice that a 2-cycle of (2.1) must satisfy

$$x + xe^{r-x} = 2r.$$

Clearly one solution is $r$. Let $\hat{f}(x) = x + xe^{r-x}$ for $x \geq 0$. Then $\hat{f}(0) = 0$ and $\hat{f}'(r) = 2 - r < 0$ implying there is another positive solution that is less than $r$. Therefore one component of a 2-cycle is less than $r$ and thus $c$ given in Proposition 2.1 must be strictly less than $r$ if $r > 2$. Moreover, $c$ depends on $r$.

Notice that in (2.1) the population per capita growth rate, $e^{r-x}$, is a decreasing function of population size $x$. It models negative density dependence of intra-specific competition between individuals within the population. Suppose now Allee effects are taken into consideration. In particular, the growth rate is zero when population size is zero and the per capita growth rate increases initially with increasing population size. In other words, density dependence has a positive effect on the population per capita growth rate when population size is small. This incorporates for example the effect of being unable to find mates when the population size is very small, but the population can grow better at least initially when population size becomes larger. As in [11,12,25], we let

$$a(x) = \frac{x}{m+x}$$

denote the probability of an individual successfully finding a mate to reproduce or a cooperative individual to exploit resources, where parameter $1/m > 0$ is an individual’s searching efficiency. Model (2.1) with Allee effects becomes

$$x_{t+1} = x_t e^{r-x_t} \frac{x_t}{m+x_t}$$

$$x_0 > 0.$$  

In the following we shall study asymptotic dynamics of (2.2).

Let $g$ be the population per capita growth rate,

$$g(x) = e^{r-x} \frac{x}{m+x} \quad \text{for } x \geq 0.$$  

A simple calculation yields

$$g'(x) = \frac{e^{r-x}(m-mx-x^2)}{(m+x)^2}.$$  

Thus

$$g'(x) \begin{cases}  > 0 & \text{if } 0 < x < \hat{x} \\  < 0 & \text{if } x > \hat{x}, \end{cases}$$

where $\hat{x}$ is uniformly persistent.
and \( g(x) \) attains its maximum at \( x = \hat{x} \), where
\[
\hat{x} = \frac{-m + \sqrt{m^2 + 4m}}{2}.
\] (2.3)

Moreover, \( g(\hat{x}) < 1 \) if and only if
\[
r < \frac{\sqrt{m^2 + 4m - m}}{2} + \ln \frac{m + 2 + \sqrt{m^2 + 4m}}{2}.
\]

Let
\[
r_0 = \frac{\sqrt{m^2 + 4m - m}}{2} + \ln \frac{m + 2 + \sqrt{m^2 + 4m}}{2}.
\] (2.4)

Then \( g(x) < 1 \) for all \( x \geq 0 \) if \( r < r_0 \) and consequently 0 is the only steady state of (2.2).

If \( r = r_0 \), then \( g(\hat{x}) = 1 \), \( g(x) < 1 \) if \( x \neq \hat{x} \), and Eq. (2.2) has a unique positive fixed point \( \hat{x} \). If \( r > r_0 \), then (2.2) has two positive fixed points \( \tilde{x}_1, \tilde{x}_2 \), where \( \tilde{x}_1 < \hat{x} < \tilde{x}_2 \), and
\[
g(x) \begin{cases} < 1 & \text{if } x \in (0, \tilde{x}_1) \cup (\tilde{x}_2, \infty) \\ > 1 & \text{if } \tilde{x}_1 < x < \tilde{x}_2. \end{cases}
\]

Since \( g \) as a function of \( r \) is increasing, we see that \( \tilde{x}_1(r) \) decreases and \( \tilde{x}_2(r) \) increases as \( r \) increases. However, as \( \frac{\tilde{x}_1}{m+\tilde{x}} < 1 \) for \( x \geq 0 \), we have \( \tilde{x}_2 < r \).

Let \( G(x) \) be the map induced by (2.2),
\[
G(x) = e^{r-x} \frac{x^2}{m+x}.
\]

Then \( G(0) = 0 \), \( \lim_{x \to \infty} G(x) = 0 \), and
\[
G'(x) = \frac{xe^{r-x}(2m + x - mx - x^2)}{(m + x)^2}.
\]

Consequently,
\[
G'(x) \begin{cases} > 0 & \text{if } 0 < x < \bar{x} \\ < 0 & \text{if } x > \bar{x}, \end{cases}
\]

where
\[
\bar{x} = \frac{1 - m + \sqrt{(m-1)^2 + 8m}}{2}.
\]

Furthermore, it is easy to see that
\[
\hat{x} < \bar{x},
\]

and both \( \hat{x} \) and \( \bar{x} \) are independent of \( r \) and only depend on \( m \). When \( r > r_0 \), it is clear that \( \tilde{x}_1 < \hat{x} < \tilde{x}_2 \). However, it is possible that either \( \bar{x} < \tilde{x}_2 \) or \( \bar{x} \geq \tilde{x}_2 \) holds (see Fig. 1(a) and (b)). For example, if we use \( r = 2.0 \) and \( m = 1.5 \), then \( \tilde{x}_1 = 0.3618, \bar{x} = 1.5, \tilde{x}_2 = 1.1794 \) and \( \hat{x} = 0.6861 \). If we vary \( r \) to \( r = 3.2 \), then \( \hat{x} \) and \( \bar{x} \) remain the same as they only depend on \( m \). But \( \tilde{x}_1 = 0.0685 \) and \( \tilde{x}_2 = 2.7668 \). Therefore, we see that it is possible for \( \bar{x} \) to be either smaller or larger than \( \tilde{x}_2 \).

