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## DISCRETE HOST-PARASITOID MODELS WITH ALLEE EFFECTS AND AGE STRUCTURE IN THE HOST

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*Dedicated to Professor Horst R. Thieme on the Occasion of his 60th Birthday*

**ABSTRACT.** We study a stage-structured single species population model with Allee effects. The asymptotic dynamics of the model depend on the maximal growth rate of the population as well as on its initial population size. We also investigate two models of host-parasitoid interaction with stage-structure and Allee effects in the host. The parasitoid population may drive the host population to extinction in both models even if the initial host population is beyond the Allee threshold.

**1. Introduction.** It has long been recognized that individuals in the population can be released from the constraints of intraspecific competition when a population is small or at low density. When population size is larger, negative density dependence takes place due to competition between individuals for resources and space. Therefore, the per-capita growth rate of the population decreases with increasing population size in most of the population models.

However, individuals of many species cooperate. They use cooperative strategies to hunt or to avoid predators. There are many other incidences in which populations would benefit from a larger population size, such as mating, etc [3]. When there are too few of individuals in a population, it may be that they will each benefit from more resources, but in many cases individuals will also suffer from a lack of conspecifics. The fitness of the population may then be reduced, the lower the population size, the lower the fitness. Such an effect is called an Allee effect, which was first proposed by W.C. Allee in the 1930s [1].

Allee effects occur when there is a positive relationship between a component of fitness and population size or density. The overall of individual fitness is positively related to population size or density. As a result, the per-capita growth rate of the population increases as population size increases, at least initially. It follows from mathematical models of Allee effects that there always exists a population threshold, the Allee threshold, such that the population will become extinct if initial population size is below the threshold. As a consequence, Allee effects play a crucial role in resource management and conservation. In addition, Allee effects have also been observed in the context of biological control, both to the introduction of the control agent and also to the extirpation of the pest requiring control [8]. Recently there is also a surge of interest and need on investigating Allee effects for epidemic

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models [7, 9, 16]. See [2, 4, 5, 6, 7, 10, 11, 12, 13, 15, 17, 18] and references cited therein for population models of Allee effects.

In this study, we propose a simple stage-structured model of a host species to study the impact of Allee effects in the population level. We also investigate two models of host-parasitoid interaction with age structure and Allee effects in the host. In the first model of host-parasitoid interaction it is assumed that parasitism occurs before density dependence. The second model assumes that density dependence occurs prior to parasitism. The single-species model and the first host-parasitoid model are generalizations of the previous models studied in [12] where specific function forms were adopted. We show that there exists a host population threshold below which both host and parasitoid populations will go extinct. If the host population size is initially greater than the threshold, then the presence of the parasitoid may also drive the host population to extinction. The parasitoid may overexploit the host population below the Allee threshold so that both populations cannot persist. This result is independent of whether density dependence occurs before or after parasitism.

In the following section, a single species model is studied. Sections 3 and 4 present models of host-parasitoid interaction and their analysis. We use numerical examples and simulations to study these systems in Section 5. The final section provides a brief discussion.

**2. Allee effects in a single species population model.** Let  $x_1(t)$  and  $x_2(t)$  be the juvenile and adult populations of a host species at time  $t$ , respectively, for  $t = 0, 1, 2, \dots$ . It is assumed that only adult population can reproduce with birth rate  $g$  depending only on the adult population size. Moreover, the survival probability  $s_1$ ,  $0 < s_1 < 1$ , from juvenile to adult over one unit of time is assumed to be independent of time and population size. Under these biological assumptions, the single species population model is given by

$$\begin{cases} x_1(t+1) = g(x_2(t))x_2(t) \\ x_2(t+1) = s_1x_1(t) \\ x_1(0), x_2(0) \geq 0. \end{cases} \quad (1)$$

We assume that the Allee effect is concentrated in the birth rate and make the following assumptions on the fertility rate  $g$ :

(H1)  $g \in C^1[0, \infty)$ ,  $g(0) = 0$ , there exists  $m > 0$  such that  $g'(x) > 0$  for  $0 \leq x < m$  and  $g'(x) < 0$  for  $x > m$ ,  $s_1g(\infty) < 1$ , and  $g(x) > 0$ ,  $\frac{d}{dx}(xg(x)) > 0$  for  $x > 0$ .

System (1) always has a trivial steady state  $E_0 = (0, 0)$ . The  $x_2$  component of an interior steady state must satisfy

$$1 = s_1g(x_2). \quad (2)$$

Therefore (2) has no positive solution if  $s_1g(m) < 1$ , has a unique positive solution  $m$  if  $s_1g(m) = 1$ , and has two positive solutions  $\bar{x}_{21}$  and  $\bar{x}_{22}$  with  $\bar{x}_{21} < m < \bar{x}_{22}$  if  $s_1g(m) > 1$ . It follows that (1) has no interior equilibrium if  $s_1g(m) < 1$ , has a unique interior equilibrium  $E_1 = (m/s_1, m)$  if  $s_1g(m) = 1$ , and has two interior equilibria  $E_{1i} = (\bar{x}_{2i}/s_1, \bar{x}_{2i})$ ,  $i = 1, 2$ , if  $s_1g(m) > 1$ . The Jacobin matrix of system (1) is given by

$$J = \begin{pmatrix} 0 & g(x_2) + g'(x_2)x_2 \\ s_1 & 0 \end{pmatrix}. \quad (3)$$

A second iteration of (1) yields the following un-coupled system

$$\begin{aligned}x_1(t+2) &= s_1g(s_1x_1(t))x_1(t) \\x_2(t+2) &= s_1g(x_2(t))x_2(t).\end{aligned}$$

Therefore 2-cycles of (1) are fixed points of

$$\begin{cases}y_1(t+1) = s_1g(s_1y_1(t))y_1(t) \\y_2(t+1) = s_1g(y_2(t))y_2(t).\end{cases} \quad (4)$$

Let  $F$  and  $G$  be defined by

$$F(x) = s_1g(s_1x)x \text{ and } G(x) = s_1g(x)x, \quad (5)$$

respectively. If  $s_1g(m) < 1$  then  $F$  and  $G$  have no nontrivial fixed points and consequently (1) has no 2-cycles. Moreover, the population will go extinct as shown below.

