



Dynamic Complexities in Host–Parasitoid Interaction

VEIJO KAITALA,^{*†‡} JANICA YLIKARJULA^{†‡§} AND MIKKO HEINO[‡]

** Department of Biological and Environmental Science, University of Jyväskylä, Box 35, FIN-40351 Jyväskylä, Finland, † Systems Analysis Laboratory, Helsinki University of Technology, Box 1100, FIN-02015 HUT, Finland and ‡ Division of Population Biology, University of Helsinki, Box 17, FIN-00014 University of Helsinki, Finland*

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In the 1970s ecological research detected chaos and other forms of complex dynamics in simple population dynamics models, initiating a new research tradition in ecology. However, the investigations of complex population dynamics have mainly concentrated on single populations and not on higher dimensional ecological systems. Here we report a detailed study of the complicated dynamics occurring in a basic discrete-time model of host–parasitoid interaction. The complexities include (a) non-unique dynamics, meaning that several attractors coexist, (b) basins of attraction (defined as the set of the initial conditions leading to a certain type of an attractor) with fractal properties (pattern of self-similarity and fractal basin boundaries), (c) intermittency, (d) supertransients, (e) chaotic attractors, and (f) “transient chaos”. Because of these complexities minor changes in parameter or initial values may strikingly change the dynamic behavior of the system. All the phenomena presented in this paper should be kept in mind when examining and interpreting the dynamics of ecological systems.

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1. Introduction

The profound discoveries by Robert May (1974, 1976) initiated a new research area dealing with the complexities in the population dynamics models. The theory of single population dynamics is now quite well understood, as compared with the dynamics of interacting populations.

The research dealing with interspecific interactions has mainly focused on continuous-time predator–prey models of two variables, where

dynamics include only stable equilibrium or limit cycles. Nevertheless, an early work by Beddington *et al.* (1975) showed that in discrete-time host–parasitoid models the dynamics can produce a much richer set of patterns than those observed in continuous-time models.

Here we analyse qualitatively the dynamic complexities in a modification of the Nicholson–Bailey model of host–parasitoid interaction (Nicholson, 1933; Nicholson & Bailey, 1935). The basic form of the complexities, which we refer to as the “complex dynamic patterns”, arising in this model is non-unique dynamics with multiple attractors. We show that several types of attractors may coexist, including

§ Author to whom correspondence should be addressed. Correspondence address: Systems Analysis Laboratory, Helsinki University of Technology, Box 1100, FIN-02015 HUT, Finland. E-mail: Janica.Ylikarjula@hut.fi.

quasiperiodic and chaotic, two different periodic, two different chaotic or periodic and chaotic attractors. Furthermore, the boundaries of the basins of attraction may have fractal properties, such as patterns of self-similarity and fractal basin boundaries, which will further increase the complexity patterns in this model. As a consequence, it can be difficult to predict the attractor into which the trajectory will converge on a basis of initial conditions. Non-unique attractors with complex basins of attraction have been earlier reported in spatial interactions modelled as coupled logistic maps (Hastings, 1993; Lloyd, 1995), and in a host–parasite model with immunized and non-immunized hosts (Kaitala & Heino, 1996).

Other complexities observed in this model are intermittency, random switches between apparently regular and chaotic motions, which is a possible explanation for the irregular behaviour of some insect pest populations (Cavaliere & Koçak, 1995), and supertransients, which exhibit unusually long convergence into an attractor (Hastings & Higgins, 1994). In addition, transients can show chaos-like dynamics.

2. Host–Parasitoid Interaction

We consider the discrete-time dynamics of host–parasitoid interaction. The starting point of our modeling studies is the well-known deterministic single species Moran–Ricker dynamics (Moran, 1950; Ricker, 1954) given as

$$N_{t+1} = N_t \exp[r(1 - N_t)], \quad (1)$$

where N_t is the prey population size in generation t , $t = 0, 1, 2, \dots$, and r is the intrinsic growth rate. The steady state of the Moran–Ricker dynamics, satisfying $N_{t+1} = N_t$, is $N^* = 1$, and the dynamics are asymptotically stable when $0 < r < 2$, unstable with different periodic attractors when $2.0 < r < 2.6924$, and chaotic (with periodic windows) when $r > 2.6924$.

