

Dynamics of a host–parasitoid model with Allee effect for the host and parasitoid aggregation

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ABSTRACT

In this paper, a discrete-time host–parasitoid model is investigated. Two biological phenomena, the Allee effect of the host population and the aggregation of the parasitism, are considered in our mathematical model. Through extensive numerical simulations, we gain some interesting findings related to Allee effect from this research. Firstly, the ranges of parameter, in which the population dynamics is chaos, are compressed when Allee effect is added. Secondly, the sensitivity to initial conditions of the host–parasitoid system decreased after adding Allee effect. Thirdly, without Allee effect, we observed two complicated dynamics, intermittent chaos and supertransients. However, when Allee effect is included, these two phenomena are replaced by another kind of phenomenon–period alternation, where chaos is eliminated. From above three novel findings, it can be concluded that dynamic complexities are alleviated by Allee effect. This conclusion is crucial in resolving the discrepancy between real population dynamics and theoretical predictions. Furthermore, the importance of this research is to help us understand the mechanisms inducing the irregular fluctuations of the natural populations.

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1. Introduction

The dynamics of natural populations are very complicated (Hassell, 1971, 1975). For example, the size of a natural population varies constantly and the variations may be small or large; sometimes regular, but in most cases irregular (Schaffer, 1985; Tilman and Wedin, 1991; Hanski et al., 1993; Dennis et al., 1995; Costantino et al., 1997). Understanding the population dynamics and the underlying mechanisms that induce the population variations is the central issue in population ecology (Royama, 1992). Some ecological models, although simple in mathematical expressions, have been designed to study the population temporal dynamics. In particular, the pioneering work in this field was initiated by May (1974, 1976). The significance of May's seminal work is inducing a new research area dealing with the complexities in the population dynamic models. Now, the theory of single-population dynamics is quite well understood compared with the dynamics of interacting populations. Traditionally, interacting populations are usually described by continuous-time models, where only simple dynamics such as stable equilibrium or limit cycles are observed (May, 1972; Segel, 1984). However, for natural

populations whose generations are non-overlapping, continuous-time model is not the best choice. Conversely, discrete-time host–parasitoid models, which are usually described by difference equations, can produce a much richer set of patterns than those observed in continuous-time model (Beddington et al., 1975).

Now, biological scientists have established many complex non-linear mathematical models to account for the dynamic behaviors of these interactions (Kaitala and Heino, 1996; Kaitala et al., 1999). However, ecologists are usually frustrated by the analytical intractability of these mathematical models since the intrinsic non-linearity. An alternative method to resolve the trouble is through numerical simulations. For different parameters and initial conditions, we can iterate the difference equations for thousands time steps and analyze the time series of population size to elucidate the regularity and mechanisms that hidden behind the population dynamics. Recently, many authors have investigated on the complexities of discrete-time host–parasitoid models. Kaitala and Heino (1996) reported the dynamic complexity of host–parasitoid interaction with immunized and non-immunized host. Kaitala et al. (1999), Tang and Chen (2002) showed that many forms of complex dynamics were observed in host–parasitoid interaction model with Holling-type functional response. Xu and Boyce (2005) also demonstrated the dynamic complexity of a mutual interference host–parasitoid model. All these researches relied on a Logistic growth function to analyze

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the dynamics of the host–parasitoid interaction and obtained some intriguing results. However, to our knowledge, two important phenomena are ignored in the previous studies, particularly in this type of host–parasitoid models.

- (1) None considers Allee effect that exists widely in natural world (Allee, 1931). Allee effect indicates scarcity in reproductive opportunities that cause negative growth rates below a critical density threshold (lower bound), which may arise from a number of sources such as difficulties in finding mates, social dysfunction and inbreeding depressing (Dennis, 1989; Lewis and Kareiva, 1993; Kunit and Iwasa, 1996; McCarthy, 1997). Thus, it is meaningful to consider the kind of biological reality in host–parasitoid interactions.
- (2) A basic assumption in above papers is that the encounter between host and parasitoid follows the Poisson distribution, where the parasitoids are distributed randomly in space. However, in the real world, there are seldom cases where the distribution pattern of species individuals can be characterized by Poisson distribution (Pielou, 1969). Generally, a more biological reasonable assumption is that the encounter between host and parasitoid follows the negative binomial distribution, which implies that the parasitoids are aggregated distributed in space (Bliss and Fisher, 1953).

In this paper, we establish a discrete-time host–parasitoid interaction model, in which both Allee effect and aggregated parasitoid are incorporated. The population dynamics will be extensively analyzed. In the next section, we will first propose the host–parasitoid model and give the explanation of all the parameters and variables. Then, a simple mathematical analysis about the stability of the system will be presented. Next, the population dynamics will be fully investigated through numerical simulations. Some interesting findings will be shown as a separate section. At last, we will conclude the results and give a short discussion.

2. Host–parasitoid model

We assume that the growth of host population without parasitoid follows Moran–Ricker dynamics (Moran, 1950; Ricker, 1954), which is given by

$$H_{t+1} = H_t \exp \left[r \left(1 - \frac{H_t}{K} \right) \right], \tag{1}$$

where H_t stands for the population size at time t , r is the intrinsic growth rate, and K is the carrying capacity of the environment.

Since the influence of Allee effect, once the population size is below the lower bound, the species will die out (Allee, 1931). Thus, it is necessary to consider the intraspecific interaction with a lower bound (Lv and Zhao, 2006). Here starting from Eq. (1), we introduce a single-species model with Allee effect. The model is described as

$$H_{t+1} = H_t \exp \left[\frac{r(1 - H_t/K)(H_t - c)}{H_t + m} \right], \tag{2}$$

where Allee effect is denoted as a new term $(H_t - c)/(H_t + m)$. The parameter c is the lower bound for the host and m can be defined as “Allee effect constant”. When H is small and c equals zero, the bigger m is, the stronger the Allee effect will be. Then the per capita growth rate of the host population is slower (the per capita growth rate of the host population is changed from r to $r(H_t/(H_t + m))$). When $c \neq 0$ and $H_t < c$, a simple calculation yields $((r(1 - H_t/K)(H_t - c))/(H_t + m)) < 0$, that implies $\exp[(r(1 - H_t/K)(H_t - c))/(H_t + m)] < 1$. Then, we have $H_{t+1} < H_t$. In other words, the host

population will go extinct, when its population size falls below the lower bound c .

There are a number of factors that may affect the host–parasitoid dynamics, such as Holling-type functional response and mutual interference functional response (Tang and Chen, 2002; Xu and Boyce, 2005). In many host–parasitoid models, the encounters between host and parasitoid are random and can be represented by Poisson distribution. The derivations of this kind of host–parasitoid models are usually based on two assumptions (Misra and Mitra, 2006). (i) following the law of mass action, the number of encounters H_e of the hosts by parasites is proportional to the product of their densities, so that $H_e = aH_tP_t$, P_t is the parasitoid population size in generation t , a is the searching efficiency of the parasitoid on the host; (ii) only the first encounter between a host and a parasite is significant and the encounter is random. We denote n as the random variable of encounters between the host and parasitoid per unit time, which follows the Poisson distribution. In this paper, we do not want to repeat this derivation process and the details can be found in Misra and Mitra (2006).