**Theorem 2.1.** *If  $s_1g(m) < 1$ , then steady state  $E_0 = (0, 0)$  is globally asymptotically stable in  $\mathbb{R}_+^2$ .*

*Proof.* Let  $(x_1(t), x_2(t))$  be a solution of (1). Since  $x_2(t+2) \leq s_1g(m)x_2(t)$  for all  $t \geq 0$  and  $s_1g(m) < 1$ ,  $\lim_{t \rightarrow \infty} x_2(t) = 0$  and thus  $\lim_{t \rightarrow \infty} x_1(t) = 0$  and  $E_0$  is globally attracting in  $\mathbb{R}_+^2$ . Moreover,  $E_0$  is locally asymptotically stable since the Jacobian matrix  $J$  at  $E_0$  is  $\begin{pmatrix} 0 & 0 \\ s_1 & 0 \end{pmatrix}$ . Therefore,  $E_0$  is globally asymptotically stable.  $\square$

Observe that  $s_1g(m)$  can be regarded as the maximal growth rate of the host population. The population will become extinct if this maximal growth rate is less than one. Suppose now  $s_1g(m) = 1$ . Then (1) has a unique interior steady state  $E_1 = (m/s_1, m)$  with Jacobian matrix at  $E_1$  given by  $\begin{pmatrix} 0 & g(m) \\ s_1 & 0 \end{pmatrix}$ . Hence,  $E_1$  is non-hyperbolic. The steady states of system (4) are:  $(0, 0)$ ,  $(m/s_1, 0)$ ,  $(0, m)$  and  $(m/s_1, m)$ . As a result, system (1) has no interior 2-cycles and there exists a unique 2-cycle on the boundary:

$$\mathcal{C}_1 = \{(m/s_1, 0), (0, m)\}. \quad (6)$$

Moreover,  $F$  and  $G$  satisfy:

$$F(x) \leq x \text{ for } x \geq 0, F(x) = x \text{ if and only if } x = 0, x = m/s_1, \quad (7)$$

and

$$G(x) \leq x \text{ for } x \geq 0, G(x) = x \text{ if and only if } x = 0, x = m. \quad (8)$$

The asymptotic dynamics of (1) restricted on the boundary of  $\mathbb{R}_+^2$  when  $s_1g(m) = 1$  are given below.

**Theorem 2.2.** *Let  $s_1g(m) = 1$  and  $(x_1(t), x_2(t))$  be a solution of (1) with either  $x_1(0) > 0, x_2(0) = 0$  or  $x_1(0) = 0, x_2(0) > 0$ .*

- (a) *Let  $x_2(0) = 0$ . If  $0 < x_1(0) < m/s_1$ , then the solution converges to  $E_0 = (0, 0)$ . If  $x_1(0) \geq m/s_1$ , then the solution has the 2-cycle  $\mathcal{C}_1$  as its  $\omega$ -limit set.*
- (b) *Let  $x_1(0) = 0$ . If  $0 < x_2(0) < m$ , then the solution converges to  $E_0$ . If  $x_2(0) \geq m$ , then the solution has  $\omega$ -limit set  $\mathcal{C}_1$ .*

*Proof.* We only prove (a). Observe that  $x_1(2t+1) = x_2(2t) = 0$  and  $x_1(2t) > 0, x_2(2t+1) > 0$  for  $t = 0, 1, \dots$ . Let  $0 < x_1(0) < m/s_1$ . It can be easily shown, using finite mathematical induction, that  $x_1(2t) < m/s_1$  and  $x_2(2t+1) < m$  for  $t \geq 0$ . Therefore, it follows from (7) and (8), we have for  $t \geq 0$

$$x_1(2t+2) = F(x_1(2t)) < x_1(2t)$$

and

$$x_2(2t+3) = G(x_2(2t+1)) < x_2(2t+1).$$

As a result,

$$\lim_{t \rightarrow \infty} x_1(2t) = x_1^* < m/s_1 \text{ and } \lim_{t \rightarrow \infty} x_2(2t+1) = x_2^* < m.$$

System (1) implies

$$x_1^* = s_1 g(x_2^*) x_1^*.$$

If  $x_1^* \neq 0$  then  $x_2^* = m$  and we obtain a contradiction. Therefore  $x_1^* = x_2^* = 0$  and the solution converges to  $E_0$ .

Suppose now  $x_1(0) \geq m/s_1$ . If  $x_1(0) = m/s_1$ , then  $x_2(1) = m$  and the result follows. Assume  $x_1(0) > m/s_1$ . We claim that

$$x_1(2t) > m/s_1 \text{ and } x_2(2t+1) > m \text{ for } t \geq 0.$$

The inequalities are clearly true if  $t = 0$ . For  $t = 1$ ,  $x_1(2) = g(x_2(1))x_2(1) > g(m)m = m/s_1$  by (H1), and  $x_2(3) > m$ , i.e., the statements hold for  $t = 1$ . Suppose the inequalities are valid for  $t = k$ . Then using (H1) it can be shown that the inequalities also hold for  $t = k+1$ . As a result, we have for  $t \geq 0$  that

$$x_1(2t+2) = F(x_1(2t)) < x_1(2t) \text{ and } x_2(2t+3) = G(x_2(2t+1)) < x_2(2t+1).$$

Therefore,

$$\lim_{t \rightarrow \infty} x_1(2t) = x_1^{**} \geq m/s_1 \text{ and } \lim_{t \rightarrow \infty} x_2(2t+1) = x_2^{**} \geq m.$$

It follows from system (1) that

$$x_1^{**} = s_1 g(x_2^{**}) x_1^{**}.$$

Since  $x_1^{**} > 0$  we must have  $x_1^{**} = m/s_1$  and  $x_2^{**} = m$ . Therefore, the 2-cycle  $\mathcal{C}_1$  is the  $\omega$ -limit set of the solution.  $\square$

The asymptotic dynamics of (1) in the interior of  $\mathbb{R}_+^2$  when  $s_1 g(m) = 1$  are given below.

**Theorem 2.3.** *Let  $s_1 g(m) = 1$  and  $(x_1(t), x_2(t))$  be a solution of (1) with  $x_1(0) > 0, x_2(0) > 0$ .*

- (a) *Let  $x_2(0) < m$ . If  $x_1(0) < m/s_1$ , then the solution converges to  $(0, 0)$ . If  $x_1(0) \geq m/s_1$ , then the solution has  $\omega$ -limit set equal the 2-cycle  $\mathcal{C}_1$ .*
- (b) *Let  $x_2(0) \geq m$ . If  $x_1(0) < m/s_1$  then the solution has  $\omega$ -limit set equal the boundary 2-cycle  $\mathcal{C}_1$ . If  $x_1(0) \geq m/s_1$ , then the solution converges to the interior steady state  $E_1 = (m/s_1, m)$ .*

*Proof.* Notice  $x_i(t) > 0$  for  $i = 1, 2$  and  $t = 0, 1, 2, \dots$ . To prove (a), first assume  $x_1(0) < m/s_1$ . Then  $x_1(1) = g(x_2(0))x_2(0) < g(m)m = m/s_1$  and  $x_2(1) < m$ . Suppose  $x_1(k) < m/s_1$  and  $x_2(k) < m$  for some  $k > 1$ . Then  $x_1(k+1) = g(x_2(k))x_2(k) < g(m)m = m/s_1$  and  $x_2(k+1) < m$ , i.e.,

$$x_1(t) < m/s_1 \text{ and } x_2(t) < m \text{ for all } t \geq 0.$$

It follows that  $x_1(t+2) = F(x_1(t)) < x_1(t)$  and  $x_2(t+2) = G(x_2(t)) < x_2(t)$  for  $t \geq 0$ . Therefore

$$\begin{aligned}\lim_{t \rightarrow \infty} x_1(2t) &= x_1^*, \lim_{t \rightarrow \infty} x_1(2t+1) = x_1^{**}, \\ \lim_{t \rightarrow \infty} x_2(2t) &= x_2^*, \lim_{t \rightarrow \infty} x_2(2t+1) = x_2^{**}\end{aligned}$$

exist with

$$x_1^*, x_1^{**} < m/s_1 \text{ and } x_2^*, x_2^{**} < m.$$

Since  $x_1^{**} = s_1 g(x_2^*) x_1^{**}$ , we must have  $x_1^{**} = 0 = x_2^*$ . Similarly, from  $x_1^* = s_1 g(x_2^{**}) x_1^*$  we have  $x_1^* = x_2^{**} = 0$  and the solution converges to  $E_0$ .