The aim of this study is to explore how the dynamics of the Moran–Ricker model change when the host population, N_t , is subjected to parasitism. The model used here is especially suited for describing the arthropod host–parasitoid systems. Denoting the parasitoid population size in generation t as P_t , the interspecific

interaction assumes the following dynamics (Holling, 1959a; Royama, 1971; Rogers, 1972)

$$N_{t+1} = N_t \exp\left[r(1 - N_t) - \frac{aTP_t}{1 + aT_h N_t}\right], \quad (2)$$

$$P_{t+1} = N_t \left[1 - \exp\left(\frac{-aTP_t}{1 + aT_h N_t}\right)\right], \quad (3)$$

where a is the instantaneous search rate, i.e. the average encounters per host per unit of searching time, T the total time initially available for search, i.e. the total time the hosts are exposed to parasitoids and T_h the handling time, i.e. the time between host being encountered and search being resumed.

In many host–parasitoid models host population is assumed to increase exponentially in the absence of parasitism. In the model (2)–(3) host population growth is limited and described by the Moran–Ricker model. The main assumptions of this model are that each parasitoid searches at random, that is irrespective of the host abundance, the average number of parasitoid progeny produced per host attacked is assumed to be one, and the functional response is of Holling type II, which is typical for insects (see e.g. Begon & Mortimer, 1982). We analyse the population dynamics in terms of the intrinsic growth rate r of the host population and the instantaneous search rate a . Parameters T and T_h assume values 100 and 1, respectively. These values are well in line with the estimated values from this model for parasitoids (see e.g. Hassell, 1978).

Assuming that the population dynamics reach a point equilibrium with both species present, the steady-state population sizes satisfy the following equations:

$$N^* = \frac{\lambda \ln \lambda}{a(T(\lambda - 1) - T_h \lambda \ln \lambda)}, \quad (6)$$

$$P^* = \frac{(\lambda - 1) \ln \lambda}{a(T(\lambda - 1) - T_h \lambda \ln \lambda)}, \quad (5)$$

where λ is the net rate of increase of the host per generation, which is in this model $\lambda = \exp[r(1 - N^*)]$. Note that the equilibrium population sizes (N^* , P^*) cannot be solved in closed form.

The point attractor with both species present is, however, only a special case, and perhaps not the most interesting one. In this work we explore the dynamic behavior of the model beyond the traditionally used local stability analysis. In addition to the sustained coexistence of both species at a steady state, the alternative dynamics in host-parasitoid interactions include sustained coexistence in a more complex manner, or extinctions of parasitoid ($P^* = 0$). We focus on the case of sustained coexistence of both species.

We begin our analysis by investigating some of the conditions under which the parasitoid cannot invade the host population. Local stability analysis (see the Appendix) shows that the steady state with $P = 0$ is locally asymptotically stable when the host growth rate and the instantaneous search rate are sufficiently low, that is when $r < 2$ and $a < 1/(T - T_h)$. In this parameter area the instantaneous search rate a is not high enough to allow a viable parasitoid population.

For different parameter values a great variety of coexistence patterns between host and parasitoid can be observed. We next use numerical simulations to identify the areas of coexistence and the different types of dynamics. A two-dimensional bifurcation diagram is developed in Fig. 1 using instantaneous search rate a and intrinsic growth rate of host population r as bifurcation parameters. The bifurcation curves were calculated by using LOCBIF Interactive local bifurcation analyser (Khibnik *et al.*, 1990–1992).