However, in natural world, most species are neither randomly distributed nor evenly distributed in space. Particularly, parasites are usually observed to be aggregated or clumped distributed, i.e., many hosts harbor a few or no parasites while a few hosts harbor large number of parasites (Begon et al., 1986). Bliss and Fisher (1953) reported that the number of parasitoid on a host usually follows the empirical statistical distribution Negative binomial. Walde and Murdough (1988), according to the data collected by Lessell (1985), reported that the diffusion and search for food of parasitoid are closely related to their attacks upon the host. Then, it is necessary for us to modify the assumptions that encounter between host and parasitoid is random so as to establish a more precise model. We confined our attention to the behavioral responses made by parasitoids whose attacks become more aggregated to host. Because encounters between host and parasitoid are assumed to be aggregated, the number of encounters n can be approximated by Negative binomial distribution, where the probability mass function is given by

$$\mathbf{P}(n) = \frac{\Gamma(k + n - 1)}{n! \Gamma(k - 1)} p^n q^{-k-n}, \quad n = 0, 1, 2, 3, \dots,$$

in which k is clumping parameter. When $k \rightarrow \infty$, Negative binomial distribution becomes Poisson distribution, while $k \rightarrow 0$, it is a logarithmic series. The smaller k is, the stronger the aggregation parasitism is. For our host–parasitoid system, p is actually aP/k . But q does not satisfy $q = 1 - p$ in Binomial distribution, instead, $q = 1 + p$ here. P is the number of parasitoid population, n is the number of encounters per unite time, and aP is the mean of encounters per unite time. So the fraction of the host that remain uninfected can be described as

$$\mathbf{P}(0) = q^{-k} = (1 + p)^{-k} = \left(1 + \frac{aP}{k} \right)^{-k}.$$

Here $n = 0$, since only the first encounter of the host is assumed to be significant and is considered to be enough for a successful transfer of the parasite egg. Thus, function response takes the form of $(1 + (aP_t/k))^{-k}$ that indicate that parasitism following the Negative binomial distribution function proposed by May (1978). Then, the host–parasitoid model with Allee effect for the host and with clumping effect for the parasitoid can be described as

$$\begin{aligned} H_{t+1} &= H_t \exp \left[\frac{r(1 - H_t/K)(H_t - c)}{H_t + m} \right] \left(1 + \frac{aP_t}{k} \right)^{-k} \\ P_{t+1} &= H_t \left[1 - \left(1 + \frac{aP_t}{k} \right)^{-k} \right]. \end{aligned} \tag{3}$$

Here we attempt to analyze the stabilizing and destabilizing effects of Allee effect of host and clumping effect of parasitoid in terms of the lower bound c , the searching efficiency a , the intrinsic growth rate r , and the clumping degree k .

3. Stability analysis

In this section, the existence and local stability analysis of the non-negative equilibria of system (3) are investigated. There are two non-negative equilibrium points for system (3). The total extinction solution whereby no species is able to survive is $E_0 = (0, 0)$ (trivial equilibrium) and the coexistence solution for the two species is $E^* = (H^*, P^*)$ (non-trivial equilibrium).

Once the steady-state solutions are obtained, we can study what happens to the dynamic variables H and P when a steady-state solution is slightly perturbed. Such knowledge is obtained by calculating the Jacobian matrix. System (3) can be rewritten in the form:

$$\begin{aligned} H(t + 1) &= F_1(H_t, P_t) \\ P(t + 1) &= F_2(H_t, P_t), \end{aligned}$$

for which the Jacobian matrix is given by

$$\begin{pmatrix} \frac{\partial F_1}{\partial H} & \frac{\partial F_1}{\partial P} \\ \frac{\partial F_2}{\partial H} & \frac{\partial F_2}{\partial P} \end{pmatrix} \quad (5)$$

The Jacobian matrix of system (3) at the equilibrium point $E_0 = (0, 0)$ is

$$J(0, 0) = \begin{pmatrix} e^{-(cr/m)} & 0 \\ 0 & 0 \end{pmatrix}$$

Accordingly, we find eigenvalues are $\lambda_1 = e^{-(cr/m)}$, $\lambda_2 = 0$. From this, it can be concluded that $E_0 = (0, 0)$ is a stable node ($|\lambda_1| < 1$).

The equilibrium point $E^* = (H^*, P^*)$ satisfies the following equations:

$$\begin{aligned} H^* &= \frac{Qk(Q^{1/k} - 1)}{a(Q - 1)} \\ P^* &= \frac{k(Q^{1/k} - 1)}{a}, \end{aligned} \quad (6)$$

where Q is the net rate of the increase in the host per generation, which in this model is

$$Q = \exp \left[\frac{r(1 - H^*/K)(H^* - c)}{H^* + m} \right]. \quad (7)$$

Note that the equilibrium point $E^* = (H^*, P^*)$ can not be solved in a closed form.

The stability of the steady state at $E^* = (H^*, P^*)$ will now be examined. Using Eqs. (6) and (7), one can calculate the Jacobian matrix (5) of system (3) at (H^*, P^*) :

$$\begin{aligned} \frac{\partial F_1}{\partial H} \Big|_{E^*} &= 1 + \frac{Q^2 k(Q^{1/k} - 1)}{Qk(Q^{1/k} - 1) + ma(Q - 1)} \left[r + \frac{rc}{K} - \frac{2Qrk(Q^{1/k} - 1)}{aK(Q - 1)} - \ln Q \right], \\ \frac{\partial F_1}{\partial P} \Big|_{E^*} &= \frac{Qk(1 - Q^{-1/k})}{1 - Q}, \\ \frac{\partial F_2}{\partial H} \Big|_{E^*} &= 1 - \frac{1}{Q}, \\ \frac{\partial F_2}{\partial P} \Big|_{E^*} &= \frac{k(1 - Q^{-1/k})}{Q - 1}. \end{aligned}$$

Consider the matrix

$$A = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix}$$

where

$$G_{11} = \frac{\partial F_1}{\partial H} \Big|_{E^*}, \quad G_{12} = \frac{\partial F_1}{\partial P} \Big|_{E^*}, \quad G_{21} = \frac{\partial F_2}{\partial H} \Big|_{E^*}, \quad G_{22} = \frac{\partial F_2}{\partial P} \Big|_{E^*}.$$

The characteristic equation is

$$\begin{vmatrix} G_{11} - \lambda & G_{12} \\ G_{21} & G_{22} - \lambda \end{vmatrix} = 0,$$

which may be rewritten in the form

$$\lambda^2 - B\lambda + C = 0, \quad (8)$$

where

$$B = G_{11} + G_{22}, \quad C = G_{11}G_{22} - G_{21}G_{12}.$$

The roots of Eq. (8) are

$$\lambda_{1,2} = \frac{1}{2}(B \pm \sqrt{B^2 - 4C}).$$

Both eigenvalues are real for (λ_R) and $|\lambda_{1,2}| < 1$ if

$$B^2 - 4C > 0 \quad \text{and} \quad -1 < \frac{1}{2}(B \pm \sqrt{B^2 - 4C}) < 1,$$

which yields

$$4C < B^2 < 4C + 4. \quad (9)$$

The eigenvalues $|\lambda_{1,2}| < 1$ become complex (λ_C) and are inside the unit circle in the complex λ -plane for

