

**COMPLEX NON-UNIQUE DYNAMICS IN A HOST-PARASITOID
MODEL INCORPORATING CLUMPING EFFECT**

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ABSTRACT: In this paper, Computer simulation is used to study the influence of clumping effect on the dynamic complexities of a discrete-time host-parasitoid model. We report here parasitoid aggregation may be a strong stabilizing or destabilizing factor. Using computer simulation, many forms of complex dynamic are observed, including Hopf bifurcation reversal, period-halving, attractor crises, chaotic bands with narrow or wide periodic windows, intermittent chaos, and supertransient behavior. Several types of attractors, e.g. point equilibrium vs. chaotic, periodic vs. quasiperiodic and quasiperiodic vs. chaotic attractors, may coexist in the same mapping. This non-uniqueness also indicates that the bifurcation diagrams, or the routes to chaos, depend on initial conditions and are therefore non-unique. The basins of attraction, defining the initial conditions leading to a certain attractor, may be fractal set. The fractal property observed is the pattern of self-similarity. The numerical results indicate that computer simulation is a useful method of investigating complex dynamic systems. We also conclude that non-unique dynamic, associated with the extremely complex structure of the basin boundaries, can have a profound effect on our understanding of the dynamical processes of nature.

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1. INTRODUCTION

Simple ecological models have been designed and studied since the pioneering work of sir. Robert May (see [1], [2]). By his profound discoveries, a new research area dealing with the complexities in the population dynamic models was initiated.

The theory of single-population dynamic is now quite clearly understood as compared with the dynamic of interactive population. Ecologists have focused on studying interspecific interaction of continuous-time host-parasitoid models of two variables, where dynamic includes only stable equilibrium or limit cycles (see [3]). Natural populations whose generations are non-overlapping can be modeled by differential equations that describe how the population evolves in discrete time-steps and in the discrete-time host-parasitoid models the dynamics can produce a much richer set of patterns than those observed in continuous-time model (see [4]). It is not easy to analyze its global stability by qualitative method, so people often study the dynamic complexity of discrete-time host-parasitoid models by computer simulation. Through simulation, one can test model parameters and find out the stability domain of the parameters, through which to optimize the system by artificial control and to improve the stability of the system. Recently, many authors have adopted computer simulation to investigate the complexities of discrete-time hostparasitoid models. Kaitala and Heino (see [5]) reported the dynamics complex of host-parasitoid interaction with immunized and non-immunized host. Tang and Chen (see [6]) and Xu and Mark (see [7]) show that many forms of complex dynamics are observed not only in host-parasitoid interaction model with Holling-type functional response but also a mutual interference host-parasitoid model. Clamer and Pugliese (see [8]) studied the dynamics of a 2 hostCparasitoid model assuming, and obtained explicit conditions for the existence of an equilibrium where the two host species coexist with the parasitoid. However, if host demography is density-independent, equilibrium coexistence is impossible. Liu and Chu Y (see [9]) proved that a discrete-time biological model and its dynamical behaviors in detail, the existence and stability of the equilibrium of the model are qualitatively discussed. Din (see [10]) discussed qualitative behavior of a discrete-time density-dependent predator-prey model, the existence and uniqueness of positive steady-state, permanence, local and global behavior of unique positive equilibrium point and the rate of convergence of positive solutions that converge to the unique positive equilibrium point of this model are studied. Din (see [11]) considered the comprehensive dynamics of a density-dependent hostCparasitoid system with the Hassell growth function for the host population.

Here, using computer simulation, the dynamic complexities of a model that includes the density-dependent response in the parasitoid were qualitatively analyzed. This density-dependent response acts on foraging ability of parasitoid. And the ex-

pression of the functional response is dependent on a clumping index that describes whether the parasitoids attacks on host become more aggregated or not. We shall demonstrate that the clumping effect not only can stabilize the dynamics but may destabilize it as well. Many complexities relating to clumping effect are observed, including Hopf bifurcation reversal, period-halving, attractor crises, chaotic bands with narrow or wide periodic windows, non-unique dynamics with multiple attractors, fractal basins of attraction, intermittent chaos, and supertransient.

2. HOST-PARASITOID INTERACTION

The starting point of our modeling studies is the well-known deterministic single-species Moran-Ricker (see [12], [13]) dynamic given as.

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

where H_t is the host population size in generation t , $t = 0, 1, 2, \dots$, r is the intrinsic growth rate, and K is the carrying capacity of the environment. The steady state of the Moran-Ricker dynamics, satisfying $H_{t+1} = H_t$, is $H^* = K$, and the dynamics are asymptotically stable when $0 < r < 2$, unstable with different periodic attractors when $2 < r < 2.6924$, and chaotic (with periodic windows) when $r > 2.6924$.

There are a number of factors that may affect the host-parasitoid dynamic. We confine our attention to the behavioral responses made by parasitoid whose attacks become more aggregated to host. Here we use function response as the form of $\left(1 + \frac{aP}{K}\right) - K$ that is the expression for parasitism following the negative binomial distribution function proposed by May (see [14]). Then, the host-parasitoid model incorporating clumping effect that we investigate follows as

$$\begin{cases} H_{t+1} = H_t \exp \left(r \left(1 - \frac{H_t}{K} \right) \right) \left(1 + \frac{aP_t}{k} \right)^{-k}, \\ P_{t+1} = H_t \left[1 - \left(1 + \frac{aP_t}{k} \right)^{-k} \right]. \end{cases} \quad (2)$$

Here P_t is the parasitoid population size in generation t , a is the searching efficiency of the parasitoid on the host, and the k is the clumping index of the negative binomial distribution. As k declines parasitoid attacks become more aggregated.