The general pattern arising from the study is that for small values of instantaneous search rate a host and parasitoid cannot coexist but parasitoid goes extinct. When increasing the value of a stable coexistence between host and parasitoid becomes possible. If the instantaneous search rate increases even further the interactions begin to show complex dynamics and possible non-uniqueness of attractors. In more detail, the area of stable coexistence on the left-hand side of Fig. 1 is bordered by vertical fold bifurcation curve $a = 1/(T - T_h)$ for $r < 2$ (see the Appendix) and by flip bifurcation curve for $r \geq 2$. These bifurcation curves are identified by an eigenvalue of the Jacobian matrix of the linearized system passing through the unit circle at $+1$ or -1 , respectively (for thorough review of different

bifurcations see e.g. Kuznetsov, 1994). Further right, a Hopf bifurcation takes place when the complex conjugate eigenvalues of the Jacobian matrix of the linearized system cross the unit circle. The Hopf bifurcation curve separates the area of stable coexistence from the area of more complex coexistence dynamics, showing periodic, quasiperiodic or chaotic dynamics. Regions of periodic solutions occur as Arnold tongues touching the Hopf bifurcation curve; some of the phase-lockings with low periods are shown in Fig. 1. We next study the dynamics of the population interaction (2)–(3).

3. One-dimensional Bifurcation Analysis

A traditional approach to gain preliminary insight into the properties of a dynamic system is to carry out 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 the initial transient phase and within which the trajectory will then remain forever.

Figure 2 illustrates the bifurcation diagram of the host population dynamics for $r = 0.2$ and for the initial values $N_0 = P_0 = 0.5$ as parameter a increases. Recall from above that, for $r = 0.2$, the host dynamics are stable in the absence of parasitism and that the single species host dynamics become unstable only at $r = 2.0$.

As the parameter a increases passing the level $a = 0.0101$, a stable coexistence between the host and parasitoid is observed. The steady-state host population size decreases and that of the parasitoid increases as the parameter a gets larger. When the parameter a further increases, a Hopf bifurcation occurs at $a \approx 0.030$. In the phase plane this appearance of a closed curve, where the points never coincide, is an indication of quasiperiodicity. Quasiperiodic range often includes frequency-lockings as in this case, too. These frequency-lockings appear as a collapse of the invariant circle to a periodic orbit. From an ecological point of view, we see from Fig. 2 that parasitism may easily destabilize stable host dynamics into more complex dynamics. Up to the r value of 1.7 this same kind of dynamic

behavior—for lower values of a equilibrium attractors, then a Hopf bifurcation, and quasiperiodic range with frequency-lockings—can be seen.

For $r = 2.1$ the coexistence between host and parasitoid becomes possible at $a \approx 0.011$ (Fig. 3). Contrary to our observation above that parasitoids may act as a destabilizing force in a

host population equilibrium attractors with both species coexisting we show here that parasitism may also act as a stabilizing factor. The nature of this stable coexistence changes as a Hopf bifurcation takes place at $a \approx 0.032$, initiating a range of complicated dynamics which are not as easy to characterize as in the case illustrated in Fig. 2. The first range, $0.032 < a < 0.051$,