Suppose  $x_1(0) = m/s_1$ . Then it can be shown that  $x_1(2t) = m/s_1$ ,  $x_2(2t+1) = m$ ,  $x_1(2t+1) < m/s_1$  and  $x_2(2t) < m$  for  $t \geq 0$ . Since  $x_1(t+2) = F(x_1(t)) \leq x_1(t)$  and  $x_2(t+2) = G(x_2(t)) \leq x_2(t)$  for  $t \geq 0$ , we have

$$\lim_{t \rightarrow \infty} x_1(2t+1) = \hat{x}_1 < m/s_1 \text{ and } \lim_{t \rightarrow \infty} x_2(2t) = \hat{x}_2 < m.$$

Since  $\hat{x}_1 = s_1 g(\hat{x}_2) \hat{x}_1$  holds, we must have  $\hat{x}_1 = 0 = \hat{x}_2$  and the solution has the boundary 2-cycle  $\mathcal{C}_1$  as its  $\omega$ -limit set.

If  $x_1(0) > m/s_1$ , then it can be shown that  $x_1(2t) > m/s_1$ ,  $x_2(2t) < m$ ,  $x_1(2t+1) < m/s_1$  and  $x_2(2t+1) > m$  for all  $t \geq 0$ . Therefore,

$$\lim_{t \rightarrow \infty} x_1(2t) = \tilde{x}_1 \geq m/s_1, \lim_{t \rightarrow \infty} x_1(2t+1) = \hat{x}_1 < m/s_1,$$

and

$$\lim_{t \rightarrow \infty} x_2(2t) = \tilde{x}_2 < m, \lim_{t \rightarrow \infty} x_2(2t+1) = \hat{x}_2 \geq m.$$

Furthermore, since  $\tilde{x}_1 = s_1 g(\tilde{x}_2) \tilde{x}_1$  and  $\tilde{x}_1 > 0$ , we have  $\hat{x}_2 = m$  and  $\tilde{x}_1 = m/s_1$ . Similarly, since  $\hat{x}_1 = s_1 g(\hat{x}_2) \hat{x}_1$  and  $\hat{x}_1 < m$ , we must have  $\hat{x}_1 = 0 = \tilde{x}_2$  and the boundary 2-cycle  $\mathcal{C}_1$  is the  $\omega$ -limit set of the solution.

To prove (b), first assume  $x_2(0) = m$  and  $x_1(0) < m/s_1$ . Then  $x_2(2t) = m$ ,  $x_1(2t) < m/s_1$ ,  $x_2(2t+1) < m$  and  $x_1(2t+1) = m/s_1$  for  $t \geq 0$ . Hence (7) and (8) imply  $x_1(t+2) \leq x_1(t)$  and  $x_2(t+2) \leq x_2(t)$  for  $t \geq 0$ . It follows that the following limits exist

$$\lim_{t \rightarrow \infty} x_1(2t) = x_1^* \text{ and } \lim_{t \rightarrow \infty} x_2(2t+1) = x_2^*$$

with

$$x_1^* < m/s_1 \text{ and } x_2^* < m.$$

We then have  $x_1^* = 0 = x_2^*$  and the solution has the boundary 2-cycle as its  $\omega$ -limit set. Suppose  $x_2(0) > m$  and  $x_1(0) < m/s_1$ . Then we have  $x_2(2t) > m$ ,  $x_1(2t) < m/s_1$ ,  $x_2(2t+1) < m$  and  $x_1(2t+1) > m/s_1$  for  $t \geq 0$ . Also,  $x_1(t+2) < x_1(t)$  and  $x_2(t+2) < x_2(t)$  hold for  $t \geq 0$ . Therefore,

$$\begin{aligned}\lim_{t \rightarrow \infty} x_1(2t) &= x_1^*, \lim_{t \rightarrow \infty} x_1(2t+1) = \hat{x}_1, \\ \lim_{t \rightarrow \infty} x_2(2t) &= x_2^*, \lim_{t \rightarrow \infty} x_2(2t+1) = \hat{x}_2\end{aligned}$$

with

$$x_1^* < m/s_1, \hat{x}_1 \geq m/s_1, x_2^* \geq m \text{ and } \hat{x}_2 < m.$$

It then follows that  $x_2^* = m$ ,  $\hat{x}_1 = m/s_1$ , and  $x_1^* = 0 = \hat{x}_2$ . Therefore the solution also has the boundary 2-cycle  $\mathcal{C}_1$  as its  $\omega$ -limit set. Similarly, it can be shown that the solution converges to  $E_1$  if  $x_1(0) \geq m/s_1$  and  $x_2(0) \geq m$  and the proof is complete.  $\square$

Suppose now  $s_1g(m) > 1$ . Then system (1) has two interior steady states  $E_{11} = (\bar{x}_{21}/s_1, \bar{x}_{21})$  and  $E_{12} = (\bar{x}_{22}/s_1, \bar{x}_{22})$ , where  $\bar{x}_{2i}$  satisfies (2) for  $i = 1, 2$  with  $\bar{x}_{21} < m < \bar{x}_{22}$ . Let functions  $F(x)$  and  $G(x)$  be defined in (5). A simple calculation yields

$$\begin{aligned} F(x) &< x \text{ if } x \in (0, \bar{x}_{21}/s_1) \cup (\bar{x}_{22}/s_1, \infty) \\ F(x) &> x \text{ if } x \in (\bar{x}_{21}/s_1, \bar{x}_{22}/s_1) \end{aligned}$$

and

$$F(x) = x \text{ if } x = 0 \text{ or } x = \bar{x}_{2i}/s_1, i = 1, 2.$$

The same is true for  $G(x)$ :

$$\begin{aligned} G(x) &< x \text{ if } x \in (0, \bar{x}_{21}) \cup (\bar{x}_{22}, \infty) \\ G(x) &> x \text{ if } x \in (\bar{x}_{21}, \bar{x}_{22}) \end{aligned}$$

and

$$G(x) = x \text{ if } x = 0 \text{ or } x = \bar{x}_{2i}, i = 1, 2.$$

Moreover, any 2-cycles of system (1) are fixed points of system (4). It can be easily seen that (4) has fixed points:  $(0, 0)$ ,  $(\bar{x}_{21}/s_1, \bar{x}_{22})$ ,  $(\bar{x}_{22}/s_1, \bar{x}_{21})$ , and  $E_{1i}$ ,  $(\bar{x}_{2i}/s_1, 0)$ ,  $(0, \bar{x}_{2i})$  for  $i = 1, 2$ . As a result, (1) has two boundary 2-cycles

$$\mathcal{C}_{1i} = \{(\bar{x}_{2i}/s_1, 0), (0, \bar{x}_{2i})\}, i = 1, 2 \quad (9)$$

and a unique interior 2-cycle

$$\mathcal{C}^* = \{(\bar{x}_{21}/s_1, \bar{x}_{22}), (\bar{x}_{22}/s_1, \bar{x}_{21})\}. \quad (10)$$