Typically, Mays model exhibits an abrupt transition from stable to oscillatory dynamic as the value of the aggregation term k , increases to values greater than 1. If $k < 1$, the host-parasitoid interaction is stable. We observed if $k \rightarrow \infty$, the function response of model (2) became $e - ap$, then the model (2) became Nicholson-Bailey (see [15]) host-parasitoid equation, which assumed the parasitoids attack to host random.

Here we will analyze the population dynamics in term of intrinsic growth rate r of the host population, the searching efficiency a and especially the clumping index k .

3. STABILITY ANALYSIS

In this section, the existence and local stability analysis of the non-negative equilibria of system (2) are investigated. There are two non-negative equilibrium points for system (2). 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).

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

$$\begin{cases} H^* = H^* \exp\left(r\left(1 - \frac{H^*}{K}\right)\right) \left(1 + \frac{aP^*}{k}\right)^{-k} \\ P^* = H^* \left[1 - \left(1 + \frac{aP^*}{k}\right)^{-k}\right] \end{cases} \quad (3)$$

Simplification formula (4) can be obtained

$$\begin{cases} H^* = K \left(1 + \frac{\ln Q}{r}\right) \\ P^* = K \left(1 + \frac{\ln Q}{r}\right) (1 - Q) \end{cases}$$

where Q is the net rate of the increase in the host per generation, which in this model is $Q = \left(1 + \frac{aP^*}{k}\right)^{-k}$.

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

In order to discuss the stability of the equilibrium point of model, the model (3) is written as follows

$$\begin{cases} H_{t+1} = F_1(H_t, P_t) \\ P_{t+1} = F_2(H_t, P_t) \end{cases}$$

At t time, a small perturbation n_t and p_t is added to the equilibrium point, and the equation evolves at $t + 1$ time is as follow

$$\begin{cases} H^* + n_{t+1} = F_1(H^* + n_t, P^* + p_t) \\ P^* + p_{t+1} = F_2(H^* + n_t, P^* + p_t) \end{cases}$$

In order to obtain the linear stability analysis, the Taylor expansion of the upper formula is

$$\begin{pmatrix} n_{t+1} \\ p_{t+1} \end{pmatrix} = \begin{pmatrix} \frac{\partial F_1}{\partial H} & \frac{\partial F_1}{\partial P} \\ \frac{\partial F_2}{\partial H} & \frac{\partial F_2}{\partial P} \end{pmatrix}_{H^*, P^*} \begin{pmatrix} n_t \\ p_t \end{pmatrix}.$$

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. For which the Jacobian matrix is given by

$$J = \begin{pmatrix} \frac{\partial F_1}{\partial H} & \frac{\partial F_1}{\partial P} \\ \frac{\partial F_2}{\partial H} & \frac{\partial F_2}{\partial P} \end{pmatrix}.$$

The Jacobian matrix of system (2) at the equilibrium point $E_0 = (0, 0)$ is

$$J(0, 0) = \begin{pmatrix} e^r & 0 \\ 0 & 0 \end{pmatrix}.$$

Accordingly, we find eigenvalues are $\lambda_1 = e^r$, $\lambda_2 = 0$. From this, it can be concluded that $E_0 = (0, 0)$ is a stable center.

The stability of the steady state at $E^* = (H^*, P^*)$ will now be examined. Using Eqs. (4) and (5), one can calculate the Jacobian matrix (3) of system (2) at $E^* = (H^*, P^*)$:

$$\begin{aligned} \frac{\partial F_1}{\partial H} \Big|_{E^*} &= 1 - r - \ln Q, \quad \frac{\partial F_1}{\partial P} \Big|_{E^*} = \frac{-aK(r + \ln Q)Q^{\frac{1}{k}}}{r}, \\ \frac{\partial F_2}{\partial H} \Big|_{E^*} &= 1 - \ln Q, \quad \frac{\partial F_2}{\partial P} \Big|_{E^*} = \frac{aK(r + \ln Q)Q^{1+\frac{1}{k}}}{r}. \end{aligned}$$

Consider the matrix

$$A = \begin{pmatrix} 1 - r - \ln Q & \frac{-aK(r + \ln Q)Q^{\frac{1}{k}}}{r} \\ 1 - \ln Q & \frac{aK(r + \ln Q)Q^{1+\frac{1}{k}}}{r} \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix}.$$

Here

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

Which can be rewritten in the following form

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

The characteristic equation is $Q(\lambda) \equiv \lambda^2 - B\lambda + C$, $Q(\lambda)$ is a concave parabola, when meets the following conditions, the roots of the equation, the balance point gradual. Where $B = G_{11} + G_{22}$, $C = G_{11}G_{22} - G_{12}G_{21}$.

In the stable: $Q(-1) > 0$, $Q(+1) > 0$, $C < 1$.

The solution stability of the $E^* = (H^*, P^*)$ positive equilibrium conditions

$$-1 - C < B < 1 + C, \quad C > 1.$$

4. BIFURCATION ANALYSIS

System (2) can not be solved explicitly. Thus, we have to study the long-term behavior of the system (2) by numerical simulation with Matlab, which is an interactive computer algebra system with great ability for symbolic evaluation, numerical calculation, etc. Its powerful function library and unique programming language provide scientific calculation and programming on an user-friendly platform.

To gain preliminary insight into the properties of the dynamical system we conducted an one-dimensional bifurcation analysis. One-dimensional bifurcation diagrams provide information about the dependence of the dynamics on a certain parameter. The analysis is called upon 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. Here we plot one-dimensional bifurcation diagrams of system (2) by computer simulation.