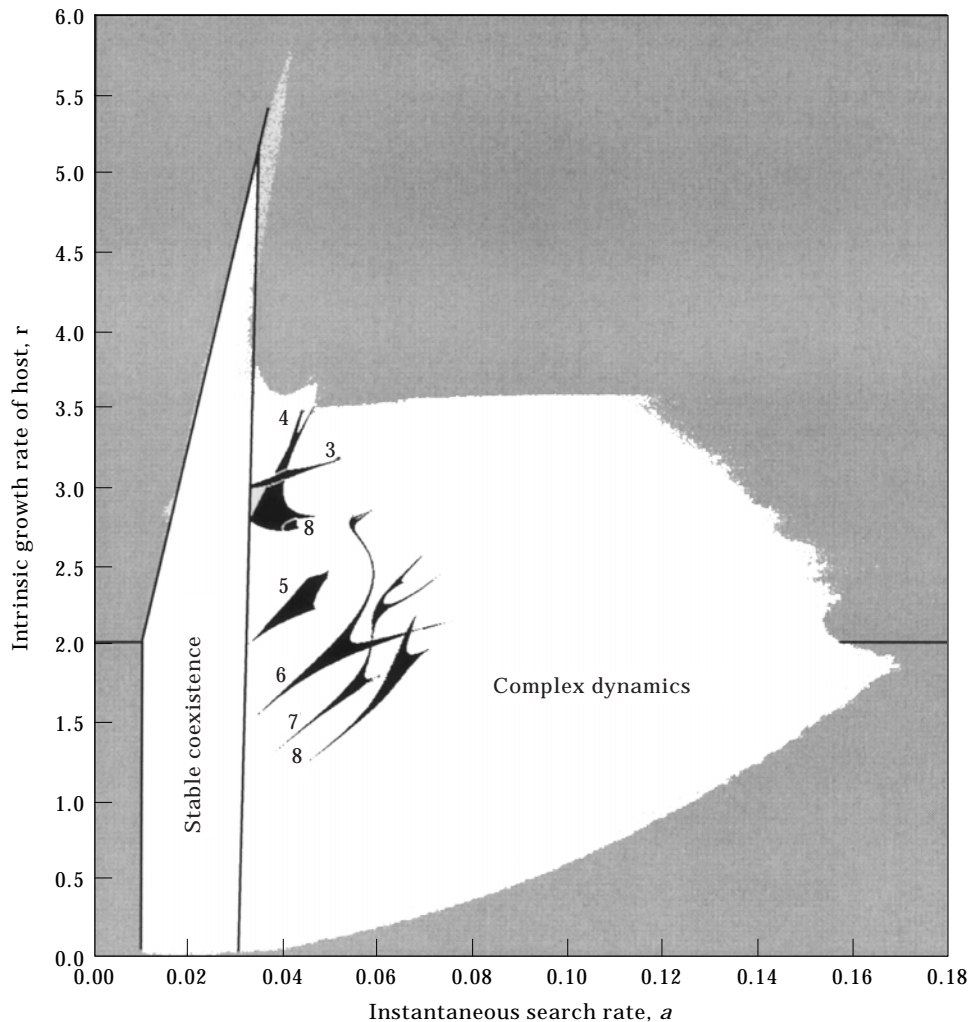


FIG. 1. Two-dimensional bifurcation diagram for the host-parasitoid system. The dynamics were traced for 2000 generations. Parasitoid was considered extinct if its cumulative population size over the following 20 generations was below 10^{-5} . Possibility of coexistence was evaluated on the basis of 25 replicate simulations with initial conditions (N_0, P_0) drawn from a uniform distribution in $([0.1, 2.1], [0.1, 2.1])$. In the shadowed region, the parasitoid population always goes extinct, after which the host population displays normal Moran-Ricker-type dynamics. The horizontal line at $r = 2$ is the first flip (pitchfork) bifurcation boundary. In the white region, the host and parasitoid populations can coexist, at least for some initial conditions. For low instantaneous search rate a , the dynamics have a stable fixed point, which undergoes a Hopf bifurcation when a is increased. Right of the Hopf bifurcation curve, the dynamics are complex—either periodic, quasiperiodic or chaotic. Periodic dynamics are caused by frequency-lockings which occur as narrow “Arnold” tongues (black regions; only the largest tongues with periods ≤ 8 are shown) touching the Hopf bifurcation curve.