The stability of these interior steady states and the 2-cycles can be easily obtained using the associated Jacobian matrix. Indeed, the stability of the 2-cycles are determined by the Jacobian matrix of system (4) evaluated at the components of the cycle, where the Jacobian matrix of (4) is given by

$$\hat{J} = \begin{pmatrix} s_1g(s_1y_1) + s_1^2g'(s_1y_1)y_1 & 0 \\ 0 & s_1g(y_2) + s_1g'(y_2)y_2 \end{pmatrix}. \quad (11)$$

In particular, at  $(0, \bar{x}_{2i})$  we have  $\hat{J} = \begin{pmatrix} 0 & 0 \\ 0 & 1 + s_1g'(\bar{x}_{2i})\bar{x}_{2i} \end{pmatrix}$ . Notice that  $g'(\bar{x}_{21}) > 0$ , we see that the boundary 2-cycle  $\mathcal{C}_{11}$  is unstable. On the other hand,  $g'(\bar{x}_{22}) < 0$  and (H1) implies  $0 < 1 + s_1\bar{x}_{22}g'(\bar{x}_{22}) < 1$ . Therefore, the other boundary 2-cycle  $\mathcal{C}_{12}$  is stable. Similarly,  $\hat{J}$  evaluated at  $(\bar{x}_{21}/s_1, \bar{x}_{22})$  is given by  $\begin{pmatrix} 1 + s_1g'(\bar{x}_{21})\bar{x}_{21} & 0 \\ 0 & 1 + s_1g'(\bar{x}_{22})\bar{x}_{22} \end{pmatrix}$ . It follows that the interior 2-cycle  $\mathcal{C}^*$  is unstable. Furthermore, from the Jacobian matrix  $J$  of system (1) evaluated at the interior steady state  $E_{1i}$  we can conclude that  $E_{11}$  is unstable while  $E_{12}$  is locally asymptotically stable.

Using these observation, the asymptotic dynamics of system (1) restricted on the boundary of  $\mathbb{R}_+^2$  when  $s_1g(m) > 1$  can be summarized below. The proofs are similar to the proofs of previous theorems and are therefore omitted.

**Theorem 2.4.** *Let  $s_1g(m) > 1$  and  $(x_1(t), x_2(t))$  be a solution of (1) with either  $x_1(0) = 0, x_2(0) > 0$  or  $x_1(0) > 0, x_2(0) = 0$ .*

- (a) *Let  $x_2(0) = 0$ . If  $0 < x_1(0) < \bar{x}_{21}/s_1$ , then the solution converges to  $E_0 = (0, 0)$ . If  $x_1(0) = \bar{x}_{21}/s_1$ , then the solution is the 2-cycle  $\mathcal{C}_{11}$ . If  $x_1(0) > \bar{x}_{21}/s_1$ , then the solution has  $\omega$ -limit set equal the boundary 2-cycle  $\mathcal{C}_{12}$ .*

- (b) Let  $x_1(0) = 0$ . If  $0 < x_2(0) < \bar{x}_{21}$ , then the solution converges to  $E_0 = (0, 0)$ . If  $x_2(0) = \bar{x}_{21}$ , then the solution is the 2-cycle  $\mathcal{C}_{11}$ . If  $x_2(0) > \bar{x}_{21}$ , then the solution has  $\mathcal{C}_{12}$  as its  $\omega$ -limit set.

Similarly, asymptotic dynamics of system (1) restricted to the interior of  $\mathbb{R}_+^2$  when  $s_1 g(m) > 1$  are summarized below without proof.

**Theorem 2.5.** *Let  $s_1 g(m) > 1$  and  $(x_1(t), x_2(t))$  be a solution of (1) with  $x_1(0) > 0$ ,  $x_2(0) > 0$ . Then the following statements are true.*

- (a) Let  $x_2(0) < \bar{x}_{21}$ . If  $x_1(0) < \bar{x}_{21}/s_1$  then the solution converges to  $E_0 = (0, 0)$ . If  $x_1(0) = \bar{x}_{21}/s_1$ , then the solution has  $\mathcal{C}_{11}$  as its  $\omega$ -limit set. If  $x_1(0) > \bar{x}_{21}/s_1$ , then the solution has  $\omega$ -limit set  $\mathcal{C}_{12}$ .
- (b) Let  $x_2(0) = \bar{x}_{21}$ . If  $x_1(0) < \bar{x}_{21}/s_1$ , then the solution has  $\omega$ -limit set  $\mathcal{C}_{11}$ . If  $x_1(0) = \bar{x}_{21}/s_1$ , then the solution is  $E_{11}$ . If  $x_1(0) > \bar{x}_{21}/s_1$ , then the solution has the interior 2-cycle  $\mathcal{C}^*$  as its  $\omega$ -limit set.
- (c) Let  $x_2(0) > \bar{x}_{21}$ . If  $x_1(0) < \bar{x}_{21}/s_1$ , then the solution has  $\omega$ -limit set  $\mathcal{C}_{12}$ . If  $x_1(0) = \bar{x}_{21}/s_1$ , then the solution has the interior 2-cycle  $\mathcal{C}^*$  as its  $\omega$ -limit set. If  $x_1(0) > \bar{x}_{21}/s_1$ , then the solution converges to the interior steady state  $E_{12}$ .

**3. A host-parasitoid model with Allee effects in the host.** In this section we shall study a model of host-parasitoid interaction. Let  $p(t)$  denote the parasitoid population at time  $t$ . An individual parasitoid must find a host to reproduce. Since the host population is stage-structured, we classify eggs and larvae as juveniles and pupae and matured host as adults as in [12]. The parasitism is usually assumed to occur during the pupae stage as discussed in [14] so that individuals of the adult class in the model may get parasitized. Moreover, it is assumed in this model that parasitism occurs before density dependence.

Let  $\beta$  be the average number of survived parasitoid that an individual parasitized adult host can reproduce. Building upon system (1), the interaction between host and parasitoid is governed by the following system of difference equations:

$$\begin{cases} x_1(t+1) = x_2(t)g(x_2(t))f(p(t)) \\ x_2(t+1) = s_1 x_1(t) \\ p(t+1) = \beta x_2(t)(1 - f(p(t))) \\ x_1(0), x_2(0), p(0) \geq 0, \end{cases} \quad (12)$$

where  $g$  satisfies the assumptions given in (H1) and  $f$  satisfies the following conditions:

(H2)  $f \in C^2[0, \infty)$ ,  $f(0) = 1$ ,  $f'(x) < 0$ ,  $f''(x) \geq 0$  for  $x \geq 0$ , and  $f(\infty) = 0$ .