**Theorem 2.2.** Solutions of (2.2) are bounded and dynamics of (2.2) are summarized below.

(a) If \( r < r_0 \) then 0 is the only steady state of (2.2) and solutions of (2.2) converge to 0.
(b) If \( r = r_0 \), then (2.2) has two steady states 0 and \( \hat{x} > 0 \). Solutions with \( x_0 < \hat{x} \) satisfy \( \lim_{t \to \infty} x_t = 0 \) and solutions with \( \hat{x} < x_0 \leq \bar{x} \) satisfy \( \lim_{t \to \infty} x_t = \hat{x} \). Solutions with \( x_0 > \bar{x} \) converge to either 0 or \( \bar{x} \).
(c) If \( r > r_0 \), then (2.2) has three steady states 0, \( \tilde{x}_1 \) and \( \tilde{x}_2 \). Solutions of (2.2) with \( x_0 < \tilde{x}_1 \) converge to 0. If we further assume \( \tilde{x}_2 \leq \tilde{x} \), then solutions converge to either 0 or \( \tilde{x}_2 \).
Theorem 2.2

(a) Also condition (c) means that (a) if \( m = 2.2 \) and solutions converge to either 0 or a positive steady state when \( r \) is roughly between 1.85 and 2.85 as demonstrated in Theorem 2.2(c) where \( \tilde{x}_2 < \tilde{x} \). A period-doubling bifurcation occurs when \( r \) is about 2.85. The next period-doubling bifurcation occurs when \( r \) is around 3.25. (d) is the bifurcation diagram of (2.2) when \( m = 2.0 \).

Proof. (a) If \( r < r_0 \), then \( g(x) < 1 \) for \( x \geq 0 \). In particular, \( g(\tilde{x}) < 1 \) and \( x_{t+1} = g(x_t) \) for \( t \geq 0 \) implies \( \lim_{t \to \infty} x_t = 0 \) for any solution \( x_t \) of (2.2).

(b) Suppose \( r = r_0 \). Let \( 0 \leq x_0 < \tilde{x} \) be given. Then \( x_1 = g(x_0)x_0 < x_0 \) and \( 0 \leq x_1 = G(x_0) < G(\tilde{x}) = \tilde{x} \). Inductively, \( \{x_t\} \) is a decreasing sequence of real numbers that is bounded below by 0. Since the sequence must converge to a fixed point of (2.2), we have \( \lim_{t \to \infty} x_t = 0 \). If \( \tilde{x} \leq x_0 \leq \tilde{x} \), then since \( G \) is increasing on \( (\tilde{x}, \tilde{x}) \) we have \( x_1 = g(x_0)x_0 < x_0 \) and \( 0 \leq x_1 = G(x_0) < G(\tilde{x}) = \tilde{x} \). Hence such a solution converges to the unique positive fixed point \( \hat{x} \). If \( x_0 > \tilde{x} \), then since \( y = G(x) \) lies below the line \( y = x \) if \( x \neq 0 \), \( \tilde{x} \), and \( G(x) \) is decreasing on \( (\tilde{x}, \infty) \), we have \( x_1 = G(x_0) < x_0 \) and \( x_1 = G(x_0) < G(\tilde{x}) = \tilde{x} \). Therefore if \( x_1 \in [\tilde{x}, \tilde{x}) \), then \( \lim_{t \to \infty} x_t = \tilde{x} \), and if \( x_1 \in (0, \tilde{x}) \), then \( \lim_{t \to \infty} x_t = 0 \). We conclude that solutions converge to either 0 or \( \tilde{x} \) if \( r = r_0 \).

(c) Suppose now \( r > r_0 \), i.e., \( g(\tilde{x}) > 1 \). Clearly if \( x_0 < \tilde{x}_1 \), then such a solution converges to 0. In addition if \( \tilde{x}_2 \leq \tilde{x} \), then similar to the previous analysis, we have solutions with either \( \tilde{x}_1 < x_0 \leq \tilde{x}_2 \) or \( \tilde{x}_2 < x_0 < \tilde{x} \) converging to \( \tilde{x}_2 \), and solutions with \( x_0 > \tilde{x} \) converging to either 0 or \( \tilde{x}_2 \) by a similar argument as in the case for \( r = r_0 \). Hence the equation has only two attractors 0 and \( \tilde{x}_2 \). □

Notice that \( r_0 \) defined in (2.4) is an increasing function of \( m \). Therefore decreasing the searching efficiency of an individual will make the population more likely to become extinct by Theorem 2.2(a). Also condition \( \tilde{x}_2 \leq \tilde{x} \) given in Theorem 2.2(c) means that \( r \) is not too large, as \( \tilde{x}_2 \) increases with increasing \( r \) and \( \tilde{x} \) is independent of \( r \). In this case since \( \tilde{x}_2 < r \) and the population will either converge to 0 or to \( \tilde{x}_2 \), the population will stabilize in a smaller level than the model without Allee effects. If \( \tilde{x}_2 > \tilde{x} \), i.e., if \( r \) is large, then the asymptotic dynamics of the solutions with \( x_0 > \tilde{x}_1 \) are much more complicated. However, it can be easily seen that if \( x_0 > \tilde{x}_2 \), then \( x_1 < \tilde{x}_2 \). Therefore the
complex dynamics of the equation originate on the initial conditions that are lying between \( x_1 \) and \( x_2 \). Fig. 1 plots the map \( y = G(x) \) for \( m = 1.5 \) and \( m = 2.0 \) along with the line \( y = x \). The corresponding bifurcation diagrams are also provided in Fig. 1, where \( r \) is the bifurcation parameter.

3. Allee effects in a host–parasitoid model

In this section we shall first introduce a host–parasitoid model based on the classical Nicholson–Bailey model (1935), but modified to incorporate overcompensatory density dependence (a Ricker-type curve) in the host population. The host–parasitoid interaction with Allee effects on the host will then be proposed. Asymptotic behavior of the solutions of both models will be studied.

Let \( N_t \) be the host population at time \( t \). The parasitoid population at time \( t \) is denoted by \( P_t \). The parasitoid in this example is a specialist, and must search for a specific host in which to deposit its eggs. Let \( \beta \) be the average number of offspring that a parasite can reproduce from a parasitized host. It is assumed that the number of encounters between host and parasitoid populations at any time \( t \geq 0 \) follows that of simple mass action, \( bN_tP_t \), where the searching efficiency \( b \) is a constant. We assume that the number of encounters is distributed randomly with a Poisson distribution. Consequently, the probability that an individual host will escape from being parasitized when the parasitoid population is of size \( P \) is \( e^{-\beta P} \). Therefore, the interaction between host and parasitoid is governed by the following system of difference equations:

\[
\begin{align*}
N_{t+1} &= N_t e^{r - N_t} e^{-bP_t} \\
P_{t+1} &= \beta N_t (1 - e^{-bP_t}) \\
N_0, P_0 &\geq 0.
\end{align*}
\]

(3.1)