Figure 1 illustrates the bifurcation diagram of the parasitoid population dynamic for $r = 3$ and for initial values $H_0 = 5$, $P_0 = 2.5$ as parameter a increase. Figure 1(a) shows a case of model (2) with parasitoids attacks on host random (aggregation absent, $k \rightarrow \infty$). As the parameter a is increased from 0.3421, a stable coexistence between the host and parasitoid is observed. When the parameter a further increase, the system first experiences a quasiperiodicity (Hopf bifurcation at $a = 0.6368$). In the phase plane this appearance of a closed curve, where the points never coincide, is an indication of quasiperiodic. Quasiperiodic range often includes frequency-lockings, as in this case, too. When the parameter a is slightly increased, the system goes through period-4, period-12, high period cycle, period-32, and to chaotic dynamic at $a = 0.8206$. We also observed the parasitoid extinct at parameter $a = 2.3764$. In contrast, the dynamics are much more simple when clumping index k is decreased (Figure 1 (b): $k = 1.5$, Figure 1 (c): $k = 0.5$). Figure 1(b) shows the case of parasitoid moderate aggregation. The host-parasitoid system begins with chaos at $a = 0.3583$. As a approaches to 0.3868, the dynamic experienced a period-doubling reversal, from period-32 at $a = 0.3868$ to period-16 at $a = 0.3870$, following period-8, period-4, period-2 and at $a = 0.4434$ the system becomes a stable coexistence. When the parameter a further increases, the system suddenly becomes period-4 at $a = 1.9768$, and then becomes period-8 at $a = 2.5596$. As a approaches to 3.1403, the chaotic dynamics appears again, and sometimes it appears period-13 window. In the case of the parasitoid aggregation strong (Figure 1 (c): $k = 0.5$), the parameter region for persistent and stable interaction increases. In Figure 1 (c), the system begins with chaos. Chaotic dynamics experiences a period-doubling reversal. At $a = 0.8384$ a stable coexistence is observed.

Figure 2 is bifurcation diagram for mode (2) with $a = 1.5$, $H_0 = 5$, $P_0 = 2.5$, and r

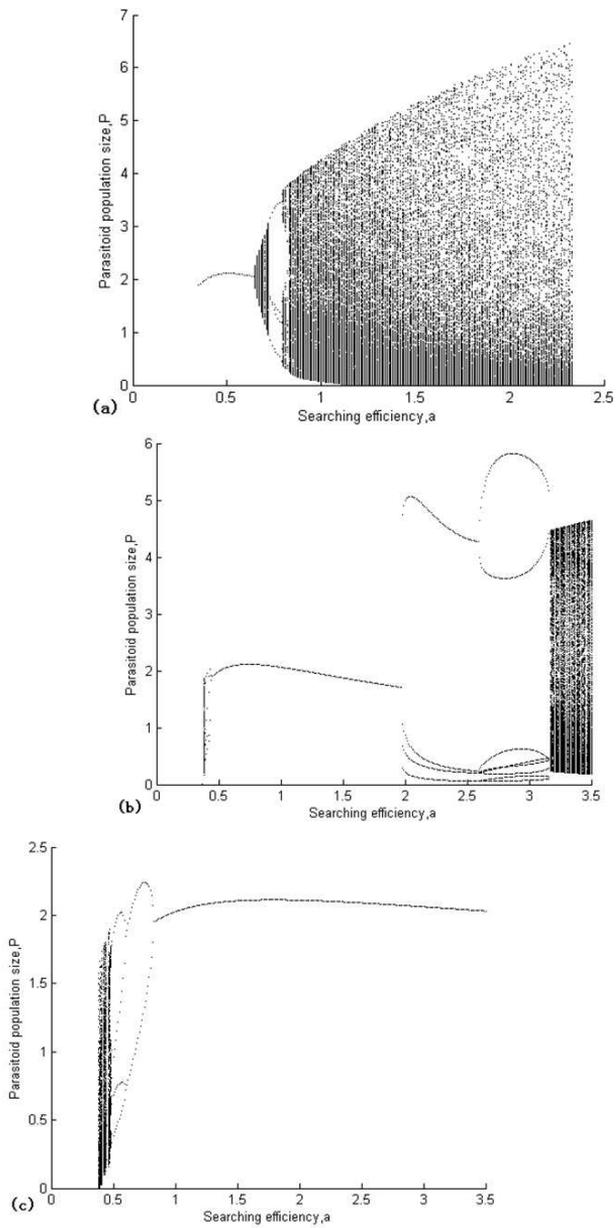


Figure 1: Bifurcation diagram of parasitoid population with respect to the searching efficiency a in the host-parasitoid model (2) for (a) $k \rightarrow \infty$; (b) $k = 1.5$; (c) $k = 0.5$; The parameters $r = 3$, $K = 5$, and the initial values $H_0 = 5$, $P_0 = 2.5$.