Let  $(x_1(t), x_2(t), p(t))$  be a solution of (12). If  $p(0) = 0$  then  $p(t) = 0$  for  $t \geq 1$  and (12) reduces to (1). Therefore we assume  $p(0) > 0$  for the remainder of the discussion. Since  $x_1(t+1) \leq x_2(t)g(x_2(t))$  holds for  $t \geq 0$ , we consider the following system

$$\begin{cases} z_1(t+1) = g(z_2(t))z_2(t) \\ z_2(t+1) = s_1 z_1(t) \\ z_1(0) = x_1(0), z_2(0) = x_2(0), \end{cases} \quad (13)$$

i.e., system (1). Then  $x_1(1) \leq z_2(0)g(z_2(0)) = z_1(1)$ ,  $x_2(1) = z_2(1)$ ,  $x_1(2) \leq z_2(1)g(z_2(1)) = z_1(2)$  and  $x_2(2) \leq z_2(2)$ . Since  $xg(x)$  is strictly increasing by (H1), inductively one can show that

$$x_i(t) \leq z_i(t) \text{ for } t \geq 1 \text{ and } i = 1, 2. \quad (14)$$



Inequalities (14) will aid us in understanding the asymptotic dynamics of system (12). Furthermore, a similar argument shows that

$$x_1(t+2) \leq F(x_1(t)) \text{ and } x_2(t+2) \leq G(x_2(t)) \quad (15)$$

hold for  $t \geq 0$ , where  $F$  and  $G$  are given in (5).

The Jacobian matrix of (12) is given by

$$\begin{pmatrix} 0 & (g(x_2) + g'(x_2)x_2)f(p) & x_2g(x_2)f'(p) \\ s_1 & 0 & 0 \\ 0 & \beta(1-f(p)) & -\beta x_2f'(p) \end{pmatrix}. \quad (16)$$

The extinction steady state  $E_0 = (0, 0, 0)$  always exists for (12). The Jacobian matrix evaluated at  $E_0$  is  $\begin{pmatrix} 0 & 0 & 0 \\ s_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$  which implies that  $E_0$  is always locally asymptotically stable. The dynamics of system (12) are discussed separately below for  $s_1g(m) < 1$ ,  $s_1g(m) = 1$  and  $s_1g(m) > 1$ . When  $s_1g(m) < 1$ , since  $(0, 0)$  is globally asymptotically stable for (1), it can be easily shown that  $E_0 = (0, 0, 0)$  is globally asymptotically stable for (12).

**Theorem 3.1.** *If  $s_1g(m) < 1$ , then  $E_0 = (0, 0, 0)$  is globally asymptotically stable for (12) in  $\mathbb{R}_+^3$ .*

*Proof.* It follows from (14) and Theorem 2.1 that  $\lim_{t \rightarrow \infty} x_i(t) = 0$ ,  $i = 1, 2$ , for any solution  $(x_1(t), x_2(t), p(t))$  of (12). Hence  $\lim_{t \rightarrow \infty} p(t) = 0$ , and  $E_0$  is globally attracting. Therefore  $E_0$  is globally asymptotically stable since it is locally asymptotically stable.  $\square$

Suppose now  $s_1g(m) = 1$ . Then in addition to  $E_0$ , (12) has another boundary steady state  $E_1 = (m/s_1, m, 0)$ , where  $E_1$  is non-hyperbolic by the Jacobian matrix given in (16) evaluated at  $E_1$ . Moreover, (12) has a unique boundary 2-cycle

$$\mathcal{S}_1 = \{(m/s_1, 0, 0), (0, m, 0)\} \quad (17)$$

and there are neither interior steady states nor interior 2-cycles. The boundary 2-cycle  $\mathcal{S}_1$  is also non-hyperbolic. By Theorems 2.2 and 2.3, solutions of system (13) satisfy  $\limsup_{t \rightarrow \infty} z_1(t) \leq m/s_1$  and  $\limsup_{t \rightarrow \infty} z_2(t) \leq m$ . As a result, solutions of (12) satisfy

$$\limsup_{t \rightarrow \infty} x_1(t) \leq m/s_1, \limsup_{t \rightarrow \infty} x_2(t) \leq m, \text{ and } \limsup_{t \rightarrow \infty} p(t) \leq \beta m. \quad (18)$$

**Theorem 3.2.** *Let  $s_1g(m) = 1$  and  $(x_1(t), x_2(t), p(t))$  be a solution of (12) with  $p(0) > 0$ .*

- (a) *Inequalities (18) hold. Moreover, if  $-\beta m f'(0) < 1$  then  $\lim_{t \rightarrow \infty} p(t) = 0$ .*
- (b) *Let  $x_1(0) = 0$ . If  $0 < x_2(0) \leq m$ , then the solution converges to  $E_0$ . If  $x_2(0) > m$ , then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t+1) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution will either converge to  $E_0$  or has the 2-cycle  $\mathcal{S}_1$  as its  $\omega$ -limit set. Let  $x_2(0) = 0$ . If  $0 < x_1(0) \leq m/s_1$ , then the solution converges to  $E_0$ . If  $x_1(0) > m/s_1$ , then  $\lim_{t \rightarrow \infty} x_1(2t+1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has  $\omega$ -limit set  $\mathcal{S}_1$ .*
- (c) *Let  $0 < x_1(0) < m/s_1$ . Then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t+1) = \lim_{t \rightarrow \infty} p(t) = 0$ . If  $0 < x_2(0) \leq m$  or if  $x_2(0) > m$  and  $p(0) > f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right)$ , then the solution converges to  $E_0$ . Let  $x_1(0) = m/s_1$ .*

If  $0 < x_2(0) \leq m$  then the solution converges to  $E_0$ . If  $x_2(0) > m$ , then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t+1) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has the 2-cycle  $\mathcal{S}_1$  as its  $\omega$ -limit set.

(d) Let  $x_1(0) > m/s_1$ . If either  $0 < x_2(0) \leq m$ , or if  $x_2(0) > m$  and  $p(0) > f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right)$ , then  $\lim_{t \rightarrow \infty} x_1(2t+1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has the 2-cycle  $\mathcal{S}_1$  as its  $\omega$ -limit set.

*Proof.* (a) It is enough to prove only the second statement. By (18) and the assumption, there exist positive constants  $\epsilon$  and  $t_0$  such that  $-\beta(m+\epsilon)f'(0) < 1$  and  $x_2(t) < m+\epsilon$  for all  $t \geq t_0$ . It follows that for  $t \geq t_0$  there exists  $\eta > 0$  depending on  $t$  such that

$$p(t+1) = -\beta x_2(t) f'(\eta) p(t) < -\beta(m+\epsilon) f'(0) p(t),$$

by (H2). Therefore,  $\lim_{t \rightarrow \infty} p(t) = 0$  is shown. The statements in (b) can be shown similarly as in Theorem 2.2 since there exists a finite  $t_1 > 0$  such that  $p(t) = 0$  for  $t \geq t_1$ .