Since \( N_{t+1} \leq N_t e^{r-N_t} \) and \( P_{t+1} \leq \beta N_t \) for \( t \geq 0 \), it follows that solutions of (3.1) are bounded. Moreover, (3.1) always has a trivial steady state \( E_0 = (0, 0) \) and a boundary steady state \( E_1 = (r, 0) \). The \( P \)-component of an interior fixed point \((N, P)\) must satisfy

\[
1 = e^{-h(P)} - bP,
\]

(3.2)

where \( h(P) = \frac{P}{\beta(1-e^{-\beta P})} \). Since \( \lim_{P \to 0^+} h(P) = \frac{1}{\beta^*} \), \( \lim_{P \to \infty} h(P) = \infty \), and \( h'(P) > 0 \) if \( P > 0 \), we see that steady state \( E_2 = (N^*, P^*) \) exists if and only if

\[
\beta br > 1,
\]

in which case the interior steady state is unique, where \( P^* \) satisfies (3.2) and \( N^* = \frac{P^*}{\beta(1-e^{-\beta P^*)}} \). Moreover, we have

\[
N^* < r
\]

whenever \( E_2 = (N^*, P^*) \) exists. The local asymptotic stability of these fixed points can be determined by the corresponding Jacobian matrix of the system. In particular, \( E_0 = (0, 0) \) is always a saddle point and \( E_1 = (r, 0) \) is locally asymptotically stable if \( r < 2 \) and \( \beta br < 1 \).

The dynamics of system (3.1) are presented in the following.

**Theorem 3.1.** Solutions of (3.1) are bounded and dynamics of system (3.1) can be summarized below.

(a) If \( 0 < r < 2 \) and \( \beta br < 1 \), then \( E_0 = (0, 0) \) and \( E_1 = (r, 0) \) are the only steady states for (3.1) and solutions with \( N_0 > 0 \) all converge to \( E_1 \).

(b) If \( 0 < r < 2 \) and \( \beta br > 1 \), then steady states \( E_0, E_1 \) and \( E_2 = (N^*, P^*) \) all exist, where \( E_0 \) is unstable and \( E_1 \) is a saddle point with global unstable manifold given in (3.5). Moreover, system (3.1) is uniformly persistent, i.e., there is \( C > 0 \) such that \( \lim \inf_{t \to \infty} N_t \geq C \) and \( \lim \inf_{t \to \infty} P_t \geq C \) for any solution \((N_t, P_t)\) of system (3.1) with \( N_0 > 0 \) and \( P_0 > 0 \). In addition if \( \beta bN^*(1 - N^*e^{-bP^*}) < 1 \), then \( E_2 \) is locally asymptotically stable.

(c) If \( r > 2 \) and \( \beta br < 1 \), then (3.1) has only two steady states \( E_0 \) and \( E_1 = (r, 0) \), where \( E_0 \) and \( E_1 \) are saddle points. The local stable manifold of \( E_1 \) is given in (3.6). In addition if \( \beta be^{-1} < 1 \), then \( \lim_{t \to \infty} P_t = 0 \) for all solutions of (3.1).
(d) If \( r > 2 \) and \( \beta br > 1 \), then (3.1) has three steady states \( E_0, E_1 \) and \( E_2 \), where \( E_0 \) is a saddle point and \( E_1 \) is a repeller. If in addition \( \beta bc > 1 \), where \( c > 0 \) is defined in Proposition 2.1, then system (3.1) is uniformly persistent.

**Proof.** It is clear that solutions of (3.1) are bounded. Indeed, \( N_t \leq e^{-t} \) and \( P_t \leq \beta e^{-t} \) for all \( t \) large. To prove (a), let \((N_t, P_t)\) be a solution of (3.1) with \( N_0 > 0 \). Since \( 0 < r < 2 \) and \( N_{t+1} \leq N_t e^{r-1} \) for \( t \geq 0 \), using (2.1), we have \( \limsup_{t \to \infty} N_t \leq r \). As \( \beta br < 1 \), we can then prove that \( \lim_{t \to \infty} P_t = 0 \). Hence it can be shown that \( \liminf_{t \to \infty} N_t \geq r \). Therefore \( \lim_{t \to \infty} N_t = r \) and solutions of (3.1) with \( N_0 > 0 \) converge to the boundary steady state \( E_1 = (r, 0) \).

(b) If \( 0 < r < 2 \) and \( \beta br > 1 \), then \( E_1 = (r, 0) \) is a saddle point and (3.1) has a unique interior steady state \( E_2 = (N^*, P^*) \) with \( N^* < r \). We proceed to estimate the local unstable manifold of \( E_1 \) [26]. A straightforward computation of an eigenvector \( v \) belonging to the eigenvalue \( \beta br \) of the Jacobian matrix evaluated at \( E_1 \) yields \( v = (1 - \frac{br}{1 - \beta br}, 1)^T \). Thus the tangent of the local unstable manifold of \( E_1 \) at \( E_1 \) has a slope of

\[
m = \frac{1 - r - \beta br}{br} < 0.
\]

We shall introduce new variables so that steady state \( E_1 \) of system (3.1) becomes the trivial steady state for the resulting new system [26]. Indeed, let

\[
x = N - r, \quad y = P.
\]

Then (3.1) is converted into

\[
\begin{cases}
x_{t+1} = (x_t + r) e^{-x_t} e^{-by_t} - r \\
y_{t+1} = \beta(x_t + r)(1 - e^{-by_t}),
\end{cases}
\]

(3.3)

where \( \hat{E} = (0, 0) \) is the corresponding steady state of (3.3). Using a second order approximation, we let

\[
y = \hat{y}(x) = mx + qx^2 + O(x^3)
\]

be the local unstable manifold of \( \hat{E} \) for \( x \) near 0. Since \( y = \hat{y}(x) \) is invariant for system (3.3), we have, by a direct computation,

\[
q = \frac{1 - r}{br^2}.
\]

Therefore the local unstable manifold of \( E_1 = (r, 0) \) with respect to the original system (3.1) is

\[
y_1^-(N) = \beta r + \frac{r - 1 - \beta br}{br} N + \frac{1 - r}{br^2} N^2 + O(N^3)
\]

(3.4)

for \( N \) near \( r \), and the global unstable manifold of \( E_1 \) can be written as

\[
\bigcup_{n>0} F^n(y_1^-),
\]

(3.5)

where \( F \) is the map induced by Eq. (3.1).