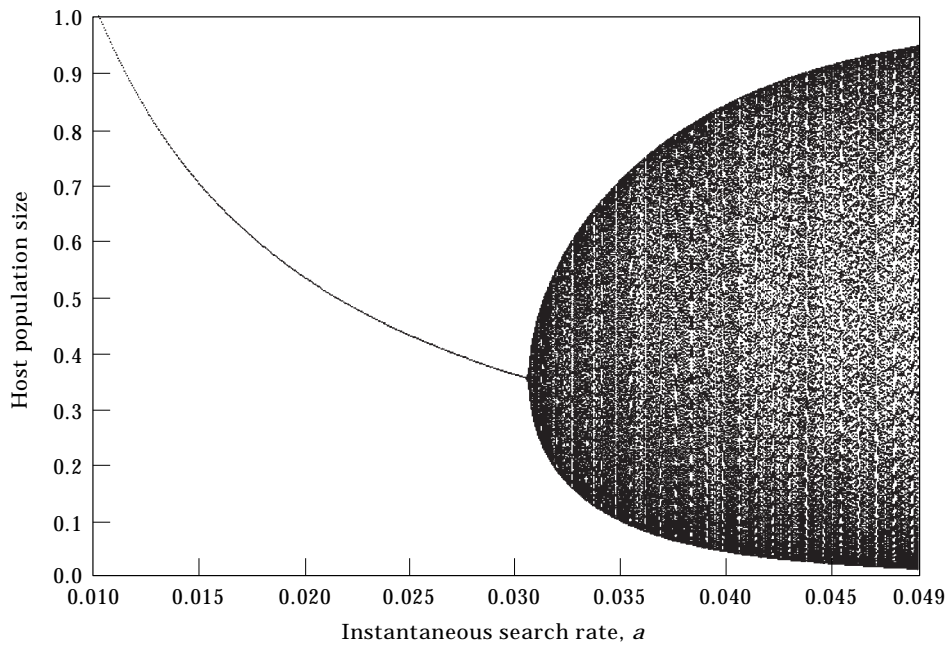


FIG. 2. Bifurcation diagram of the host population in the host-parasitoid interaction for $r = 0.2$, $0.01 < a < 0.049$ and initial values $N_0 = 0.5$, $P_0 = 0.5$. For each a , the 20000 first simulated host population values were omitted to remove the initial transients, and only the next 300 host population values were plotted.

represents quasiperiodic attractors with frequency-lockings.

At the first time chaotic attractors can be seen after a frequency-locking for $a \approx 0.051$. Chaos can be determined by calculating the dominant

Lyapunov exponent, which quantifies the average growth of infinitesimally small deviations of initial point. For $a = 0.051$ the dominant Lyapunov exponent of the system is positive, 0.0339, indicating chaotic behavior. Some of

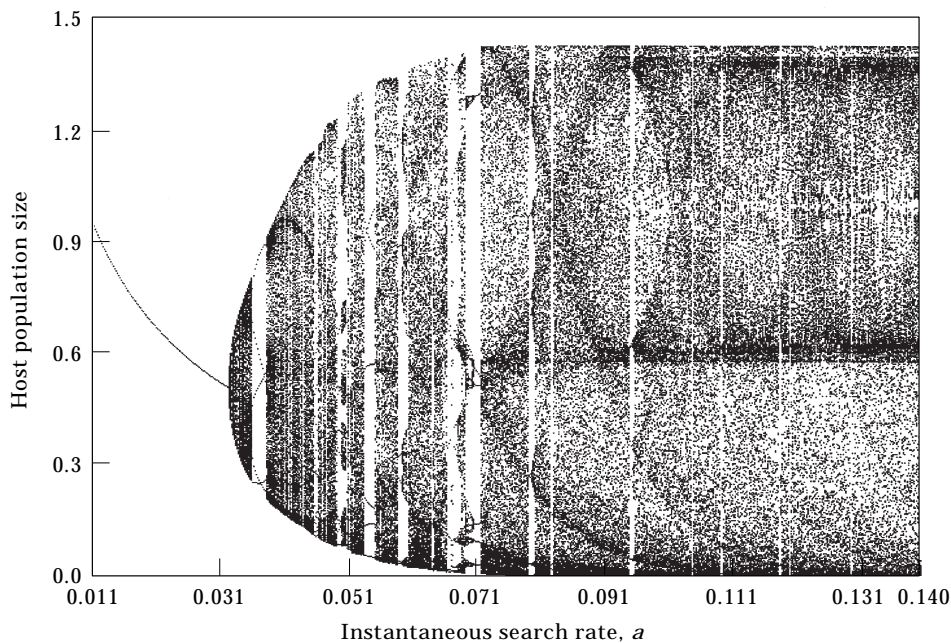


FIG. 3. Bifurcation diagram of the host population in the host-parasitoid interaction for $r = 2.1$, $0.011 < a < 0.14$ and initial values $N_0 = 0.5$, $P_0 = 0.5$.