$$B^2 - 4C < 0 \quad \text{and} \quad B^2 + (4C - B^2) < 4,$$

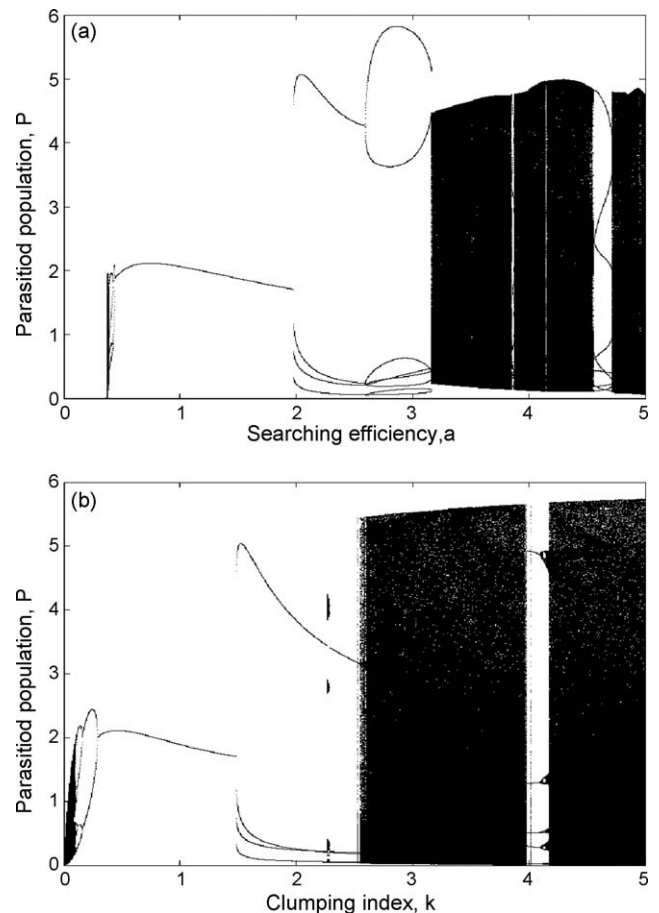


Fig. 1. Bifurcation diagram of parasitoid population in model (3) without Allee effect ($c = 0, m = 0$): (a) respect to the searching efficiency a , the parameters $r = 3, K = 5, k = 1.5$, and the initial values $H_0 = 5, P_0 = 2.5$; (b) respect to the clumping index k , the parameters $r = 3, a = 2, K = 5$, and the initial values $H_0 = 5, P_0 = 2.5$.

which yields

$$B^2 < 4C < 4. \tag{10}$$

If conditions (9) or (10) is satisfied, positive equilibrium point $E^* = (H^*, P^*)$ is stable.

4. Bifurcation analysis

System (3) is a transcendental equation, therefore, we can not obtain the solutions explicitly. Alternatively, to gain preliminary insight into the properties of the dynamical system, we conducted a one-dimensional bifurcation analysis. One-dimensional bifurcation diagrams give information about the dependence of the dynamics on a certain parameter. The analysis is expected to reveal the type of attractor to which the dynamics will ultimately settle down after passing an initial transient phase and within which the trajectory will then remain forever. In this paper, for each numerical simulation, the first 4000 steps are omitted to remove the initial transients, and only the next 1000 steps are used to draw the bifurcation diagrams.

Firstly, we will show the bifurcation diagrams for the two major parameters a and k , where Allee effect is not included ($m = 0, c = 0$). Fig. 1(a) is plotted as a function of the bifurcation parameter a , while Fig. 1(b) is a bifurcation diagram of parasitoid population with respect to the clumping index k . These two bifurcation diagrams are similar to classical bifurcation diagrams, where the routes to chaos is through periodic-doubling and crisis. Particularly, for a large range of these parameters, the host and

parasitoid can coexist, although the system dynamics are chaotic and non-periodic. The first question that we are interested in is what the dynamics is when Allee effect is incorporated. In other word, whether these chaotic attractors persist or disappear when Allee effect is included? In the following paragraphs, our major concern is to elucidate the influence of Allee effect in this host-parasitoid system.

Our first aim is to illustrate how the system dynamics respond to the principle parameter—the lower bound c . As Fig. 2 shows, it seems that the lower bound is an important factor affecting the host-parasitoid dynamics. From Fig. 2(a), we see the host-parasitoid system begins with period-4 fluctuations. As c approaches to 0.02913, system experienced a period-doubling, from period-4 to period-8. Unlike the common period-doubling route to chaos, here we observe period-8 within a small region. Then it experienced a period-halving bifurcations, from period-8 to period-4 at $c = 0.05315$. When the parameter c further increases, the system suddenly changes into quasiperiodic at $c = 0.05688$. In the phase plane this appearance of a closed curve, where the points never coincide, is an indication of quasiperiodic. After that, from Fig. 2(b) (details plotted in Fig. 2(a)), quasiperiodic attractor abruptly disappears and goes period-5 at $c = 0.12352$, thus constituting a type of attractor crisis. Lastly, parasitoid suddenly vanishes at $c = 0.15964$. As we can see, when the parameter c increases, although the steady states were replaced by some unstable dynamics, there is not evidence of occurrence of chaos. Meanwhile, we also frequently observed the sudden changes of attractors (crisis), where multiple attractors coexist (see the following section).

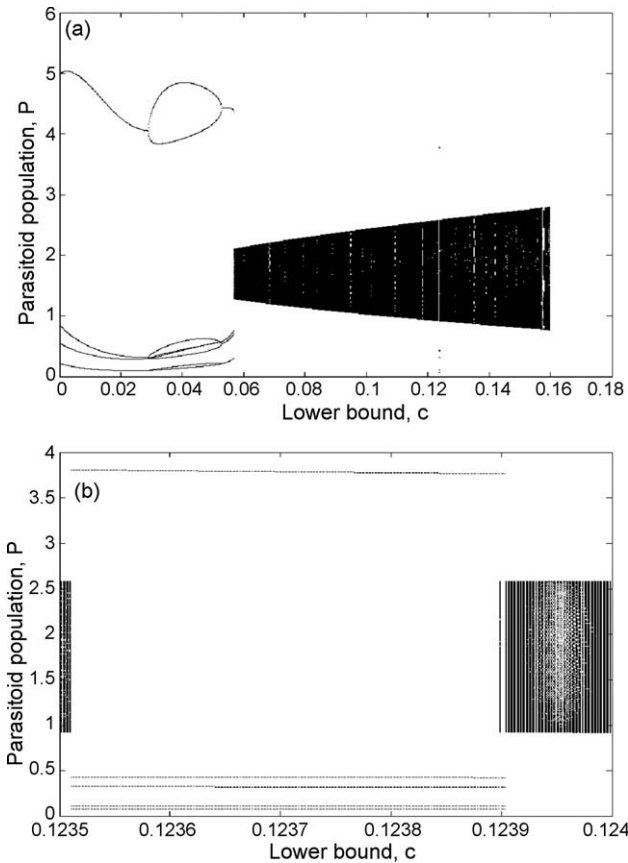


Fig. 2. Bifurcation diagram of parasitoid population P with respect to the lower bound c in model(3). (a) parasitoid population size P and (b) gives details of (a). The parameters $r = 3, a = 2, K = 5, k = 1.5, m = 0.0002$, and the initial values $H_0 = 5, P_0 = 2.5$.