The proof of uniform persistence is straightforward by using [24]. Notice that (3.1) has a global attractor \( X \). Let \( Y = \{(N, P) \in \mathbb{R}_+^2 : N = 0 \text{ or } P = 0 \} \). Then \( Y \) is closed in \( \mathbb{R}_+^2 \) and \( \mathbb{R}_+^2 \setminus Y \) is positively invariant for (3.1). The maximal compact invariant set \( M \) in \( Y \) consists of \( E_0 = (0, 0) \) and \( E_1 = (r, 0) \). Clearly \( M \) is isolated in \( X \). It is also very easy to verify that the stable set of \( M \), \( \{(N_t, P_t) \in \mathbb{R}_+^2 : (N_t, P_t) \to M \text{ as } t \to \infty\} \), is contained in \( Y \). Indeed, if there exists \((N_0, P_0)\) with \( N_0, P_0 > 0 \) such that \( \lim_{t \to \infty}(N_t, P_t) = E_0 \), then since for any \( \epsilon > 0 \) we can find \( t_0 > 0 \) such that \( N_t, P_t < \epsilon \) for \( t \geq t_0 \), we have \( N_{t+1} > N_t e^{-\epsilon - be} \) for \( t \geq t_0 \). Since \( r > 0 \), we can choose \( \epsilon > 0 \) so that \( r - \epsilon - be > 0 \). Hence \( N_{t+1} > N_t \) for \( t \geq t_0 \) and contradicts \( \lim_{t \to \infty} N_t = 0 \). Similarly, if there exists \((N_0, P_0)\) such that \( N_0, P_0 > 0 \) and \( \lim_{t \to \infty}(N_t, P_t) = E_1 \), then let \( \epsilon > 0 \) be such that \( \beta b(r - \epsilon) > 1 \). For this \( \epsilon > 0 \) we can find \( t_1 > 0 \) such that \( N_t > r - \epsilon \) for \( t \geq t_1 \). But then \( P_{t+1} > \beta(r - \epsilon)(1 - e^{-by}) \) for \( t \geq t_1 \) implies \( \liminf_{t \to \infty} P_t > 0 \). We obtain another contradiction and conclude that the stable set of \( M \) lies in \( Y \). Therefore [24, Theorem 4.1] implies that system (3.1) is uniformly persistent.
To show local asymptotic stability of $E_2$, notice that the linearization of (3.1) at $E_2$ yields the following Jacobian matrix:

$$J^* = \begin{pmatrix} 1 - N^* & -bN^* \\ P^* / N^* & \beta b N^* e^{-b P^*} \end{pmatrix},$$

with $\text{tr} J^* = 1 - N^* + \beta b N^* e^{-b P^*}$ and $\det J^* = (1 - N^*) \beta b N^* - b P^* = \beta b N^* - \beta b (N^*)^2 e^{-b P^*}$. It follows from the Jury conditions that $E_2$ is locally asymptotically stable if $|\text{tr} J^*| < 1 + \det J^* < 2$ [23]. Observe that $\text{tr} J^* < 1 + \det J^*$ if and only if $\beta b (N^* + 1) e^{-b P^*} < \beta b + 1$. Notice that $P^* = \beta b N^* (1 - e^{-b P^*}) < \beta N^* b P^*$ implies $\beta b N^* > 1$. Moreover, $\beta b N^* e^{-b P^*} < 1$ if and only if $b P^* < e^{b P^*} - 1$, which is trivially true. Hence $\beta b (N^* + 1) e^{-b P^*} = \beta b N^* e^{-b P^*} + \beta b e^{-b P^*} < 1 + \beta b$ and $\text{tr} J^* < 1 + \det J^*$ is valid. On the other hand, $-1 - \det J^* < \text{tr} J^*$ if and only if $N^* + \beta b (N^*)^2 e^{-b P^*} < 2 + \beta b N^* + \beta b N^* e^{-b P^*}$. Since $N^* < r < 2$, the inequality is trivial, and also $\det J^* < 1$ by our assumption $\beta b N^* (1 - N^* e^{-b P^*}) < 1$. Consequently, $E_2$ is locally asymptotically stable if $\beta b N^* (1 - N^* e^{-b P^*}) < 1$.

(c) Suppose now $r > 2$ and $\beta b r < 1$. Then $E_1 = (r, 0)$ is a saddle point and (3.1) has no interior steady state. Similar to the case when $0 < r < 2$ and $\beta b r > 1$, we can approximate the local stable manifold of $E_1$:

$$\gamma_1^+(N) = \beta r + \frac{r - 1 - \beta b r}{\beta r} N + \frac{1 - r}{\beta r^2} N^2 + O(N^3) \quad (3.6)$$

for $N$ near $r$. However, since the determinant of the Jacobian matrix of system (3.1) is

$$\beta b N e^{P - N} e^{-b P} (1 - N e^{-b P}),$$

which vanishes if either $N = 0$ or $P = \frac{1}{\beta} \ln N$ for $N \geq 1$, the map may not be locally one-to-one in the interior of $\mathbb{R}^2_+$. Therefore the map induced by system (3.1) may not be invertible and the global stable manifold of $E_1$ may not exist. Notice that if $\beta b e^{-1} < 1$, then since $N_t \leq e^{-1}$ for all $t$ large, we have by the first equation of (3.1) that $\lim_{t \to \infty} P_t = 0$ for all solutions of (3.1).