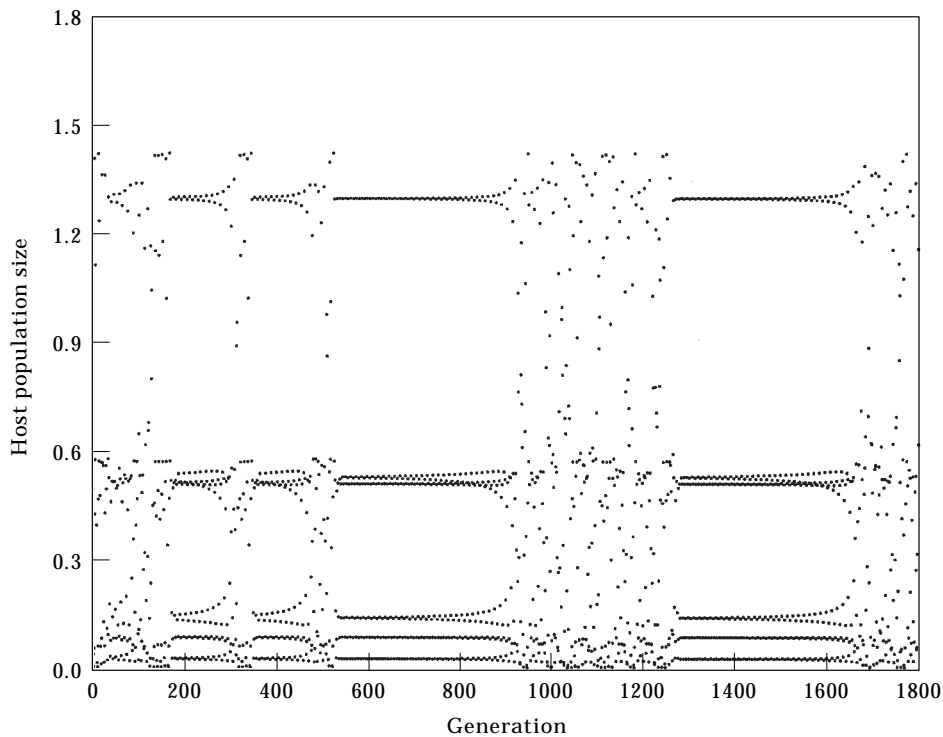


FIG. 4. Intermittent chaos—host dynamics for $r = 2.1$, $a = 0.0717$ and initial values $N_0 = 0.5$, $P_0 = 0.5$.

these chaotic solutions belong to the class of intermittency, as illustrated in Fig. 4. 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 (Hilborn, 1994). 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. It should be noted that intermittency is a basic characteristic of chaos even in the discrete-time single species models, where it can be found, for example before the onset of a periodic window in a bifurcation diagram.

Taking a closer look at the range $0.066 \leq a \leq 0.072$ shows that this window is not a periodic window with its own cascade of period-doublings, but that this range includes more complex dynamic patterns. It appears that here the attractor is non-unique. For example at $a = 0.0671$ the alternative attractors are two different types of periodic attractors (see below). Thus, choosing the initial conditions differently

will produce a slightly different bifurcation diagram since the attractors depend on the initial conditions.

An interesting feature is the thickenings in the chaotic area for very low values of host population size and around host population sizes of 0.6 and 1.4. The two latter ones are approximately the same values as the host population size would have without parasitism, i.e. for $r = 2.1$ the Moran–Ricker model exhibits periodic motion between values 0.6293 and 1.3707. The same phenomenon can be seen in part of the other bifurcation diagrams as well. This indicates that the host dynamic patterns without parasitism have a strong effect also when the parasitism is added.

Increasing further the value of the growth rate r shows slightly different dynamics. For $r = 2.8$ there can be seen first stable coexistence, then a Hopf bifurcation and quasiperiodic range with major period-four frequency-locking. After this chaotic range begins. In Fig. 5 only part of the range of coexistence is shown so that the non-uniqueness of the attractors between values 0.0425 and 0.0445 can be clearly seen.