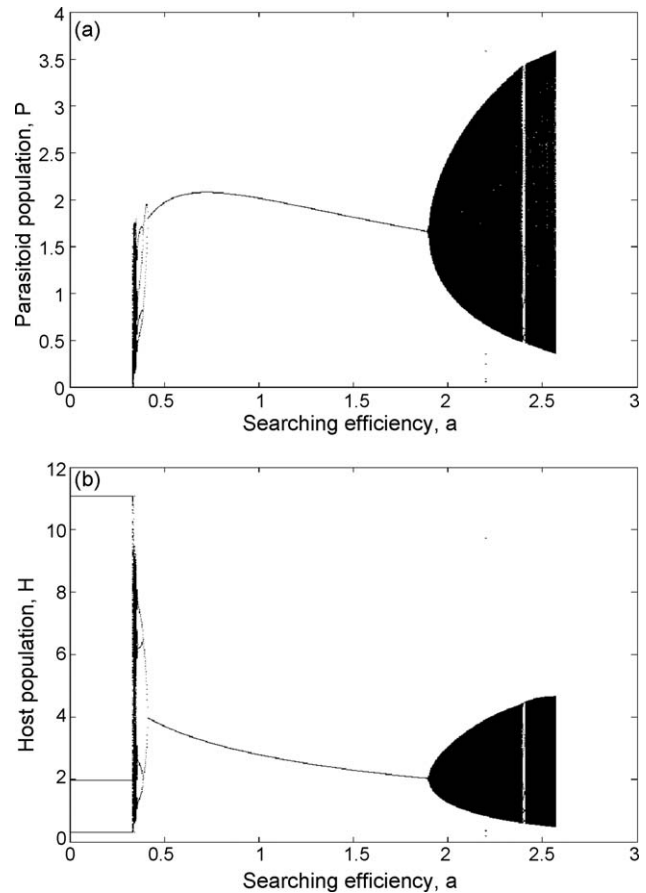


Fig. 3. Bifurcation diagram of parasitoid population and host population with respect to the searching efficiency a in model (3). (a) parasitoid population size P and (b) host population size H . The parameters $r = 3, K = 5, k = 1.5, c = 0.1, m = 0.0002$, and the initial values $H_0 = 5, P_0 = 2.5$.

Now, we are in position to show how the bifurcation diagrams in Fig. 1 are changed, when Allee effect is included. For the purpose of comparison, we will draw the bifurcation diagrams for both a and k . In order to illustrate the system dynamics explicitly, the bifurcation diagrams will also be given here.

(1) Fig. 3 illustrates the bifurcation diagram of model (3) for the parasitoid and the host population dynamics. The bifurcation diagrams are almost similar except the left part, where parasitoid goes extinct and host is 3-period dynamics, so only parts of Fig. 3(a) is magnified in Fig. 4. The parasitoid population size is plotted as a function of the bifurcation parameter a and the parameter values are $c = 0.1$, $m = 0.0002$. From Fig. 3(a), we see that the system experiences a period-doubling reversal from chaotic dynamics at $a = 0.3335$ to

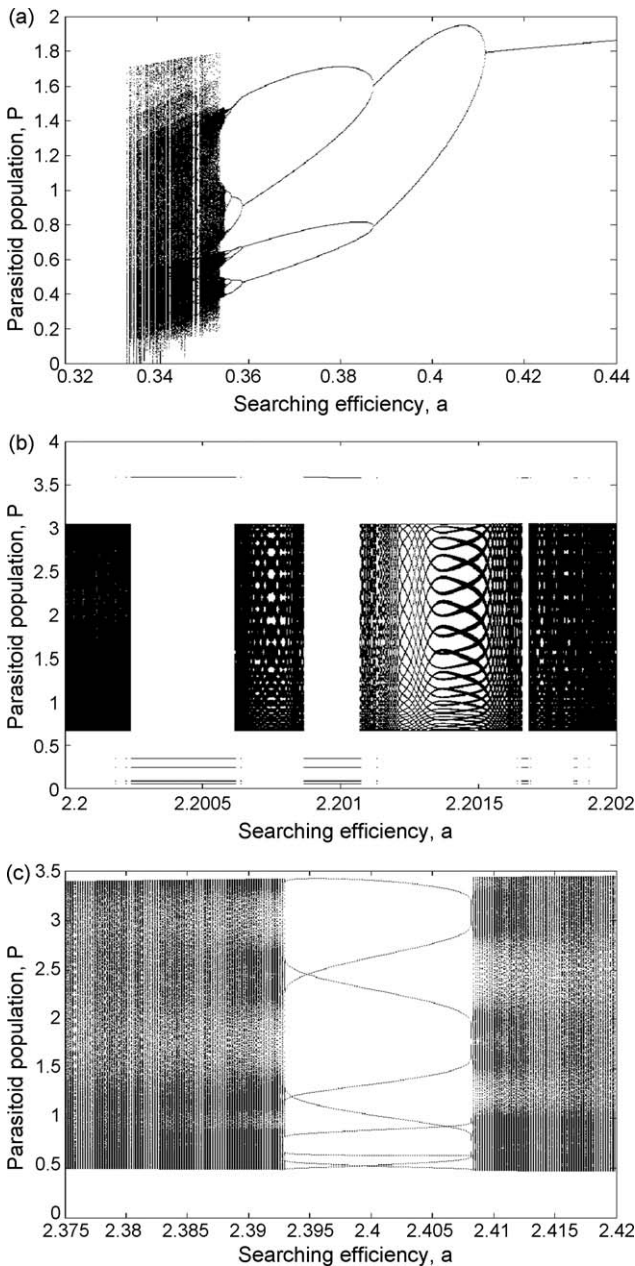


Fig. 4. Magnification of part of Fig. 3(a): (a) $0.32 < a < 0.44$; (b) $2.2 < a < 2.202$; and (c) $2.375 < a < 2.42$.

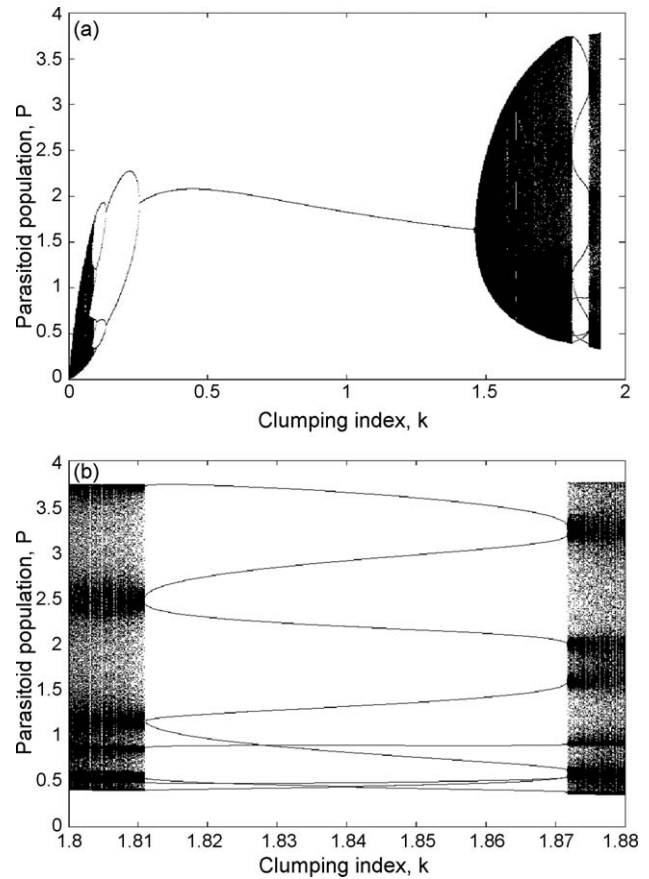


Fig. 5. Bifurcation diagram of parasitoid population with respect to the clumping index k in the host–parasitoid model (3) for (a) parasitoid population size P and (b) give details of (a). The parameters $r = 3$, $a = 2$, $K = 5$, $c = 0.1$, $m = 0.0002$, and the initial values $H_0 = 5$, $P_0 = 2.5$.

period-32, period-16, period-8 and then period-4, period-2, and at $a = 0.4134$ stable coexistence (details plotted in Fig. 4(a)). When the parameter a further increases, the system dynamics will quasiperiodic through a Hopf bifurcation (the