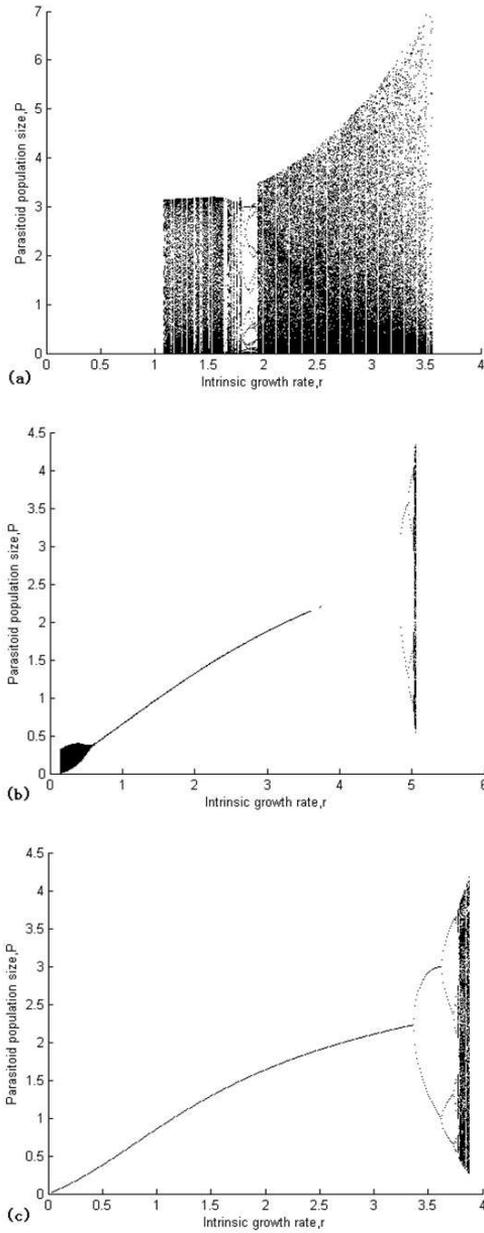


Figure 2: Bifurcation diagram of parasitoid population with respect to the intrinsic growth rate r in the host-parasitoid model (2) for (a) $k \rightarrow \infty$; (b) $k = 1.5$; (c) $k = 0.5$. The parameters $a = 1.5$, $K = 5$, and the initial values $H_0 = 5$, $P_0 = 2.5$.

as the bifurcation parameter. Like Figure 1, we show varying degrees of aggregation: Figure 2 (a) shows parasitoid random attack (aggregation absent $k \rightarrow \infty$). The dynamics of model (2) is very complicated, including many chaotic bands, pitchfork and tangent bifurcation, periodic windows, and attractor crises. This conclusion is the same with host-parasitoid model without mutual interference (see [7]). We also note recent study of Holling type II host-parasitoid model (see [6], [14]), in which, similar complexities have been found. Figure 2 (b) (c) show parasitoid moderate aggregation (Figure 2 (b): $k = 1.5$) and parasitoid aggregation strong (Figure 2(c): $k = 0.5$). For $k = 1.5$ (Figure 2 (b)) there is a Hopf bifurcation reversal of parameter r before a stable coexistence between host and parasitoid at $r = 1.2748$. The stable coexistence persists until parameter r approaches 3.559. In the range of $[3.559, 4.8486]$, parasitoid goes extinct. When parameter $r = 4.8486$, the system suddenly changes into period-2, and then, system experiences a Feigenbaum cascade of period-doubling bifurcations to chaos at $r5.047$. This chaos last for a short time. After that, parasitoid suddenly goes extinct and host dynamics become chaos. For $k = 0.5$ (Figure 2 (c)), Host and parasitoid experiences stable coexistence for long region of parameter r , and as r further increases, the system goes through a Feigenbaum cascade of period-doubling bifurcation leading to chaos at $r3.7650$. This chaotic region with periodic windows also suddenly disappears. Unlike the common Feigenbaum cascade of period-doubling leading to chaos which persists for a long time (see [7]), in Figure 2(b) (c), we observe the sudden extinct of parasitoid after its dynamics become chaos shortly. As we show before, the clumping index k can stabilize the dynamics and decrease of k made the stabile dynamic more strong.

We observe from Figure 3 that the clumping index k also may act as a strong destabilizing factor. Figure 3 is the bifurcation diagram for model (2) with $r = 3$ and k is the bifurcation parameter. The parameter of Figure 3(a) is $H_0 = 5, P_0 = 2.5K = 5, a = 2.0$. We see the system experiences a period-doubling reversal from chaotic dynamics with periodic window to period-32, period-16, period-8 and then period-4, period-2, and at $k = 0.2928$ stable coexistence. The stable coexistence suddenly changes into period-4 at $k = 1.4860$. As k increases further, we see that suddenly changes from one type of attractor to another occurs in range of $[2.2668, 2.2886]$, where multiple attractors coexist (see the following section). As k approaches 2.2668, the period-4 becomes into 12 piece of quasiperodicity Hopf bifurcation. Especially, these quasiperodicity Hopf bifurcations are reversal (details plotted in Figure 3(b)). At $k = 2.2886$, the system changes back to period-4, and then the system dynamics become chaos at $k2.5948$. When the parameters change to $H_0 = 0.49, P_0 = 0.81, a = 1.95$ (Figure 3(c)), then bifurcation diagram looks the same with Figure 3(a), but details are different. At $k = 2.1100$, the sudden change of attractors is from period-4 into period-12, and then pitchfork bifurcation occurs in