(d) If $r > 2$ and $\beta b r > 1$, then $E_1$ is a repeller and system (3.1) has a unique interior fixed point $E_2$. We claim that system (3.1) is uniformly persistent if $r > 2$ and $\beta b e > 1$, where $e > 0$ is the constant given in Proposition 2.1. The proof is very similar to the proof of uniform persistence for (3.1) when $0 < r < 2$ and $\beta b r > 1$. Recall that $\liminf_{t \to \infty} x_t \geq c$ and $\limsup_{t \to \infty} x_t \leq c - e^{-1}$ for any solution $x_t$ of (2.1) with $x_0 > 0$. Let $X$ and $Y$ be defined as above. Then the maximal compact invariant set $M_0$ of $Y$ is contained in

$$\{ E_0 \} \cup \{(N, 0) : c \leq N \leq e^{e^{-1}} \}.$$

The proof of the stable set of $E_0$ lying in $Y$ can be easily carried out. Similarly, suppose there exist $N_0$, $P_0 > 0$ such that $(N_t, P_t) \to M_0 \setminus \{ E_0 \}$. Then for any $\epsilon > 0$, there exists $t_0 > 0$ such that $N_t > c - \epsilon$ for $t \geq t_0$. We choose $\epsilon > 0$ so that $\beta b (c - \epsilon) > 1$. But then $P_{t+1} > \beta (c - \epsilon) (1 - e^{-b P_t})$ for $t \geq t_0$ implies $\liminf_{t \to \infty} P_t > 0$ and we obtain a contradiction. Hence the stable set of $M_0$ is contained in $Y$ and system (3.1) is therefore uniformly persistent. ■

Fig. 2(a) and (b) provide bifurcation diagrams for system (3.1) when $b = 0.03$ and $\beta = 25$. Notice that the parasitoid population becomes extinct as $r$ is increased somewhat beyond 3. Therefore the system is not uniformly persistent if $r$ is large as noted in Theorem 3.1(d).

Suppose now the host population experiences Allee effects but not the parasitoid population. Similar to model (2.2), we let $\frac{N}{m + N}$ be the probability of a host individual successfully finding a mate or a cooperative individual when the host population is of size $N$. The host–parasitoid interaction now takes the following form

$$\begin{cases}
N_{t+1} = N_t e^{r - N_t} \frac{N_t}{m + N_t} e^{-b P_t} \\
P_{t+1} = \beta N_t (1 - e^{-b P_t}) \\
N_0, \quad P_0 > 0.
\end{cases} \quad (3.7)$$

It is clear that solutions of (3.7) are bounded and thus (3.7) is point dissipative. Moreover, the map induced by (3.7) is asymptotically smooth. It follows from [27] that (3.7) has a global attractor [27].

Notice that system (3.7) has a trivial steady state $E_0 = (0, 0)$ for all parameter values. If $r < r_0$, then $E_0$ is the only steady state for (3.7) as (2.2) has only the trivial steady state 0 when $r < r_0$. It can then be easily shown that
Fig. 2. (a) and (b) plot $N$ and $P$-bifurcation diagrams for system (3.1) respectively when $\beta = 5$ and $b = 0.003$. Notice that $\beta be^{-1} \leq \beta be^4 = 0.81897225 < 1$ and parasitoid population becomes extinct. (c) and (d) provide one solution of system (3.7) when $r = r_0$. Notice that $N_0 = P_0 = 1$, where host population can survive but parasitoid becomes extinct.

$E_0$ is globally asymptotically stable by using a simple comparison argument. The proof of the following theorem is omitted.

**Theorem 3.2.** If $r < r_0$, then $E_0 = (0, 0)$ is the only steady state for system (3.7) and all solutions of (3.7) converge to $E_0$.

Comparing Theorems 3.1 and 3.2 we see that both populations are more likely to become extinct when Allee effects are incorporated into this host–parasitoid interaction.

If $r = r_0$, then system (3.7) has two steady states $E_0 = (0, 0)$ and $E_1 = (\hat{N}, 0)$, where $\hat{N} = \hat{x}$ was defined in (2.3), and there is no interior fixed point. The Jacobian matrix of (3.7) evaluated at $E_1$ yields

$$J(E_1) = \begin{pmatrix} J_{11}(E_1) & -be^{r-\hat{N}} \frac{\hat{N}^2}{m + \hat{N}} \\ 0 & \beta b \hat{N} \end{pmatrix},$$

where

$$J_{11}(E_1) = -e^{r-\hat{N}} \frac{\hat{N}^2}{m + \hat{N}} + e^{r-\hat{N}} \frac{\hat{N}^2 + 2m \hat{N}}{(m + \hat{N})^2}$$

$$= 1 + \frac{m - m \hat{N} - \hat{N}^2}{m + \hat{N}}.$$
Since
\[ m - m\hat{N} - \hat{N}^2 = 0, \]
steady state \( E_1 = (\hat{N}, 0) \) is non-hyperbolic. Moreover,
\[ \Omega = \{(N, P) \in \mathbb{R}_+^2 : N \leq \hat{N}\} \]
is positively invariant for system (3.7) as the map \( G \) induced by (2.2) is increasing on \((0, \hat{N})\) and
\[ N_{t+1} \leq \frac{N_t e^{r-N_t}}{m + N_t} \]
for \( t \geq 0 \). Therefore, \( \lim_{t \to \infty} N_t = 0 \) if \( N_0 \leq \hat{N} \) by using Theorem 2.2(b). As a result, solutions converge to the trivial steady state \( E_0 \) if \( N_0 \leq \hat{N} \).

Furthermore, since solutions of (2.2) all converge to either 0 or \( \hat{x} \) when \( r = r_0 \) as shown in Theorem 2.2(b), solutions of (3.7) satisfy
\[ \limsup_{t \to \infty} N_t \leq \hat{N}. \]

The dynamics of system (3.7) when \( r = r_0 \) can be summarized below.

**Theorem 3.3.** If \( r = r_0 \), then (3.7) has two steady states \( E_0 = (0, 0) \) and \( E_1 = (\hat{N}, 0) \), where \( E_0 \) is locally asymptotically stable and \( E_1 \) is non-hyperbolic.

(a) If \( \beta b \hat{N} > 1 \), then solutions of (3.7) all converge to \( E_0 \).

(b) If \( \beta b \hat{N} < 1 \), then solutions of (3.7) satisfy \( \lim_{t \to \infty} P_t = 0 \). In addition if either \( N_0 \leq \hat{N} \) or if \( N_0 > \hat{N} \) and \( P_0 \) satisfies (3.8), then the solution converges to \( E_0 \).