To prove (c), let  $0 < x_1(0) < m/s_1$ . Then inductively one has  $x_1(2t) < m/s_1$  and  $x_2(2t+1) < m$  for  $t \geq 0$ . Using (15), we see that  $x_1(2t)$  and  $x_2(2t+1)$  monotonically decrease to 0. Therefore,  $\lim_{t \rightarrow \infty} p(2t) = 0$  and thus  $\lim_{t \rightarrow \infty} p(2t+1) = 0$ , i.e.,  $\lim_{t \rightarrow \infty} p(t) = 0$ . It is clear that the solution converges to  $E_0$  if  $0 < x_2(0) \leq m$ . Suppose  $x_2(0) > m$ . Setting  $x_1(1) = x_2(0)g(x_2(0))f(p(0)) < m/s_1$  and solving for  $p(0)$ , yields

$$p(0) > f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right),$$

where  $\frac{m}{s_1 x_2(0) g(x_2(0))} \in (0, 1)$ . It follows that  $x_1(t) < m/s_1$  and  $x_2(t+1) < m$  for all  $t > 0$  and the solution also converges to  $E_0$ . The remainder of the statements can be proved similarly as in Theorem 2.3.  $\square$

Suppose now  $s_1 g(m) > 1$ . The second iteration of system (12) yields the following system

$$\begin{cases} x_1(t+2) = s_1 x_1(t) g(s_1 x_1(t)) f(\beta x_2(t)(1-f(p(t)))) \\ x_2(t+2) = s_1 x_2(t) g(x_2(t)) f(p(t)) \\ p(t+2) = \beta s_1 x_1(t) (1-f(\beta x_2(t)(1-f(p(t))))). \end{cases} \quad (19)$$

In addition to  $E_0 = (0, 0, 0)$ , system (12) has two more boundary steady states:

$$E_{1i} = (\bar{x}_{2i}/s_1, \bar{x}_{2i}, 0), \quad i = 1, 2$$

where  $\bar{x}_{21} < m < \bar{x}_{22}$  satisfy (2), and three boundary 2-cycles:

$$\mathcal{S}_{1i} = \{(\bar{x}_{2i}/s_1, 0, 0), (0, \bar{x}_{2i}, 0)\}, \quad i = 1, 2 \quad (20)$$

and

$$\mathcal{S}_2 = \{(\bar{x}_{21}/s_1, \bar{x}_{22}, 0), (\bar{x}_{22}/s_1, \bar{x}_{21}, 0)\}. \quad (21)$$

The Jacobian matrix of system (19) evaluated at  $(\bar{x}_{2i}/s_1, 0, 0)$ , a component of  $\mathcal{S}_{1i}$ , is given by

$$\begin{pmatrix} 1 + s_1^2 \bar{x}_{2i} g'(\bar{x}_{2i}) & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

It follows that  $\mathcal{S}_{11}$  is unstable and  $\mathcal{S}_{12}$  is stable. Similarly, the Jacobian matrix of (19) evaluated at  $(\bar{x}_{21}/s_1, \bar{x}_{22}, 0)$ , a component of  $\mathcal{S}_2$ , is given by

$$\begin{pmatrix} 1 + s_1 \bar{x}_{21} g'(\bar{x}_{21}) & 0 & * \\ 0 & 1 + s_1 \bar{x}_{22} g'(\bar{x}_{22}) & * \\ 0 & 0 & \beta^2 \bar{x}_{21} \bar{x}_{22} (f'(0))^2 \end{pmatrix},$$

where \*'s denote some unimportant expressions. Therefore  $\mathcal{S}_2$  is unstable. Since solutions of (13) satisfy

$$\limsup_{t \rightarrow \infty} z_1(t) \leq \bar{x}_{22}/s_1 \text{ and } \limsup_{t \rightarrow \infty} z_2(t) \leq \bar{x}_{22},$$

solutions of (12) satisfy

$$\limsup_{t \rightarrow \infty} x_1(t) \leq \bar{x}_{22}/s_1, \limsup_{t \rightarrow \infty} x_2(t) \leq \bar{x}_{22} \text{ and } \limsup_{t \rightarrow \infty} p(t) \leq \beta \bar{x}_{22}. \quad (22)$$

The asymptotic dynamics of system (12) when  $s_1 g(m) > 1$  are described below. The proof is similar to the previous proofs and is omitted.

**Theorem 3.3.** *Let  $s_1 g(m) > 1$  and  $(x_1(t), x_2(t), p(t))$  be a solution of (12) with  $p(0) > 0$ . Then the following are true.*

- (a) *Solutions of (12) satisfy (22). Moreover, if  $-\beta \bar{x}_{22} f'(0) < 1$  then  $\lim_{t \rightarrow \infty} p(t) = 0$ .*
- (b) *Let  $x_1(0) = 0$ . If  $0 < x_2(0) \leq \bar{x}_{21}$ , then the solution converges to  $E_0 = (0, 0, 0)$ . If  $x_2(0) > \bar{x}_{21}$ , then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t + 1) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set. Let  $x_2(0) = 0$ . If  $0 < x_1(0) \leq \bar{x}_{21}/s_1$ , then the solution converges to  $E_0$ . If  $x_1(0) > \bar{x}_{21}/s_1$ , then  $\lim_{t \rightarrow \infty} x_1(2t + 1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set.*
- (c) *Let  $0 < x_1(0) \leq \bar{x}_{21}/s_1$ . Then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t + 1) = \lim_{t \rightarrow \infty} p(t) = 0$ . If either  $0 < x_2(0) \leq \bar{x}_{21}$  or if  $x_2(0) > \bar{x}_{21}$  and  $p(0) > f^{-1}\left(\frac{\bar{x}_{21}}{s_1 x_2(0) g(x_2(0))}\right)$ , then the solution converges to  $E_0$ .*
- (d) *Let  $x_1(0) > \bar{x}_{21}/s_1$ . If either  $0 < x_2(0) \leq \bar{x}_{21}$  or if  $x_2(0) > \bar{x}_{21}$  and  $p(0) > f^{-1}\left(\frac{\bar{x}_{21}}{s_1 x_2(0) g(x_2(0))}\right)$ , then solutions satisfy  $\lim_{t \rightarrow \infty} x_1(2t + 1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set.*

**4. A host-parasitoid model where density dependence occurs before parasitism.** In this section we consider a similar host-parasitoid interaction with Allee effects and age structure in the host. Since it is often difficult to determine when density dependence really occurs, in contrast to the earlier model (12), we study the situation when density dependence of the host occurs prior to parasitism. The model then becomes

$$\begin{cases} x_1(t+1) = x_2(t)g(x_2(t))f(p(t)) \\ x_2(t+1) = s_1 x_1(t) \\ p(t+1) = \beta x_2(t)g(x_2(t))(1 - f(p(t))) \\ x_1(0), x_2(0), p(0) \geq 0, \end{cases} \quad (23)$$

where  $g$  satisfies (H1) and  $f$  satisfies (H2).

It is clear that solutions of (23) also satisfy inequalities (14) and (15), and system (23) always has the extinction steady state  $E_0 = (0, 0, 0)$ , where both populations cannot survive. We also assume  $p(0) > 0$  for the remainder discussion since (23) reduces to (1) if  $p(0) = 0$ . It is straightforward to show that both populations will go extinct if the maximal growth rate of the host population,  $s_1g(m)$ , is less than one.

**Theorem 4.1.** *If  $s_1g(m) < 1$ , then  $E_0 = (0, 0, 0)$  is globally asymptotically stable for system (23).*

When  $s_1g(m) = 1$ , then system (23) has another boundary steady state  $E_1 = (m/s_1, m, 0)$  and one boundary 2-cycle  $\mathcal{S}_1$  given in (17), where the parasitoid population is absent. In this case, solutions of (23) satisfy

$$\limsup_{t \rightarrow \infty} x_1(t) \leq m/s_1, \limsup_{t \rightarrow \infty} x_2(t) \leq m, \text{ and } \limsup_{t \rightarrow \infty} p(t) \leq \beta m/s_1. \quad (24)$$

We have the following asymptotic behavior for (23) which are similar to that of system (12) when  $s_1g(m) = 1$ .