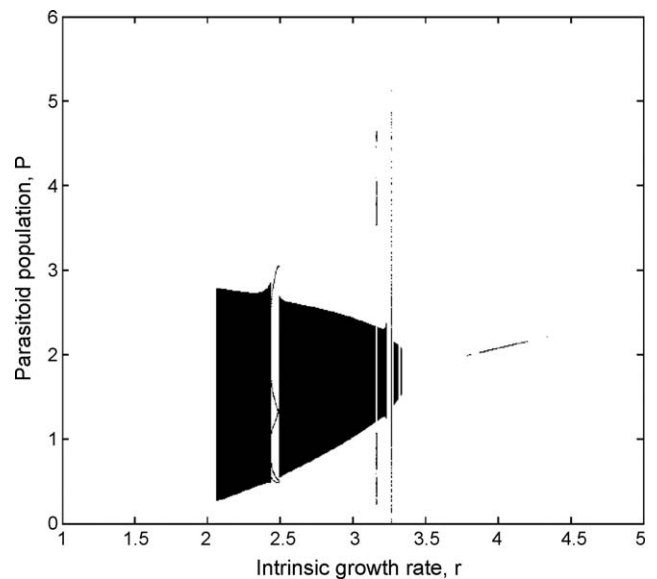


Fig. 6. Bifurcation diagram of parasitoid population with respect to the intrinsic growth rate r in the host–parasitoid model (3). The parameters $a = 2$, $K = 5$, $k = 1.5$, $c = 0.1$, $m = 0.0002$, and the initial values $H_0 = 5$, $P_0 = 2.5$.

critical value is $a = 1.6362$). Generally, frequency-lockings usually accompany with quasiperiodicity. Here, this phenomenon is also observed. As the bifurcation diagram Fig. 4(b) shows, when a is slightly increased beyond 2.2003, the quasiperiodic attractor abruptly disappears, thus constituting a type of attractor crisis. At the same time, period-5 attractor arises. When a increases beyond 2.394, crisis occurs again (details plotted in Fig. 4(c)).

(2) For the parameter k , bifurcation diagrams for model (3) illustrates the stabilizing effect of the aggregation of parasitoid attacks. Fig. 5(a) shows that the system will first experience a period-doubling reversal from chaotic dynamics with periodic windows to period-32, period-16, period-8, period-4, period-2, and then becomes stable at $k = 0.2568$. It can be clearly observed that host and parasitoid can coexist stably in the range of $[0.2568, 1.4349]$. As the parameter increases from 1.4349, the model (3) goes through quasiperiodicity with

frequency-lockings that includes period-50, period-41, period-32, attractor crisis. Fig. 5(b) illustrates an example of periodic window within the region of quasiperiodicity. Finally, parasitoid goes extinct at $k = 1.9147$. Through extensive numerical simulations, we find that the clumping effect can be considered as a stabilizing factor, especially for moderate clumping level.

Next, we will shed light on another important parameter r . In Fig. 6, the parasitoid population is plotted as a function of intrinsic growth rate r , and the initial values are $H_0 = 5, P_0 = 2.5$. Fig. 7 gives details of Fig. 6, and it shows a complex dynamical structure containing bifurcation phenomena. Fig. 7(a) shows a periodic window with a cascade of periodic attractors. Fig. 7(b) shows the window, which is not a periodic window with a cascade of periodic

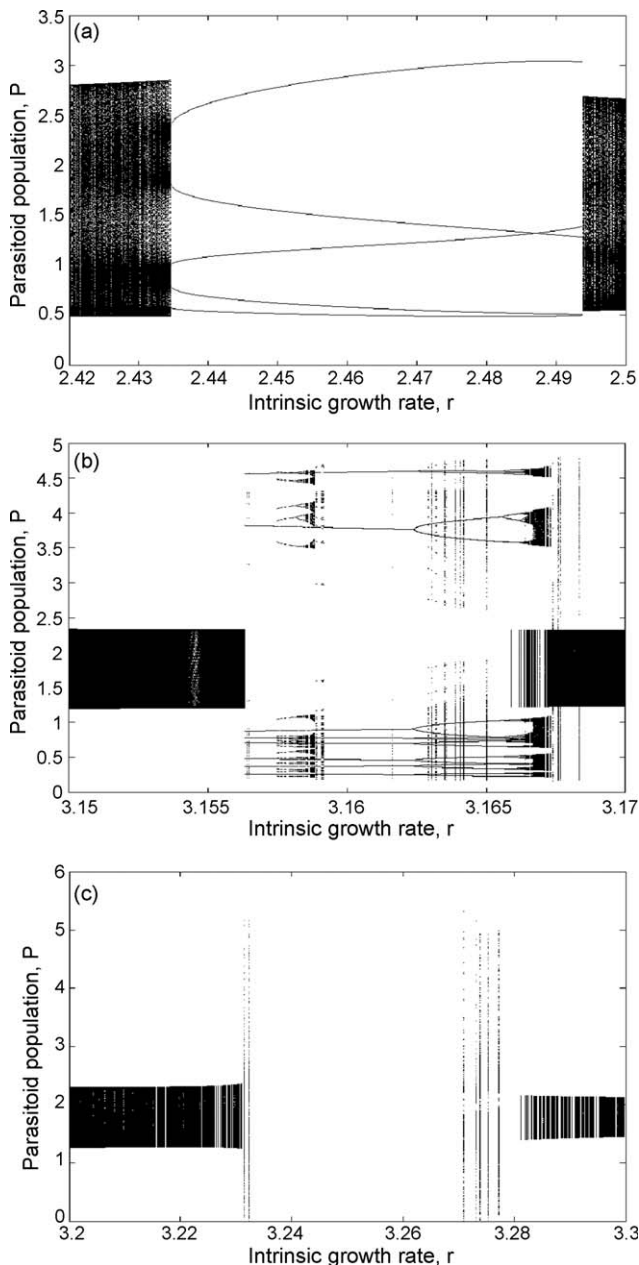


Fig. 7. Magnification of part of Fig. 6: (a) $2.42 < r < 2.5$; (b) $3.15 < r < 3.17$; and (c) $3.2 < r < 3.3$.