**Proof.** The first statement of the Theorem follows from the above discussion. To prove (a), suppose \( \beta b \hat{N} > 1 \) and there exists a solution \((N_t, P_t)\) of (3.7) with \( N_t > \hat{N} \) for \( t \geq 0 \). Then \( \lim_{t \to \infty} N_t = \hat{N} \), and using the first equation of (3.7), we have \( \lim_{t \to \infty} P_t = 0 \). We claim that this is impossible. Indeed, for any given \( \epsilon > 0 \), there exists \( t_0 > 0 \) such that \( N_t > \hat{N} - \epsilon \) for \( t \geq t_0 \). We can choose \( \epsilon > 0 \) so that \( \beta b(\hat{N} - \epsilon) > 1 \). Thus
\[ P_{t+1} \geq \beta(\hat{N} - \epsilon)(1 - e^{-bP_t}) \]
for \( t \geq t_0 \) implies \( \liminf_{t \to \infty} P_t > 0 \), and hence obtain a contradiction. Consequently, solutions will enter \( \Omega \) in finite time and thus converge to \( E_0 \).

To prove (b), suppose \( \beta b \hat{N} < 1 \). Recall \( \lim_{t \to \infty} (N_t, P_t) = E_0 \) if \( N_0 \leq \hat{N} \). Since \( \limsup_{t \to \infty} N_t \leq \hat{N} \) as derived earlier, \( \lim_{t \to \infty} P_t = 0 \) for all solutions of (3.7). Moreover, if \( N_0 > \hat{N} \) and \( P_0 > 0 \) is such that
\[ P_0 \geq \frac{1}{b} \ln \frac{N_0^2 e^{-N_0}}{N(m + N_0)}, \quad (3.8) \]
then \( N_1 \leq \hat{N} \) and hence the solution also converges to \( E_0 \). \( \blacksquare \)

It follows from Theorem 3.3 that when \( r = r_0 \) the parasitoid will always go to extinction and the host may survive only if \( \beta b \hat{N} < 1 \) and \( N_0 > \hat{N} \). Notice that the right-hand side of the above inequality approaches \(-\infty \) when \( N_0 \) goes to \( \infty \). Therefore one may conclude that if \( N_0 \) is large enough, then inequality (3.8) is always true and hence solutions with large \( N_0 \) converge to \( E_0 = (0, 0) \). We illustrate Theorem 3.3(b) by a numerical example. Let \( m = 5.2, b = 0.05 \) and \( \beta = 10 \). Then \( r_0 = 2.8125 \) and \( \hat{N} = 0.8583 \). Setting \( r = r_0 \) and choosing \( N_0 = P_0 = 1 \), we run the simulation. Fig. 2(c) and (d) plot host and parasitoid populations, respectively, against time. It is clear that the host population can survive while the parasitoid becomes extinct. In this example we have \( r = r_0, \beta b \hat{N} < 1 \), and \( N_0 > \hat{N} \) is small.

Suppose now \( r > r_0 \). Then in addition to \( E_0 \), system (3.7) has two other boundary steady states \( E_{11} = (\hat{N}_1, 0) \) and \( E_{12} = (\hat{N}_2, 0) \), where \( \hat{N}_i = \hat{x}_i \) for \( i = 1, 2 \). Similar to the Jacobian matrix \( J(E_1) \), the \((1, 1)\) entry of the Jacobian matrix of the system evaluated at \( E_{11}, J_{11}(E_{11}) \), is
\[ J_{11}(E_{11}) = 1 + \frac{m - m\hat{N}_1 - \hat{N}_1^2}{m + \hat{N}_1}. \]
for $i = 1, 2$. Since $\tilde{N}_1 < \hat{N}$, we have $m - m\tilde{N}_1 - \tilde{N}_1^2 > 0$. Thus $J_{11}(E_{11}) > 1$ and $E_{11}$ is always unstable. Steady state $E_{11}$ is a saddle point if $\beta b \tilde{N}_1 < 1$, and a repeller if $\beta b \tilde{N}_1 > 1$. On the other hand, since $\tilde{N}_2 > \hat{N}$, we have $m - m\tilde{N}_2 - \tilde{N}_2^2 < 0$ and thus $J_{11}(E_{12}) < 1$. Notice that $J_{11}(E_{12}) > -1$ if and only if
\[-\tilde{N}_2^2 + (2 - m)\tilde{N}_2 + 3m > 0.\] (3.9)
Thus $E_{12}$ is locally asymptotically stable if (3.9) holds and $\beta b \tilde{N}_2 < 1$. If inequality (3.9) is reversed then $E_{12}$ is unstable, and a period-doubling bifurcation occurs when $-\tilde{N}_2^2 + (2 - m)\tilde{N}_2 + 3m = 0$.

Recall that $\tilde{N}_1 = \tilde{x}_1 < \tilde{x} < \hat{x}$ and the map $G(x)$ is increasing on $(0, \tilde{x})$. Therefore
\[\Omega_1 = \{(N, P) \in \mathbb{R}_+^2 : N \leq \tilde{N}_1\}
\]
is forward invariant for system (3.7) and we can conclude that if $N_0 \leq \tilde{N}_1$ then the solution converges to $E_0 = (0, 0)$. Moreover, if $N_0 > \tilde{N}_1$ and $P_0$ satisfies
\[P_0 \geq \frac{1}{b} \ln \frac{N_0^2 e^{-N_0}}{\tilde{N}_1 (m + N_0)},\] (3.10)
then $N_1 \leq \tilde{N}_1$ and such a solution also converges to $E_0 = (0, 0)$.

The above discussion is summarized in the following proposition.

Proposition 3.4. Let $r > r_0$. Then in addition to $E_0 = (0, 0)$, system (3.7) has two other boundary steady states $E_{11} = (\tilde{N}_1, 0)$ and $E_{12} = (\tilde{N}_2, 0)$, where $E_{11}$ is a saddle point if $\beta b \tilde{N}_1 < 1$ and a repeller if $\beta b \tilde{N}_1 > 1$. Steady state $E_{12}$ is locally asymptotically stable if $\beta b \tilde{N}_2 < 1$ and (3.9) holds. Moreover, for any solution of (3.7) with $N_0 > 0$, $\lim_{t \to \infty} (N_t, P_t) = (0, 0)$ if either $N_0 \leq \tilde{N}_1$ or if $N_0 > \tilde{N}_1$ and $P_0$ satisfies (3.10).

Let $(N_t, P_t)$ be an arbitrary solution of (3.7) with $N_0 > \tilde{N}_1$ and $P_0$ does not satisfy inequality (3.10). We shall separate our brief discussion into three cases: $\beta b \tilde{N}_2 < 1$, $\beta b \tilde{N}_1 < 1 < \beta b \tilde{N}_2$, and $\beta b \tilde{N}_1 > 1$.