**Theorem 4.2.** *Let  $s_1g(m) = 1$  and  $(x_1(t), x_2(t), p(t))$  be a solution of (23) with  $p(0) > 0$ .*

- (a) *Solutions of (23) satisfy (24). Moreover, if  $-\beta mg(m)f'(0) < 1$  then  $\lim_{t \rightarrow \infty} p(t) = 0$ .*
- (b) *Assume either  $x_1(0) = 0$  or  $x_2(0) = 0$ . If  $x_1(0) = 0$  and  $0 < x_2(0) \leq m$  or  $x_2(0) = 0$  and  $0 < x_1(0) \leq m/s_1$ , then the solution converges to  $E_0$ . Otherwise,  $\lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converge to  $E_0$  or has the boundary 2-cycle  $\mathcal{S}_1$  as its  $\omega$ -limit set.*
- (c) *Let  $0 < x_1(0) \leq m/s_1$ . Then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t + 1) = \lim_{t \rightarrow \infty} p(t) = 0$ . In particular, if either  $0 < x_2(0) \leq m$  or if  $x_2(0) > m$  and  $p(0) > f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right)$ , then the solution converges to  $E_0$ . Otherwise, the solution either converges to  $E_0$  or has  $\mathcal{S}_1$  as its  $\omega$ -limit set.*
- (d) *Let  $x_1(0) > m/s_1$ . If either  $0 < x_2(0) \leq m$  or if  $x_2(0) > m$  and  $p(0) > f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right)$ , then  $\lim_{t \rightarrow \infty} x_1(2t + 1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has  $\mathcal{S}_1$  as its  $\omega$ -limit set.*

When  $s_1g(m) > 1$ , then in addition to  $E_0$ , system (23) has two other boundary states  $E_{1i} = (\bar{x}_{2i}/s_1, \bar{x}_{2i}, 0)$ ,  $i = 1, 2$ , and three boundary 2-cycles  $\mathcal{S}_{1i}$  ( $i = 1, 2$ ) and  $\mathcal{S}_2$  given by (20) and (21), respectively. Local stability analysis of these steady states and 2-cycles yields that  $E_0$  is locally asymptotically stable,  $E_{11}$  is unstable,  $E_{12}$  is locally asymptotically stable if  $-\beta \bar{x}_{22} g(\bar{x}_{22}) f'(0) < 1$  and unstable if the inequality is reversed,  $\mathcal{S}_{11}$  is unstable,  $\mathcal{S}_{12}$  is stable, and  $\mathcal{S}_2$  is unstable. Moreover, solutions of (23) also satisfy

$$\limsup_{t \rightarrow \infty} x_1(t) \leq \bar{x}_{22}/s_1, \limsup_{t \rightarrow \infty} x_2(t) \leq \bar{x}_{22}, \limsup_{t \rightarrow \infty} p(t) \leq \beta \bar{x}_{22}/s_1. \quad (25)$$

The asymptotic dynamics of (23) are similar to system (12) when  $s_1g(m) > 1$ . We also omit the proof of the following theorem.

**Theorem 4.3.** *Let  $s_1g(m) > 1$  and  $(x_1(t), x_2(t), p(t))$  be a solution of (23) with  $p(0) > 0$ . Then the following are true.*

- (a) Solutions of (23) satisfy (25). Moreover, if  $-\beta\bar{x}_{22}g(\bar{x}_{22})f'(0) < 1$  then  $\lim_{t \rightarrow \infty} p(t) = 0$ .
- (b) Let  $x_1(0) = 0$ . If  $0 < x_2(0) \leq \bar{x}_{21}$ , then the solution converges to  $E_0$ . If  $x_2(0) > \bar{x}_{21}$ , then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t+1) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set. Let  $x_2(0) = 0$ . If  $0 < x_1(0) \leq \bar{x}_{21}/s_1$ , then the solution converges to  $E_0$ . If  $x_1(0) > \bar{x}_{21}/s_1$ , then  $\lim_{t \rightarrow \infty} x_1(2t+1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set.
- (c) Let  $0 < x_1(0) \leq \bar{x}_{21}/s_1$ . Then  $\lim_{t \rightarrow \infty} x_1(2t) = \lim_{t \rightarrow \infty} x_2(2t+1) = \lim_{t \rightarrow \infty} p(t) = 0$ . If either  $0 < x_2(0) \leq \bar{x}_{21}$  or if  $x_2(0) > \bar{x}_{21}$  and  $p(0) > f^{-1}\left(\frac{\bar{x}_{21}}{s_1 x_2(0) g(x_2(0))}\right)$ , then the solution converges to  $E_0$ . Otherwise, the solution will either converge to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set.
- (d) Let  $x_1(0) > \bar{x}_{21}/s_1$ . If either  $0 < x_2(0) \leq \bar{x}_{21}$  or if  $x_2(0) > \bar{x}_{21}$  and  $p(0) > f^{-1}\left(\frac{\bar{x}_{21}}{s_1 x_2(0) g(x_2(0))}\right)$ , then solutions satisfy  $\lim_{t \rightarrow \infty} x_1(2t+1) = \lim_{t \rightarrow \infty} x_2(2t) = \lim_{t \rightarrow \infty} p(t) = 0$  and the solution either converges to  $E_0$  or has a boundary 2-cycle  $\mathcal{S}_{1i}$  as its  $\omega$ -limit set.

**5. Numerical simulations.** In this section we briefly use numerical examples and simulations to study models (12) and (23). Let

$$g(x) = \frac{3x}{1+x^2}. \quad (26)$$

Then  $g$  satisfies (H1) with  $m = 1$ . A well known example of  $f$  follows that of Poisson distribution as was considered by May et al. [14]:

$$f(x) = e^{-cx}, \quad (27)$$

where  $c > 0$ . Here we use  $c = 1$  for our simulations.

We first let  $s_1 = 2/3$  and  $\beta = 1.5$ . Then  $s_1 g(m) = 1$  and  $-\beta m f'(0) = 1.5 > 1$ . System (12) has two steady states  $E_0 = (0, 0, 0)$  and  $E_1 = (1.5, 1, 0)$  and a unique 2-cycle  $\mathcal{S}_1 = \{(1.5, 0, 0), (0, 1, 0)\}$ . We choose initial condition  $(x_1(0), x_2(0), p(0)) = (5, 2, 0)$ . Then since  $x_1(0) > m/s_1$  and  $x_2(0) > m$ , Theorem 2.3 implies that the solution converges to the steady state  $E_1 = (1.5, 1, 0)$ . The time evolution of the solution is plotted in Figure 1(a). A simple calculation yields  $f^{-1}\left(\frac{m}{s_1 x_2(0) g(x_2(0))}\right) = 0.47$ . We then use initial condition  $(x_1(0), x_2(0), p(0)) = (5, 2, 1)$ , where the parasitoid population has initial population size larger than 0.47. According to Theorem 3.2(c), the solution will either converge to  $E_0$  or  $\mathcal{S}_1$ . Numerical simulations suggest that the parasitoid population drives the host population to extinction as shown in Figure 1(b) and as a result the parasitoid population also cannot survive, i.e., the solution converges to  $E_0 = (0, 0, 0)$ .