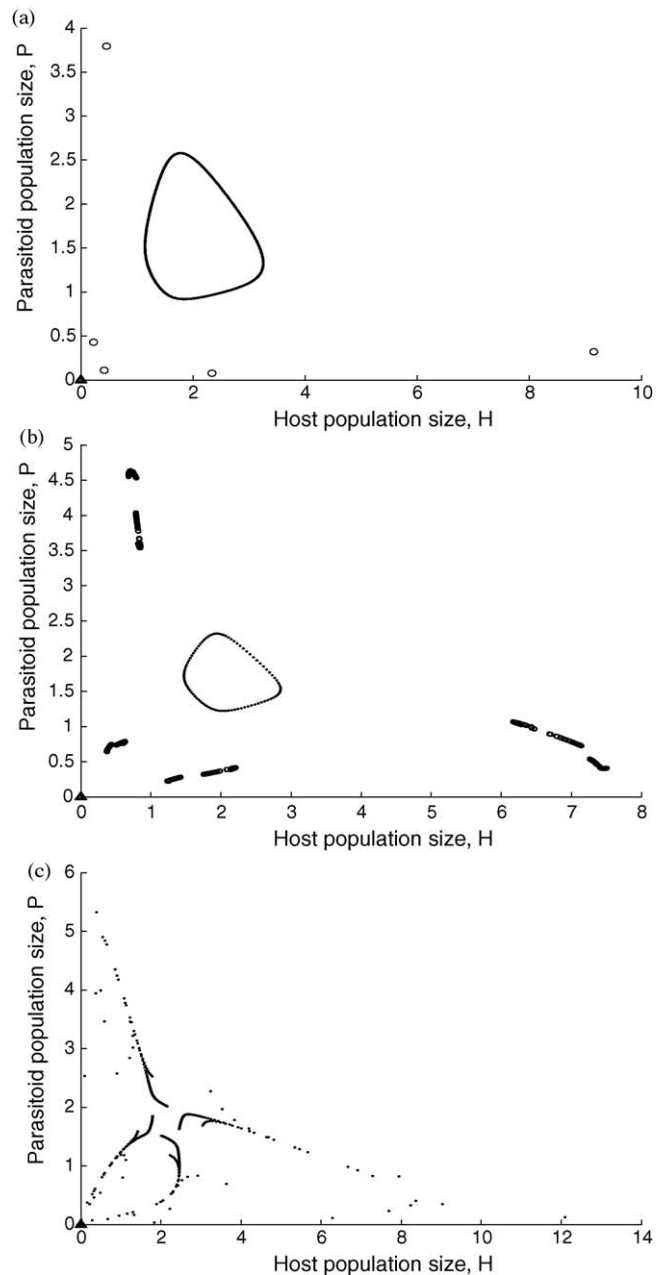


Fig. 8. Multiple attractors coexist in system: (a) $r = 3, a = 2, K = 5, k = 1.5, m = 0.0002$: point equilibrium, period-5 and quasiperiodic attractors at $c = 0.1236$; (b) $a = 2, K = 5, c = 0.1, m = 0.0002$: point equilibrium, quasiperiodic and chaotic attractors at $r = 3.167$; (c) $a = 2, K = 5, c = 0.1, m = 0.0002$: point equilibrium and chaotic attractors at $r = 3.27336$.

attractors in the range of $r \in [3.1563, 3.1683]$, includes other complex dynamic patterns. Fig. 7(c) shows another complex dynamics of attractor crisis. As r increases from 3.231 to 3.2812, quasiperiodicity attractor abruptly disappears and parasitoids go extinct. But for several concrete r , such as $r = 3.27136$, $r = 3.27137$, parasitoid persist in the form of chaos. Another strange phenomenon that attracts our interest is the coexistence of multi-attractors, where system are sensitive to initial conditions. When initial conditions are slightly changed, the system dynamics will be qualitatively different. We will give more detailed descriptions in the next section.

After a tedious bifurcation analysis, we can draw a short conclusion without further excessive discussions. By comparing the bifurcations diagrams with and without Allee effect, we notice that the chaotic parameter range shrinks, although complicated dynamics are not thoroughly removed. As we know, sensitivity to initial conditions is another important characteristic of complex dynamics (Kaitala and Heino, 1996). Actually, many interesting phenomena are also observed in the host–parasitoid system with Allee effect and aggregation. In the next section, we will investigate the influence of Allee effect on host–parasitoid system from the perspective of dynamic complexities.

5. Non-unique attractors and period alternation

First, we will give an example of coexistent attractors. Revising Fig. 2, there are sensitive ranges where multiple attractors coexist. As Fig. 8(a) shows, trivial equilibrium and period-5 coexist with quasiperiodic attractors at $c = 0.1236$. Another example comes from the bifurcation diagrams (Fig. 7(b) and (c)) with respect to the parameter r , there are also several ranges where multiple attractors coexist. In the range of $[3.1563, 3.1683] \cup [3.231, 3.2812]$, two or more attractors coexist, i.e., trivial equilibrium, quasiperiodic and chaotic attractors at $r = 3.167$ (Fig. 8(b)), trivial equilibrium and chaotic attractors at $r = 3.27336$ (Fig. 8(c)). Here, the equilibrium point is trivial, which means that the population goes extinct. There are so many examples of coexistent attractors in the host–parasitoid system that we can not illustrate all of them explicitly. In fact, what we are really interested is the basins of attraction, especially complex structure of basins of attraction (Grebogi et al., 1983; Testa and Held, 1983; Peitgen et al., 1992; Kaitala and Heino, 1996; Kaitala et al., 1999).

Now, we will give an example to illustrate the basins of attraction with and without Allee effect. Fig. 9(a)–(c) show the basins of attraction of two coexisting attractors. Through magnify

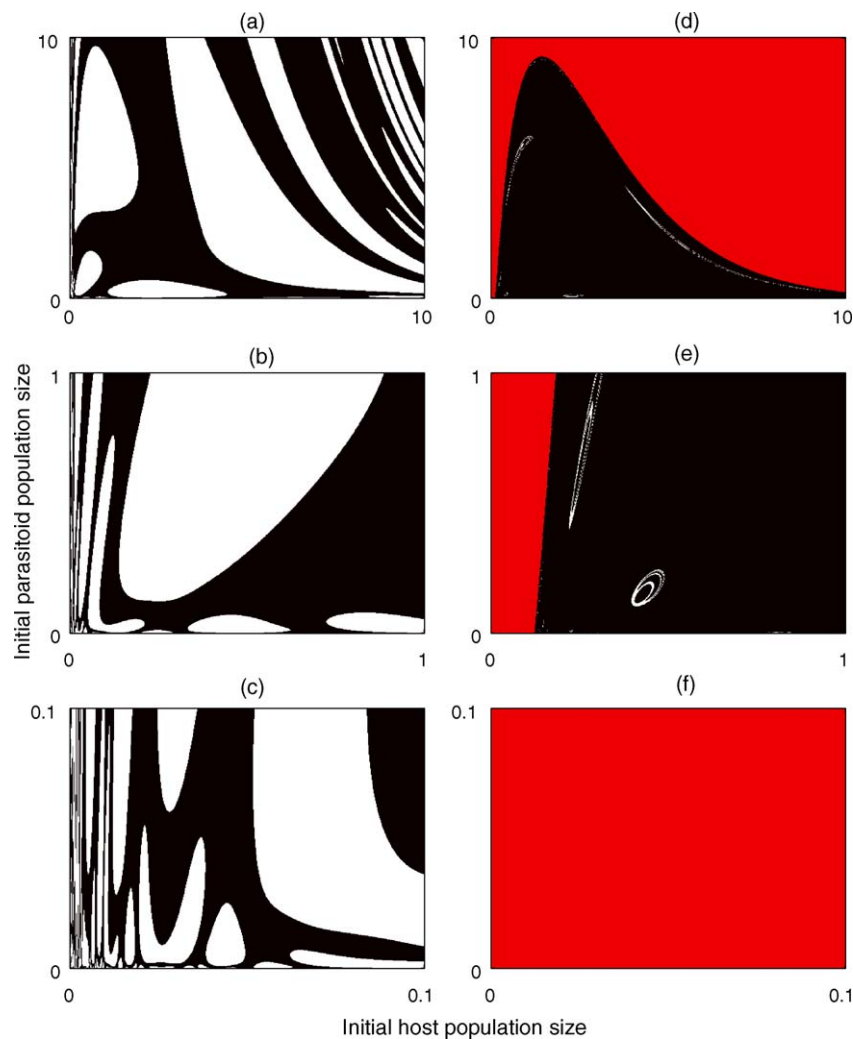


Fig. 9. The basins of attraction for Non-unique attractors ($r = 3$, $a = 2$, $K = 5$, $k = 1.5$): the step-size in the initial values: (a and d) 0.02; (b and e) 0.002; (c and f) 0.0002. The scopes of initial values: (a and d) (0, 10]; (b and e) (0, 1]; (c and f) (0, 0.1]. (a–c) host–parasitoid model without lower bound for the host ($c = 0$, $m = 0$): the white and black areas are the basins of attraction for period-4 and non-trivial equilibrium. (d–f) host–parasitoid model incorporating Allee effect ($m = 0.0002$, $c = 0.1236$, others parameters is same as (a–c)): the red area: the basins of trivial equilibrium; white area: the basins of period-5.