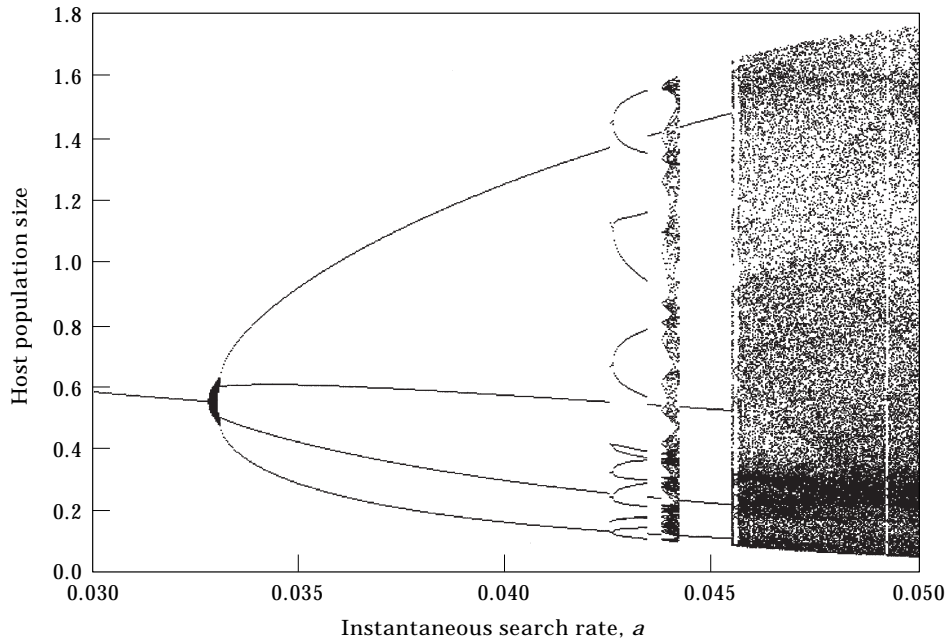


FIG. 5. Bifurcation diagram of the host population in the host-parasitoid interaction for $r = 2.8$, $0.03 < a < 0.05$ and initial values $N_0 = 0.5$, $P_0 = 0.5$.

4. Non-unique Attractors and Fractal Basin Boundaries

A typical feature of bifurcation diagrams is the occurrence of sudden changes in the types of the attractors. In one-dimensional mappings, these sudden changes are usually related to periodic windows in the middle of the chaotic range of attractors. In the two-dimensional mapping such windows may be related to frequency-lockings within quasiperiodic range.

Reviewing back the bifurcation diagram for the parasitoid population in Fig. 5 we see that sudden changes from one type of an attractor to another do occur quite often. One obvious change occurs at $a \approx 0.043$. Here a period-four attractor changes to an attractor which shows period-16 type dynamics. A more detailed numerical analysis reveals that the question is not only about windows of frequency-lockings or periodic windows in the middle of chaos. Instead, it appears that the attractor is non-unique: in this case the alternative attractors are, for example period-four and period-16 attractors (Fig. 6). Obviously, which one of the attractors is reached depends on the initial conditions (see below). Multiple attractors are known to be possible, and probably common, in

nonlinear discrete-time matrix population models (Caswell, 1989).

We have observed the following pairs of coexisting attractors in the model (2)–(3): for $r = 2.1$: period-eight and period-15 attractors at $a = 0.0671$, period-16 and period-45 attractors at $a = 0.06719$, chaotic and six-piece chaotic attractors at $a = 0.0693$; for $r = 2.4$: period-seven and period-21 attractors at $a = 0.0648$,