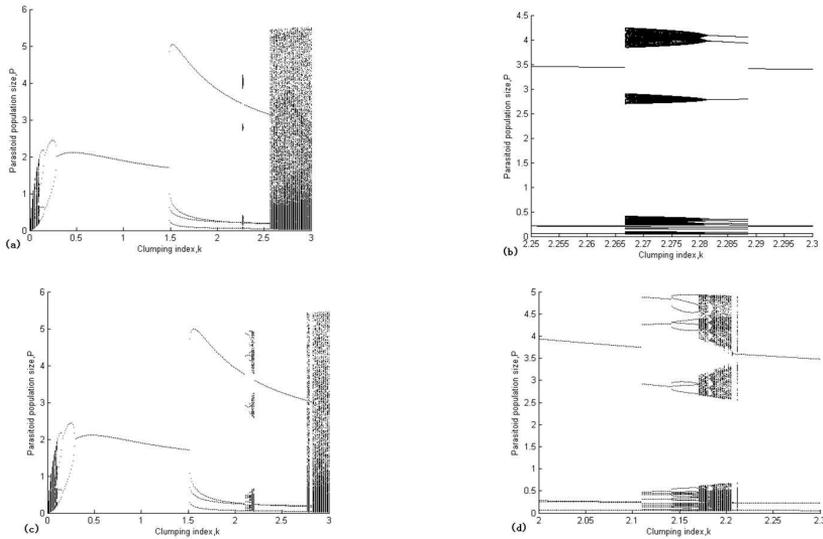


Figure 3: Bifurcation diagram of parasitoid population with respect to the clumping index k in the host-parasitoid model (2) for (a) $H_0 = 5, P_0 = 2.5, a = 2$; (b) give details of (a); (c) $H_0 = 0.49, P_0 = 0.81, a = 1.95$; (d) give details of (c). The parameters $r = 3, K = 5$.

each of these period-12 components, (details plotted in Figure 3 (d)). The frequent occurrence of sudden changes of attractors (crises) are also observed at parameter $k=2.3067$ and $k=2.3096$, where multiple attractors coexist.

4.1. NON-UNIQUE ATTRACTOR AND FRACTAL BASIN BOUNDARIES

A typical feature of bifurcation diagrams is the occurrence of sudden changes in the type of the attractors. In Figure 3 we see that sudden changes from one type of attractor to another occurs quite often. A more detailed numerical analysis reveals that the question is neither about windows of frequency-lockings within the quasiperiodic range usually occurring in two-dimensional mapping nor about periodic windows in the middle of chaos usually occurring in one-dimensional mapping. Instead, it appears that the attractor of dynamics for a certain parameter combination may not be unique. In Figure 3(a) (b), there is a sensitive range where multiple attractors coexist. In the range from $k = 2.2668$ to 2.2886 , two-attractors coexist, i.e., period-4 and 12-piece quasiperiodicity attractors at $k = 2.2668$, period-4 and period-12 attractors at $k = 2.282$. In Figure 3(c) (d), in the range from $k = 2.1100$ to 2.2033 , we also find non-unique attractor coexist.

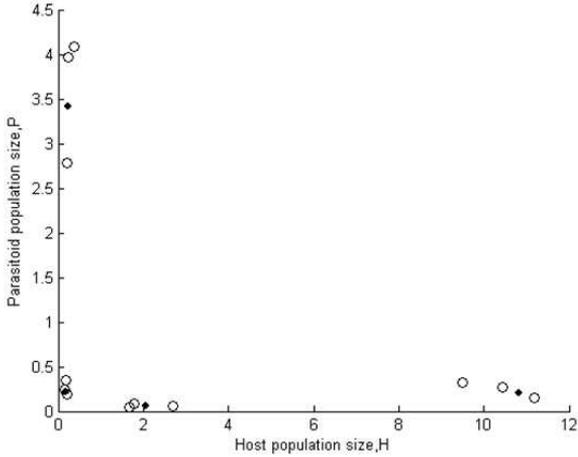


Figure 4: Two alternative attractors for $r = 3$, $a = 2$, $K = 5$, and $k = 2.2668$: 4-cycle and 12-cycle.

The basins of attraction defined as the set of the initial conditions whose trajectories asymptotically approach that attractor as time increases (see [17]). Complex basins of attraction for two coexistent attractors have been investigated by several authors (see [5], [7] and [16]), [17], [18], [19]. Figure 4 illustrates the basins of attraction for two alternatives: period-4 and period-12. The basins of attraction are fractal sets, indicating the sensitive dependence of the final state, or the attractor, on the initial state. Figure 5 shows the properties of self-similarity and fractal basin boundaries of the basins of attraction.

4.2. INTERMITTENT CHAOS AND SUPERTRANSIENTS

We also found other important properties such as intermittency and supertransient, as illustrated in Figure 6 and Figure 7. Intermittency is characterized by switches between apparently regular and chaotic behavior even though all the control parameters are constant and no external noise is present (see [20]). The switching seems random although the difference equations are deterministic. The behavior is completely aperiodic and chaotic although the system seems to switch between periodic and chaotic behavior. Supertransients are used to denote an unusually long convergence to an attractor. These transient dynamics are considerably longer than the timescale of significant environmental perturbations (see [21]). The timescale of ecological interest is tens or hundreds of generations, while supertransient can persist thousands of generations or even longer. In Figure 7, the host population size suddenly stabilizes