Suppose $\beta b \tilde{N}_2 < 1$. Since $\tilde{x}$ satisfies $\tilde{x}^2 + (m - 1)\tilde{x} - 2m = 0$, (3.9) holds if $\tilde{N}_2 < \tilde{x}$. In this case since solutions of (2.2) converge to either $0$ or $\tilde{x}_2$, solutions $(N_t, P_t)$ of (3.7) satisfy $\lim_{t \to \infty} N_t \leq \tilde{N}_2$. As a result, $\lim_{t \to \infty} P_t = 0$. Therefore the $\omega$-limit set of solutions of (3.7) lies on the $N$-axis. Moreover, $E_{11}$ is a saddle point and we can estimate its local stable manifold as we did for system (3.1) with approximation given below:
\[y_{11}'(N) = \beta \tilde{N}_1 + (2\beta - m_0)N + \frac{\beta + m_0}{\tilde{N}_1} N^2 + O(N^3)\] (3.11)
for $N$ near $\tilde{N}_1$, where $m_0 = \frac{(\tilde{N}_1 + m)(J_{11}(E_{11}) - \beta b \tilde{N}_1)}{\beta e^{-\tilde{N}_1}} > 0$. Furthermore, system (3.7) has no interior steady state if $\beta b \tilde{N}_2 < 1$. Indeed, if an interior fixed point $(N^*, P^*)$ exists, then $\tilde{N}_1 < N^* < \tilde{N}_2$ and $P^*$ must satisfy
\[P = \beta N^*(1 - e^{-bP})\]
Therefore if $\beta b \tilde{N}_2 < 1$ then $\beta b N^* < 1$ and the equation for $P$ above has no positive solution. Since the $\omega$-limit set of solutions of system (3.7) lies in the $N$-axis, one would suspect that except those initial conditions lying on the local stable manifold of $E_{11}$, solutions converge to either $E_0$ or $E_{12}$ if $\beta b \tilde{N}_2 < 1$ and $\tilde{N}_2 < \hat{N}$. If $\tilde{N}_2 \geq \hat{N}$, then inequality (3.9) may not hold and period-doubling bifurcations will occur. However, $\lim_{t \to \infty} P_t = 0$ remains true for all solutions of (3.7).

Proposition 3.5. Let $r > r_0$ and $\beta b \tilde{N}_2 < 1$. Then system (3.7) has no interior steady state. Steady state $E_{11}$ is a saddle point with local stable manifold given in (3.11) and $E_{12}$ is locally asymptotically stable if $\tilde{N}_2 < \hat{N}$. Moreover, solutions $(N_t, P_t)$ of (3.7) satisfy $\lim_{t \to \infty} P_t = 0$.

Suppose now $\beta b \tilde{N}_1 < 1 < \beta b \tilde{N}_2$ and (3.9) holds. Then $E_{11}$ and $E_{12}$ are saddle points and we can approximate the global unstable manifold of $E_{12}$:
\[\bigcup_{n > 0} H^n(y_{12}),\] (3.12)
where the local unstable manifold of $E_{12}$ is

$$\gamma_{12}(N) = \beta \hat{N}_2 + (-2\beta - m_1)N + \frac{\beta + m_1}{\hat{N}_2}N^2 + O(N^3)$$

for $N$ near $\hat{N}_2$, $m_1 = \frac{(\hat{N}_2 + m)(J_{11}(E_{12}) - \beta \hat{N}_2)}{be^{-\hat{N}_2}} < 0$ and $H$ is the map induced by system (3.7). The local stable manifold of $E_{11}$ is also given in (3.11). Similarly, period-doubling bifurcation can occur if (3.9) does not hold.

When $\beta N \hat{N}_2 > 1$, $E_{11}$ is a repeller and $E_{12}$ is a saddle point with global unstable manifold given in (3.12). It cannot be resolved analytically as to whether system (3.7) has no interior steady state or has multiple interior fixed points when $\beta N \hat{N}_2 > 1$. If (3.7) has an interior steady state $E_2 = (N^*, P^*)$ which may occur if $\beta N \hat{N}_2 > 1$, then the Jacobian matrix of system (3.7) evaluated at $E_2$ has the following form

$$J^* = \begin{pmatrix} -N^* + \frac{2m + N^*}{m + N^*} & -bN^* \\ \frac{P^*}{N^*} & \beta bN^*e^{-bP^*} \end{pmatrix},$$

where $(N^*, P^*)$ satisfies

$$\begin{cases} 1 = e^{-N^*}N^*e^{-rP^*} \\ P^* = \beta N^*(1 - e^{-bP^*}). \end{cases}$$

(3.13)

Using (3.13), a straightforward calculation yields

$$\text{tr}J^* = -N^* + 1 + \frac{m}{m + N^*} + \beta bN^*e^{-bP^*}$$

and

$$\text{det}J^* = \beta bN^* - \beta b(N^*)^2e^{-bP^*} + \frac{\beta bmN^*}{m + N^*}e^{-bP^*}.$$ 

Applying Jury conditions we see that $E_2$ is locally asymptotically stable if $|\text{tr}J^*| < 1 + \text{det}J^* < 2$ [23]. Recall that $N_1 < N^*$ and $N < \hat{N}_2$. If $N^* = \hat{N}$, then $\text{det}J^* = \beta bN^*\left[1 - (N^* - \frac{m}{m+N^*})e^{-bP^*}\right] = \beta bN^* > 1$ and hence $E_2$ is unstable. Similarly, if $N^* < \hat{N}$, then $\text{det}J^* > \beta bN^* > 1$ and $E_2$ is unstable. Since $N^*$ depends on the parameter $r$ and $\hat{N}$ depends only on $m$, we can vary $r$ and keep all other parameters fixed so that $N^*(r) > \hat{N}$ and $\text{det}J^* = 1$ hold. On the other hand, it is easy to prove that $\text{tr}J^* > 0$ if $N^* < \hat{N}$ and $\text{tr}J^* < \text{det}J^* + 1$ if $\beta bN^*e^{-bP^*} < 1$. Therefore under the conditions that $\hat{N} < N^* < \hat{N}$ and $\beta bN^*e^{-bP^*} < 1$, there exists an $r$ so that $\text{det}J^* = 1$, and the Neimark–Sacker [28,29] or the discrete Hopf bifurcation [23] may occur for these parameter values.