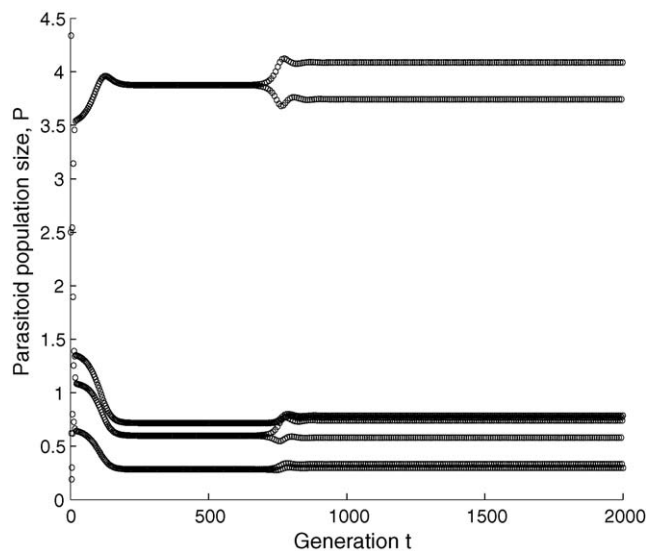


Fig. 10. Period alternation of Parasitoid population dynamics for $r = 3$, $K = 5$, $k = 2$, $c = 0.1$, $m = 0.0002$, $a = 1.4$, and the initial values $H_0 = 5$, $P_0 = 2.5$.

a corner of the basin step by step, we found that the structure of these basins are similar. Although we do not test the fractal strictly, the self-similarity is obviously. However, when Allee effect is added, the property of self-similarity is disrupted. Fig. 9(d)–(f) give the basins of attraction with the same parameters in (a)–(c) except c and m . Unlike the left column (a)–(c), the basin boundaries of attractions are almost simple sets. Although the non-ubiquity of attractors are not totally eliminated, the structure of the basin of attraction is altered. The example here gives us a clue about the influence of Allee effect on dynamical complexity of host–parasitoid system. Strictly speaking, we can not arbitrarily declare that self-similarity is eliminated by Allee effect. But at least, we can say that the sensitivity of the population dynamics to initial conditions is reduced. In one word, Allee effect still plays a positive role in stabilizing host–parasitoid system in a broad sense.

Another dynamical complexities in many host–parasitoid system are intermittent chaos and Supertransients (Kaitala and Heino, 1996; Kaitala et al., 1999; Tang and Chen, 2002; Xu and Boyce, 2005; Lv and Zhao, 2006; Zhu and Zhao, 2007). Intermittency is characterized by switches between apparently regular and chaotic behavior. The behavior is completely aperiodic and chaotic. Supertransients are used to denote an unusually long convergence to an attractor. Intermittent chaos and Supertransients are two routes leading to chaos. When Allee effect is not incorporated, both the two phenomena are observed. Here, we do not want to give these examples as figures. However, we find both these phenomena are eliminated when Allee effect is included. Unexpectedly, we indeed find another important property—abrupt changes of periodic attractors over the long time-scale. Fig. 10 shows the abrupt alternation of period. We can see that after about 700 generations 4-period fluctuation is suddenly changed to 8-period. The changes of attractor is from one periodic attractor to another periodic attractor, which is inconsistent with intermittent chaos or Supertransients. Even though the abrupt change is also one kind inconsistency of attractors, the dynamical complexity is more or less reduced. At least, chaos is eliminated in the process of change. Similarly, we notice that the dynamical complexity of host–parasitoid system is reduced in a sense by Allee effect.

6. Conclusion and discussion

In this paper, we established a brand-new discrete-time host–parasitoid model, in which both Allee effect for the host and

aggregated parasitoid are simultaneously incorporated. Generally speaking, our model is more biological reasonable than some previous host–parasitoid models. Since the strong non-linearity, we can hardly obtain any meaningful information about the stability of the equilibrium from mathematical analysis. However, an extensive bifurcation analysis through numerical simulations still elucidate all possible dynamics that the system can exhibit. Particular, we can gain some basic imagination about the role of Allee effect on host–parasitoid system. Now, we will give a short discussion based on the conclusions obtained from this study.

Our first conclusion is about the relationship between dynamical complexity and Allee effect. First, we have to admit that the host–parasitoid model can exhibit many kind of complex dynamics. However, through comparing the bifurcation diagrams without and with Allee effect, we find that the range of chaos are compressed, when Allee effect is included. Therefore, Allee effect can be considered as one stabilizing effect to some extent. However, another inharmonious phenomenon, in this study is the occurrence of quasiperiodicity the bifurcation diagram with respect to parameter c . Although the dynamics is unstable, there is not evidence of occurrence of chaos. We notice that the occurrence of quasiperiodicity does not qualitatively change the conclusion.

Moreover, as long as the stabilizing effect of Allee effect, there exist supporting evidence from two aspects. The first is related to basins of attraction. The basins of attraction were defined as the set of the initial conditions whose trajectories asymptotically approach that attractor as time increases. The properties of self-similarity and fractal basin boundaries of the basins of attraction were found in many other models (Kaitala and Heino, 1996; Kaitala et al., 1999; Tang and Chen, 2002; Xu and Boyce, 2005) except host–parasitoid model with Allee effect. Fractal basins of attraction implies the dynamics of the host–parasitoid system will change alternately among different attractors, when a small external perturbation is induced. However, in this study, a comparison between the basins of attraction with and without Allee effect shows that the sensitivity to initial conditions was reduced. In other word, population dynamics become resistable to external disturbances. The second evidence is in relevance to the changes of attractors. Two kinds of change of attractors changes are included: intermittent chaos and Supertransients. Intermittent chaos and Supertransients are two approaches from stable period to chaos and were also reported in discrete-time single-species models (Murdoch and Oaten, 1975), epidemiological models (Koella and Doebeli, 1999), spatially structured ecological models (Hastings and Higgins, 1994), and Holling-type functional response host–parasitoid models (Kaitala et al., 1999; Tang and Chen, 2002). However, we find that all these two kinds of changes are altered when Allee effect is considered. The new kind of change of attractor in this study is from periodic attractor to periodic attractor. It means Allee effect in host exclude the presence of chaos in the dynamics. Natural populations usually fluctuate irregularly in both period and amplitude. The mechanisms leading to this irregular fluctuations include two aspects—internal and external. The internal mechanism is referred to as the intrinsic interactions, such as interspecific and intraspecific interactions. The most important feature of internal mechanisms is non-linearity, which caused many complex dynamics in deterministic models. The external mechanism is referred to as the disturbance from the environment, which is also called as environmental noises. The debate between these mechanisms last for a true long time, and we do not intend to mention this topics too much here. Our intention is to link the real data and the mathematical models together. Generally, the dynamics predicted from these mathematical models is usually very intrigued, while the dynamic behavior of real data is much simpler. Since this obvious discrepancy, many ecologists refused to accept the predictions from the deterministic

mathematical models and prefer to accept environmental noise as the major driving force. However, our deterministic model, where Allee effect is added, can produce more simpler dynamics. Our result, although can not fully solve the discrepancy, can at least strengthen the utility of mathematical models in exploring populations.