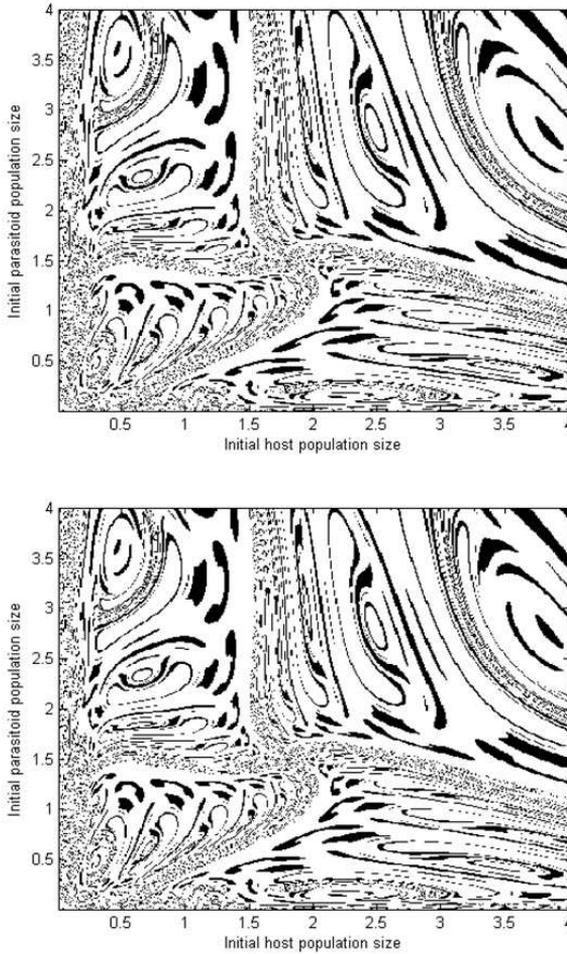


Figure 5: The basins of attraction for the two alternative attractors—the white and black areas are the basins of attraction for period-4, period-12, respectively, illustrated in *Figure 4*. The patterns of self-similarity and fractal basin boundaries indicate that the basins of attraction are fractals.

into a period-4 attractor after about 2100 generations of complicated fluctuations resembling an intermittent trajectory.

It should be noted that intermittency is a basic characteristic of chaos, even in discrete-time single-species models (see [21]) and some epidemiological models with discrete host generations (see [22]). Intermittency, chaos, and supertransients were also reported in spatially structured ecological models (see [22]), Holling-type functional response host-parasitoid models (see [6], [16]), and mutual interference host-parasitoid

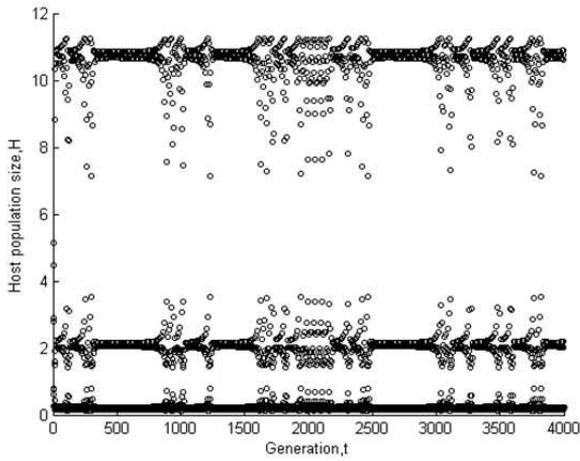


Figure 6: Intermittent chaos of host dynamics for $r = 3$, $a = 1.95$, $K = 5$, $k = 2.3615$, and the initial values $H_0 = 0.81$, $P_0 = 0.49$.

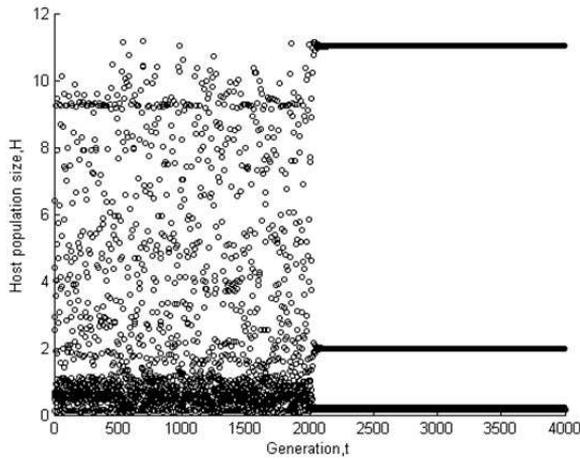


Figure 7: Supertransient behavior of host population for $r = 3$, $a = 1.95$, $K = 5$, $k = 2.7153$, and the initial values $H_0 = 0.81$, $P_0 = 0.49$.

model (see [7]).

5. CONCLUSION

In this paper, we have examined the dynamic complexities in a parasitoid aggregation host-parasitoid model by computer numerical simulation. We found the parasitoid aggregation may be a strong stabilizing or destabilizing factor. Parasitoid aggregation can extend the parameter range of host-parasitoid stable coexistence. Analysis of host-parasitoid model with clumping effect reveals that parasitoid aggregation often leads to the suppression of quasiperiodicity and the reversal with Hopf bifurcation (Figure 2 (b)) and it also leads to the suppression of chaos and the reversal with period-doubling (Figure 1(b) (c)). The phenomenon of period-halving occurs in models of the crown-of-thorns starfish (see [24]), insect population (see [25], [26]), annual plant populations (see [27]), genetic selection (see [28]), microbial predator-prey chemostats (see [29]), cardiac cell stimulation (see [30]), coevolutionary host-parasite models (see [31]) and mutual interference host-parasitoid model (see [7]). The presence of reversals has also been documented in other areas of research, ranging from models of magnetoconvection (see [32]) and rotating galaxies (see [33]), to a neuronal model of psychotic human behaviour (see [34]). Also notable is Swinney's classic study (see [35]) of chemical reaction in stirred flow reactor yielding important empirical confirmation. On the other hand, clumping effect might actually strongly destabilize the dynamics. The parasitoid aggregation leads to many forms of dynamic behavior. Some complexities in the dynamics are related to chaotic bands with periodic windows, pitchfork bifurcations attractor crises. Some are related to the non-uniqueness of the dynamics, or multiple attractors with fractal basins of attraction. Other complexities are related to intermittency with random switches between apparently regular and chaotic behavior or chaotic transient dynamics towards the attractors. We note some similar observations that the evolution of protective immunity against parasites or diseases, or any other comparable life-history trait under evolution (see [5]), or the mutual interference between host and its parasitoid (see [7]), may be a strong stabilizing or destabilizing factor in ecological interactions.