Mathematical analysis for the case of $r > r_0$ is very limited. Nevertheless, it was shown that solutions converge to the trivial steady state $E_0 = (0,0)$ when initial host population sizes are small, and the system may undergo a Hopf bifurcation when an interior steady state exists. We rely on numerical simulations to study the model. To compare systems (3.1) and (3.7), we provide bifurcation diagrams for system (3.7) using $m = 0.5$, $\beta = 25$ and $b = 0.03$. The plots are given in Fig. 3(c) and (d). From Fig. 3 one may conclude that the host population is more likely to become extinct when the population experiences the Allee effects.

4. Summary

In summary, a single-species discrete-time model with non-overlapping generations and overcompensatory density dependence can lead to chaos for $r > 2$. When Allee effects are added, populations with an initial population size less than a threshold level will go to extinction, regardless of $r$. Above the threshold initial population size, populations with low $r$ can either stabilize or go to extinction. At moderate levels of $r$, the population enters a 2-cycle, which leads to a 4-cycle then continues on to chaos as $r$ increases. At high levels of $r$, the population crashes to extinction. Increase in the searching efficiency for conspecifics (for example mates or cooperators) that decrease the probability of Allee effects decreases the level of $r$ at which bifurcations, chaos, and the eventual population crash occurs (comparing Fig. 1(c) and (d)).
In a host–parasitoid model system with overcompensatory density dependence and no Allee effects, the coexistence of the two populations depends on characteristics of both the parasitoid and host populations. The important characteristics of the host population are $r$ (the intrinsic rate of growth of the host population), and $c$, the minimum population size of the host. The important characteristic of the parasitoid population, which we will call the ‘parasitoid potential’, equals the product of $\beta$ (the fecundity of the parasitoid), and $b$ (the search efficiency of the parasitoid). The product of the parasitoid potential and the population growth rate of the host ($\beta br$) must be greater than 1, or the parasitoid population will go extinct, even at high levels of $r$. When $r$ is small ($r < 2$) and $\beta br$ is above the threshold of 1, then the host and parasitoid populations will coexist. When $r$ is somewhat $> 2$, the host population will have a stable 2-cycle, but at high levels of $r$ ($r \gg 2$), the dynamics of both populations are chaotic. Therefore, coexistence or extinction of the host and parasitoid populations at high levels of $r$ depends on initial conditions, with some combinations of initial conditions leading to the extinction of the parasitoid (while the host population persists). A larger parasitoid potential is needed for persistence of the parasitoid population if $r$ is large.

When Allee effects in the host are incorporated into the host–parasitoid model, then the dynamics once again depend on the intrinsic growth rate of host, the population size of the host, and the parasitoid potential. When the growth rate of the host is below a threshold level $r_0$ of $r$, then both populations go extinct, since the host population succumbs to Allee effects and the parasitoid population cannot survive without the host. When the host growth rate equals the threshold level of $r > 2$, there is also a minimum population size of the host $c$ that is necessary for the parasitoid population to exist, such that $\beta bc$ must be greater than 1. When $r$ is somewhat $> 2$, the host population will have a stable 2-cycle, but at high levels of $r$ ($r \gg 2$), the dynamics of both populations are chaotic. Therefore, coexistence or extinction of the host and parasitoid populations at high levels of $r$ depends on initial conditions, with some combinations of initial conditions leading to the extinction of the parasitoid (while the host population persists). A larger parasitoid potential is needed for persistence of the parasitoid population if $r$ is large.

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host population size is above the threshold size and the product of the parasitoid potential and the host population size is low i.e., $\beta b \hat{N}_2 < 1$, then the host population may survive but the parasitoid population goes extinct. If $r$ is above the threshold $r_0$ but $\beta b \hat{N}_2 > 1$, then mathematical analysis was very limited. However, it is known that period-doubling bifurcations will occur for some parameter values.

Compared to host–parasitoid systems with Ricker-type density dependence and no Allee effects, the models with Allee effects show a shrinking in the range of $r$ and population sizes at which the host population and consequently the parasitoid population can survive. Decreasing the searching efficiency of host organisms in finding mates or cooperators (i.e. increasing $m$) strengthens the Allee effect and results in a further shrinking in the range of $r$ values at which persistence occurs. Although it is expected that the host population and therefore the parasitoid population cannot persist at low levels of $r$ or low population sizes, the host population crash at high levels of $r$ was somewhat unexpected. This population crash at high $r$ occurs because the chaotic fluctuations caused by overcompensatory dynamics in the host population drive the population below the minimum level needed for population persistence (cf. [25]), which in turn causes extinction in the parasitoid.

In the host–parasitoid system, the parasitoid potential is a major factor in the coexistence of the host and parasite populations, with or without Allee effects. If the parasitoid is inefficient in finding hosts or cannot reproduce efficiently, then the parasitoid population goes extinct, regardless of the intrinsic rate of growth or the population size of the host. If the parasitoid potential is large, then a parasitoid can drive the host population to extinction, particularly if the host population is subject to Allee effects. An example of the importance of the parasitoid potential in nature was the introduction of a parasitoid (Sphecophaga vesparum) as a biological control agent of the common wasp (Vespula vulgaris) in New Zealand [30]. The common wasp, which was considered a nuisance species due to its detrimental ecological impacts at high densities, was found to have overcompensatory dynamics due to competition among queens and usurpation of nests. A total of 108,000 parasitoid cocoons were released over a three-year period, but the parasitoid was only found in subsequent years to be established at low levels at 2 of the 40 release sites. No parasitoids were found at the other 38 release sites. The authors concluded that low parasitoid potential (called the parasitoid’s effective ratio of increase by the authors) made the parasitoid an unsuccessful biological control agent.

Comparing Eq. (2.2), the single-species population model with overcompensatory dynamics, with the single-species model using compensatory dynamics in [11], we see that overcompensatory mechanism can drive the population into extinction even when the initial population size is large. This is one major difference between the two single-species models with Allee effects. The difference remains true when host–parasitoid interaction is considered. In addition to the above observation, the overcompensatory models with Allee effects show a shrinking in the range of $r$ and population sizes at which the host population and consequently the parasitoid population can survive. This phenomenon does not occur for the compensatory models investigated in [11,12].

References