When we let  $s_1 = 3/4$ , then  $s_1 g(m) > 1$ ,  $\bar{x}_{21} = 0.6096$  and  $\bar{x}_{22} = 1.6404$ . Consequently, system (12) has steady states  $E_0 = (0, 0, 0)$ ,  $E_{11} = (0.8128, 0.6096, 0)$ ,  $E_{12} = (2.1872, 1.6404, 0)$  and boundary 2-cycles  $\mathcal{S}_{11} = \{(0.8128, 0, 0), (0, 0.6096, 0)\}$ ,  $\mathcal{S}_{12} = \{(2.1872, 0, 0), (0, 1.6404, 0)\}$  and  $\mathcal{S}_2$ , where  $\mathcal{S}_2 = \{(0.8128, 1.6404, 0), (2.1872, 0.6096, 0)\}$ . We choose initial condition  $(x_1(0), x_2(0), p(0)) = (1, 2, 0)$ . The

solution converges to the steady state  $E_{12} = (2.1872, 1.6404, 0)$  according to Theorem 2.5(c). This simulation is shown in Figure 1(c). Moreover,  $f^{-1}\left(\frac{\bar{x}_{21}}{s_1 x_2(0)g(x_2(0))}\right) = 0.6127$ . As we increase  $p(0)$  to 0.2, i.e., we use the initial condition  $(1, 2, 0.2)$ , then the solution converges to the boundary 2-cycle  $S_{12} = \{(0, 1.6404, 0), (2.1872, 0, 0)\}$  as given in Figure 1(d). When we increase  $p(0)$  to 2, then Theorem 3.3(c) implies that the solution will either converge to  $E_0$  or has a boundary 2-cycle  $S_{1i}$  as its  $\omega$ -limit set. Our numerical simulations demonstrate that both populations become extinct. The same conclusion remains as we vary  $x_1(0)$ ,  $x_2(0)$  and keep  $p(0) = 2$ . These plots are not presented here. We also simulate system (23) using the above function forms and parameter values. Similar conclusions are obtained and the simulations are not presented in the manuscript.

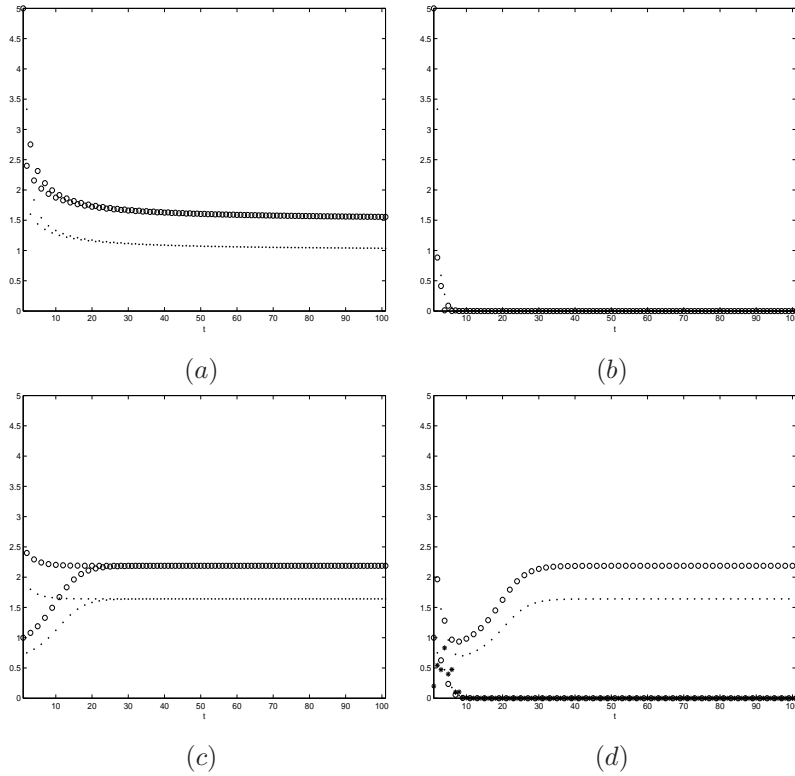


FIGURE 1. (a) and (b) plot solutions of system (12) when  $s_1 g(m) = 1$  with initial condition  $(5, 2, 0)$  for (a) and  $(5, 2, 1)$  for (b). We see that the presence of parasitoid population can drive the host population to extinction. (c) and (d) plot solutions of (12) when  $s_1 g(m) > 1$  with initial condition  $(1, 2, 0)$  for (c) and  $(1, 2, 0.2)$  for (d). Although the parasitoid does not drive the host to extinction, the presence of parasitoid population can reduce the host population from an equilibrium state to an oscillating state. Here “o” denotes  $x_1$ , “.” denotes  $x_2$ , and “\*” denotes the  $p$  population.

**6. Discussion.** Allee effects can occur in natural populations because of mating limitation or lack of cooperative individuals to explore resources efficiently when population densities are low. See [3] for various biological examples of Allee effects. Population models without stage structure implicitly assume that individuals within the population are identical. However, it has been observed that the vital rates of an individual, such as survival and fertility rates, depend on the stage of an individual. In this manuscript we proposed and studied a two-stage single species population model with Allee effects and two models of host-parasitoid interaction with Allee effects and age structure in the host. The single species model (1) and the first two species model (12) extend those models considered in an earlier work by the author [12]. In addition, we also investigated a model of host-parasitoid interaction, system (23), in which density dependence of the host occurs prior to parasitism.

For the single species two-stage population model, global analysis of its dynamical behavior are obtained. The analysis is given in terms of the threshold,  $s_1g(m)$ , which can be regarded as the maximal growth rate of the host population. It is the maximum number of offsprings that an individual host can reproduce during its life time. The host population cannot survive if  $s_1g(m) < 1$  as illustrated in Theorems 2.1, 3.1 and 4.1. When  $s_1g(m) = 1$  and there is no parasitoid present initially, the host population can survive if its initial population size is beyond the Allee threshold. See results of Theorems 2.2 and 2.3. Our numerical simulations illustrate this analytical finding. See Figure 1(a). When there is parasitoid population initially, then the parasitoid population may drive the host population to extinction as given in Theorems 3.2 and 4.2. Our numerical example presented in Figure 1(b) confirms this mathematical result. When  $s_1g(m) > 1$  and there is no parasitoid population present, the host population also can persist if its initial population size is beyond the threshold as presented in Theorems 2.4 and 2.5 and given in Figure 1(c). However, if parasitoid population is present initially, then the parasitoid population may overexploit the host population to extinction even if the initial host population size is large. See Theorems 3.3 and 4.3. Our numerical simulations although not presented in this manuscript do demonstrate this possibility.

It is usually very difficult if not impossible to determine when intra-specific competition within a population really occurs. For this reason, we also proposed and studied a model of host-parasitoid interaction in which density dependence occurs prior to parasitism. However, we conclude from this study that such a host-parasitoid interaction also has the same qualitative behavior as the model when parasitism occurs before intra-specific competition.

Since Allee effects act primarily in small or sparse populations, they are particularly vital for the survival of rare, declining, endangered, or fragmented populations. Therefore, Allee effects play a crucial role in conservation and management of natural resources. They affect how we can manage populations for suitable exploitation such as fishing, hunting and harvesting. Our present study suggests that there is a serious consequence of overexploit our natural resources. The populations may become extinct due to over-exploitation of the populations to below the Allee thresholds.

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