We find sudden changes of attractor (crisis) in model (2). The phenomena of crisis in which chaotic attractors can suddenly appear or disappear, or change size discontinuously as a parameter smoothly raises was first extensively analyzed by Grebogi et al. (see [17]), and it was observed in many others discrete-time host-parasitoid models (see [6], [7]). We also find that the attractor of dynamics for a certain parameter combination may not be unique. Because of the coexistence of non-chaotic attractors, i.e., two- or three-periodic attractors, in ecological interaction, the presence of chaotic dynamics cannot be judged solely on the basis of the sensitivity. Similarly, the presence of strong periodicity in population dynamics does not exclude the possible presence of chaos in the dynamics (see [37]).

The dynamic behavior of a population may dramatically be affected by small changes in values of the parameters (e.g., frequency-lockings or attractor crises). Even if the parameter values and initial conditions remain unchanged, the trajectory may change significantly as time passes (e.g., intermittency and supertransient behavior). This shows that if the time series is too short, only a part of the dynamic structure may be detected. Unfortunately, as the existence of supertransients implies, it may be difficult to determine the appropriate and reliable length for a time series.

Complex dynamic patterns have been observed in spatial logistic models in which local populations are connected by migration (see [38], [39]) and in two-species interactions of hosts and parasites (see [5]). In spatial predator-prey or host-parasitoid system, complex spatial patterns could be incurred by the predation or parasitism interactions and migration of individuals. Dynamic complexities also have been reported in periodically forced continuous-time predator-prey models (see [37], [40], [41], [42], [43]). As has been stated above, the dynamic complexities of ecosystem have already received considerable attention. However, as far as the authors are aware, the present study is one of analysis of the functional response of the parasitoid aggregation attacks to host discrete-time ecosystem models. The functional response also acts on foraging ability of the parasitoid and influences *PP* (predator pursuit). *PP* indicates that predators migrate not only from patches of higher predator density to those of lower predator density but also from patches of lower prey density to those of higher prey density. McCann (see [44]) found that *PP* can lead to static spatial pattern and local population outbreak in host-parasitoid metapopulation. Li and Gao (see [45]) have investigated the influence of *PP* (predator pursuit) and *PE* (prey evasion) on the spatial synchrony of a predator-prey metapopulation and have shown that *PP* and *PE* incurring spatial chaos. We find that clumping effect can incur complex dynamic patterns and it also can exclude the possible presence of chaos in the dynamics. Elsewhere, predators have been proposed to cause chaos-like oscillations in the dynamics of small rodents (see [46]). Nevertheless, identifying complicated, possibly chaotic, dynamics in population data has remained a major challenge in ecological studies (see [47], [48]). The increasing number of potential complexities predicted by the theory seems to make this task more difficult. Computer numerical simulation would facilitate the examination of the dynamic complexities of the model and would promise to uncover the complex mechanisms in the ecosystems.

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REFERENCES

- [1] R.M. May, Biological population with non-overlapping generations: stable point, stable cycle and chaos, *Science.*, **186** (1974), 645-647.
- [2] R.M. May, Simple mathematical models with very complicated dynamics, *Nature.*, **261** (1974), 645-647.
- [3] R.M. May, Limit cycles in predator-prey communities, *Science.*, **177** (1972), 900-902.
- [4] J.R. Beddington, C.A. Free, J.H. Lawton, Dynamic complexity in predator-prey models framed in difference equations, *Nature.*, **255** (1975), 58-60.
- [5] V. Kaitala, M. Heino, Complex non-unique dynamics in simple ecological interactions, *Proc R. Soc Lond B.*, **263** (1996), 1011-1015.
- [6] S.Y. Tang, L.S. Chen, Chaos in functional response host-parasitoid ecosystem models, *Chaos Solitons and Fractals.*, **13** (2002), 875-884.
- [7] C.L. Xu, S. Mark, Boyce, Dynamic complexities in a mutual interference host-parasitoid model, *Chaos Solitons and Fractals.*, **13** (2005), 175-182.
- [8] V Clamer, A Pugliese, D Liessi, et al., Host coexistence in a model for two host-one parasitoid interactions, *Journal of Mathematical Biology.*, **75(2)** (2017), 419.
- [9] X Liu, Y Chu, Y Liu. Bifurcation and chaos in a host-parasitoid model with a lower bound for the host, *Advances in Difference Equations*, **2018(1)** (2018), 31.
- [10] Q Din, Global Stability of Beddington Model, *Qualitative Theory of Dynamical Systems*, **16(2)** (2016), 1-25.
- [11] Q Din, Qualitative analysis and chaos control in a density-dependent host-parasitoid system, *International Journal of Dynamics and Control*, **3** (2017), 1-21.
- [12] P.A.P. Moran, Some remarks on animal population dynamics, *Biometrics.*, **6** (1950), 250-258.
- [13] W.E. Ricker, Stock and recruitment, *J. Fish Res Board Can.*, **11** (1954), 559-623.
- [14] R.M. May, Host-parasitoid system in patchy environments: a phenomenological model, *J. Anim. Ecol.*, **47** (1978), 833-843.
- [15] A.J. Nicholson, V.A. Bailey, The balance of animal populations, *Part I Proc Zool Soc, London.*, (1935), 551-598.
- [16] V. Kaitala, J. Ylikarjula, M. Heino, Dynamic complexities in host-parasitoid interaction, *J. Theor. Biol.*, **197** (1999), 331-341.
- [17] C. Grebogi, E. Ott, J.A. Yorke, Fractal basin boundaries, long-lived chaotic transients, and unstable-unstable pair bifurcation, *Phys. Rev. Lett.*, **50** (1983), 935-938.