Dynamic complexities are the common characteristics in a variety of population models. Identifying the complex dynamics in natural population data has remains a major challenge in ecological studies. For example, chaos is usually observed in mathematical models, but detecting chaos from real population data is a tough work. There is no clear evidence that chaos actually exists in natural populations. As far as chaos in natural populations, there are two controversial viewpoints. On the one hand, some scientists insisted that chaos does exist in natural world, but can not clearly detected from short time series of real data (May, 1972; May and Oster, 1976). One the other hand, other scientists proposed that, as one outcome of non-linear density dependence, chaos can be eliminated by the interspecific interactions, such the mutual interaction within a food web, immigration, omnivory and habitat-heterogeneity (Turchin and Taylor, 1992; Ellner and Turchin, 1995; Patten, 1997; Xu and Li, 2002a, b). However, besides chaos, a variety of other dynamic complexities are observed in many population models (Kaitala and Heino, 1996; Kaitala et al., 1999; Tang and Chen, 2002; Xu and Boyce, 2005). The increasing number of potential complexities predicted by the theoretical models causes investigating natural population dynamics more difficult. From our study, we verified that dynamic complexities are reduced by incorporating one intraspecific mechanism-Allee effect. Our finding suggests that dynamic complexities might be eliminated through some balancing efforts in the nature, that is the reason why the data from the natural population looks simpler. This conjecture is more or less similar to some previous viewpoints (Turchin and Taylor, 1992; Ellner and Turchin, 1995). From this perspective of linking real data and theoretical predictions, we speculate that the task in modeling population dynamics is to avoid dynamic complexities rather to introduce them.

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References

- Allee, W.C., 1931. *Animal Aggregations: A Study in General Sociology*. University of Chicago Press, Chicago.
- Beddington, J.R., Free, C.A., Lawton, J.H., 1975. Dynamic complexity in predator-prey models framed in difference equations. *Nature* 255, 58–60.
- Begon, M., Harper, J.L., Townsend, C.R., 1986. *Ecology: Individual, Populations and Communities*. Blackwell Scientific Publications, London.
- Bliss, C.I., Fisher, R.A., 1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. *Biometrics* 9, 176–200.
- Costantino, R.F., Desharnais, R.A., Cushing, J.M., Dennis, B., 1997. Chaotic dynamics in an insect population. *Science* 275, 389–391.
- Dennis, B., 1989. Allee effects: population growth, critical density, and the chance of extinction. *Nat. Resour. Model* 3, 481–538.
- Dennis, B., Desharnais, R.A., Cushing, J.M., Costantino, R.F., 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. *Ecol. Monogr.* 65, 261–281.
- Ellner, S., Turchin, P., 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Natural.* 145, 343–375.
- Grebogi, C., Ott, E., Yorke, J.A., 1983. Fractal basin boundaries, long-lived chaotic transients, and unstable-unstable pair bifurcation. *Phys. Rev. Lett.* 50, 935–938.
- Hanski, I., Turchin, P., Korpimi, E., Henttonen, H., 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364, 232–235.
- Hassell, M.P., 1971. Mutual interference between searching insect parasites. *J. Anim. Ecol.* 40, 473–486.
- Hassell, M.P., 1975. Density-dependence in single-species populations. *J. Anim. Ecol.* 44, 283–295.
- Hastings, A., Higgins, K., 1994. Persistence of transients in spatially structured ecological models. *Science* 263, 1133–1136.
- Kaitala, V., Heino, M., 1996. Complex non-unique dynamics in simple ecological interactions. *Proc. R. Soc. Lond. B* 263, 1011–1015.
- Kaitala, V., Ylikarjula, J., Heino, M., 1999. Dynamic complexities in host-parasitoid interaction. *J. Theor. Biol.* 197, 331–341.
- Koella, J.C., Doebeli, M., 1999. Population dynamics and the evolution of virulence in epidemiological models with discrete host generations. *J. Theor. Biol.* 198, 461–475.
- Kunin, W.E., Iwasa, Y., 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theor. Popul. Biol.* 49, 232–263.
- Lessell, C.M., 1985. Parasitoid foraging: should parasitism be density dependent. *J. Anim. Ecol.* 54, 27–41.
- Lewis, M.A., Kareiva, P., 1993. Allee dynamics and the spread of invading organisms. *Theor. Popul. Biol.* 43, 141–158.
- Lv, S.J., Zhao, M., 2006. The dynamic complexity of a host-parasitoid model with a lower bound for the host. *Chaos Solitons Fractals*.
- May, R.M., 1972. Limit cycles in predator-prey communities. *Science* 177, 900–902.
- May, R.M., 1974. Biological population with non-overlapping generations: stable points, stable cycles and chaos. *Science* 186, 645–647.
- May, R.M., 1976. Simple mathematical models with very complicated dynamics. *Nature* 261, 459–467.
- May, R.M., Oster, G.F., 1976. Bifurcations and dynamic complexity in simple ecological models. *Am. Natural.* 110, 573–599.
- May, R.M., 1978. Host-parasitoid system in patchy environments: a phenomenological model. *J. Anim. Ecol.* 47, 833–843.
- McCarthy, M.A., 1997. The Allee effect, finding mates and theoretical models. *Ecol. Model.* 103, 99–102.
- Misra, J.C., Mitra, A., 2006. Instabilities in single-species and host-parasite systems: period-doubling bifurcations and chaos. *Comput. Math. Appl.* 52, 525–538.
- Moran, P.A.P., 1950. Some remarks on animal population dynamics. *Biometrics* 6, 250–258.
- Murdoch, W.W., Oaten, A., 1975. Predation and population stability. *Adv. Ecol. Res.* 9, 1–25.
- Patten, B.C., 1997. Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus pallasi*) in the Adirondack Mountains of New York. *Ecol. Model.* 100, 11–42.
- Peitgen, H.O., Jürgens, H., Saupe, D., 1992. *Chaos and Fractals*. New Frontier of Science. Springer-Verlag, New York.
- Pielou, E.C., 1969. *An Introduction to Mathematical Ecology*. Wiley-Interscience, New York.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish Res. Board Can.* 11, 559–623.
- Royama, T., 1992. *Analytical Population Dynamics*. Chapman & Hall.
- Segel, L., 1984. *Modeling Dynamic Phenomena in Molecular and Cellular Biology*. Cambridge University Press, Cambridge.
- Schaffer, W.M., 1985. Order and chaos in ecological systems. *Ecology* 66, 93–106.
- Tang, S.Y., Chen, L.S., 2002. Chaos in functional response host-parasitoid ecosystem models. *Chaos Solitons Fractals* 13, 875–884.
- Testa, J., Held, G.A., 1983. Study of a one-dimensional map with multiple basins. *Phys. Rev. A* 28, 085–089.
- Tilman, D., Wedin, D., 1991. Oscillations and chaos in the dynamics of a perennial grass. *Nature* 353, 653–655.
- Turchin, P., Taylor, A.D., 1992. Complex dynamics in ecological time series. *Ecology* 73, 289–305.
- Walde, S.J., Murdoch, W.W., 1988. Spatial density dependence in parasitoid. *Ann. Rev. Entomol.* 33, 441–446.
- Xu, C.L., Boyce, M.S., 2005. Dynamic complexities in a mutual interference host-parasitoid model. *Chaos Solitons Fractals* 24, 175–182.
- Xu, C.L., Li, Z.Z., 2002a. Effect of diffusion and spatially varying predation risk on the dynamics and equilibrium density of a predator-prey system. *J. Theor. Biol.* 219, 73–82.
- Xu, C.L., Li, Z.Z., 2002b. Influence of intraspecific density dependence on a three-species food chain with and without external stochastic disturbances. *Ecol. Model.* 155 (1), 71–83.
- Zhu, L., Zhao, M., 2007. Dynamic complexity of a host-parasitoid ecological model with the Hassell growth function for the host. *Chaos Solitons Fractals*.