- [18] J. Testa, G.A. Held, Study of a one-dimensional map with multiple basins, *Phys. Rev. A.*, **28** (1983), 3085-3089.
- [19] H.O. Peitgen, H. Jrgens, D. Saupe, Chaos and fractals, *New frontier of science, Springer-Verlag, New York.*, 1992.
- [20] R.C. Hilborn, Chaos and nonlinear dynamics: an introduction for scientists and engineers, *Oxford University Press, New York.*, 1994.
- [21] A. Hastings, K. Higgins, Persistence of transients in spatially structured ecological models, *Science.*, **263** (1994), 1133-1136.
- [22] W.W. Murdoch, A. Oaten, Predation and population stability, *Adv. Ecol. Res.*, **9** (1975), 1?25.
- [23] J.C. Koella, M. Doebeli, Population dynamics and the evolution of virulence in epidemiological models with discrete host generations, *J. Theor. Biol.*, **198** (1999), 461-475.
- [24] H.I.J. McCallum, Effects of immigration on chaotic population dynamicstheor, *Biol.*, **154** (1992), 277-284.
- [25] M.P. Hassell, J.H. Lawton, R.M. May, Patterns of dynamical behaviour in single-species populations, *J. anim. Ecol.*, **45** (1976), 471-486.
- [26] T, S, Jr. Bellows, The descriptive properties of some models for density dependence, *J. Anim. Ecol.*, **50** (1981), 139-156.
- [27] S.W. Pacala, J.A. Silander, Neighborhood Models of Plant Population Dynamics, *I. Single-Species Models of Annuals, Am. Nat.*, **125** (1985), 385-411.
- [28] L. Altenberg, Chaos from Linear Frequency-Dependent Selection, *Am. Nat.*, (1991), 138-151.
- [29] M. Kot, G.S. Saylor, T.W. Schultz, Complex dynamics in a model microbial system, *Bull. Math. Biol.*, **54** (1992), 619-648.
- [30] M.R. Guevara, L. Glass, A. Shrier, Phase locking, period-doubling bifurcations, and irregular dynamics in periodically stimulated cardiac cells, *Science.*, **214** (1981), 1350-1353.
- [31] R.M. May, R.M. Anderson, Epidemiology and genetics in the coevolution of parasites and hosts, *Proc. R. Soc. B.*, **219** (1983), 281-313.
- [32] E. Knobloch, N.O. Weiss, Bifurcations in a model of magnetoconvection, *Physica. 9D.*, (1983), 379-407.
- [33] G. Contopoulos, Inverse Feigenbaum sequences in Hamiltonian systems, *Lett Nuovo Cimento.*, **37** (1983), 149-153.
- [34] R. King, J.D. Barchas, B.A. Huberman, Chaotic Behavior in Dopamine Neurodynamics, *Proc Natn Acad Sci USA.*, **81** (1984), 1244-1247.
- [35] H.L. Swinney, Observations of Order and Chaos in Nonlinear Systems, *Physica.*, (1983), 3-15.

- [36] K. Coffman, W.D. McCormick, H.L. Swinney, Multiplicity in a Chemical Reaction with One-Dimensional Dynamics, *Phys. Rev. Lett.*, **56** (1986), 999-1002.
- [37] W.M. Schaffer, Perceiving order in the chaos of nature, In: *Evolution of life histories of mammals*, Boyce MS, New Haven: Yale University Press, 1988, 313-350.
- [38] A. Hastings, Complex interactions between dispersal and dynamics: lessons from coupled logistic equations, *Ecology.*, **74** (1993), 1362-1372.
- [39] C.L Xu, Z.Z. Li, Effect of diffusion and spatially varying predation risk on the dynamics and equilibrium density of a predator-prey system, *J. Theor. Biol.*, **219** (2002), 73-82.
- [40] M. Inoue, H. Kamifukumoto, Scenarios leading to chaos in a forced Lotka-Volterra model, *Prog. Theor. Phys.*, **71** (1984), 930-937.
- [41] S. Rinaldi, S. Muratori, YuA. Kuznetsov, Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities, *Bull. Math. Biol.*, **55** (1993), 15-35.
- [42] G.C.W. Sabin, D. Summer, Chaos in a periodically forced predator-prey ecosystem model, *Math. Biosci.*, **113** (1993), 91-113.
- [43] S. Gakkhar, R.K. Naji, Chaos in seasonally perturbed ratio-dependent prey-predator system, *Chaos Solitons and Fractals.*, **15** (2003), 107-118.
- [44] K. McCann, A. Hastings, S. Harrison, W. Wilson, Population outbreaks in a discrete world, *Theor. Popul. Biol.*, **57** (2000), 97-108.
- [45] Z.Z. Li, M. Gao, H. Cang, H. Xiao-zhuo, S. Honghua, Impact of predator pursuit and prey evasion on synchrony and spatial patterns in metapopulation, *Ecol. Model.*, **185** (2005), 245-254.
- [46] I. Hanski, P. Turchin, E. Korpimki, H. Henttonen, Population oscillations of boreal rodents: regulation by mustelid predators lead to chaos, *Nature.*, **364** (1993), 232-235.
- [47] G. Sugihara, R.M. May, Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series, *Nature.*, **344** (1990), 734-741.
- [48] L. Stone, Coloured noise or low-dimensional chaos. *Proc. R. Soc. Lond B.*, **250** (1992), 77-81.