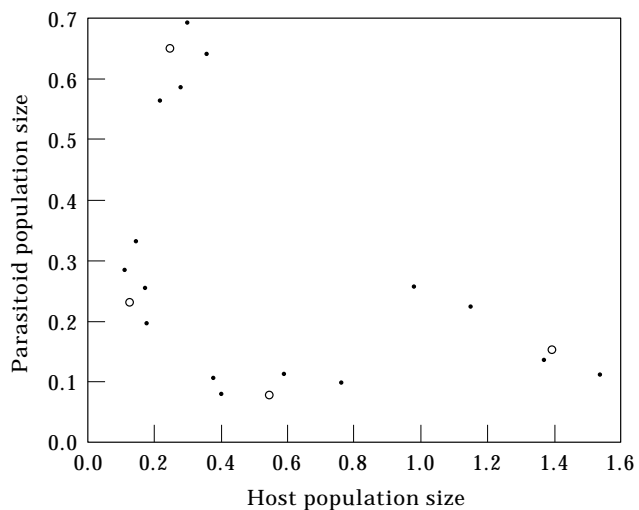


FIG. 6. Two alternative attractors for $r = 2.8$, $a = 0.043$: four-cycle and 16-cycle.

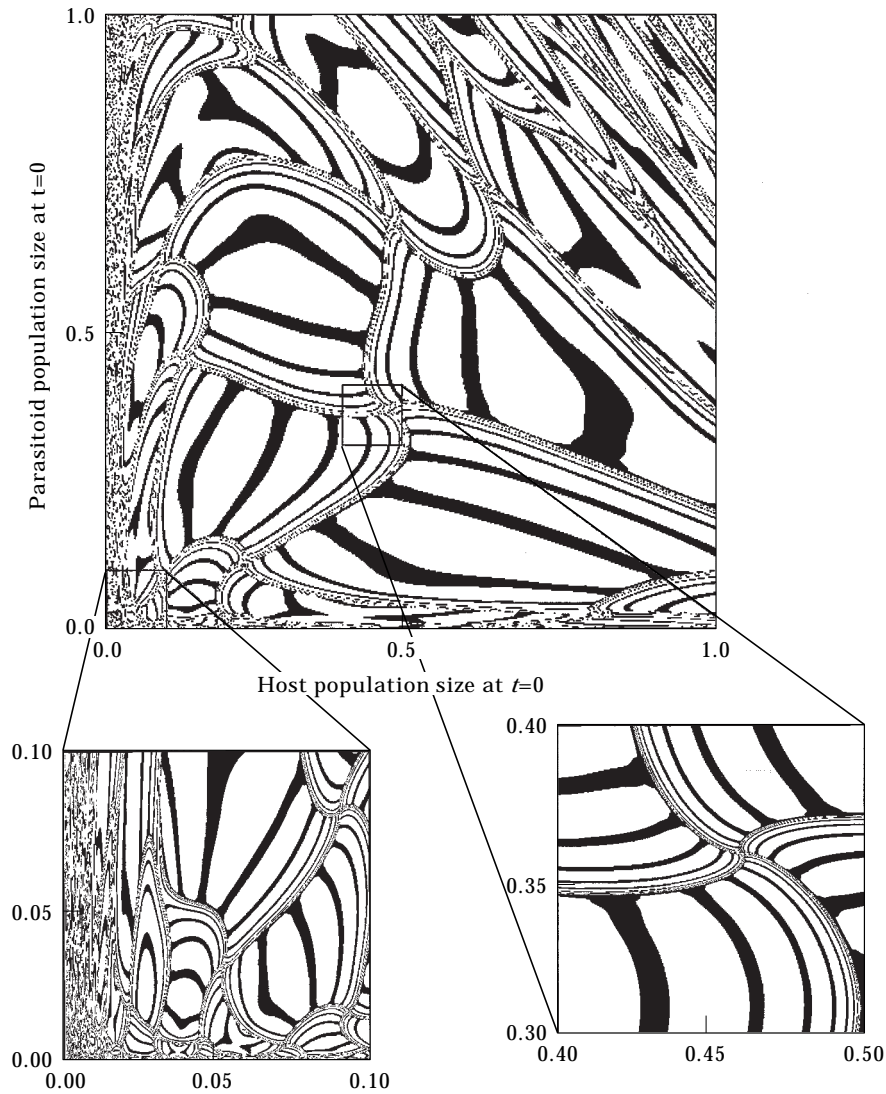


FIG. 7. The basins of attraction for the two alternative attractors—the black and white areas are the basins of attraction for period-four and period-16, respectively, illustrated in Fig. 5. The patterns of self-similarity and fractal basin boundaries indicate that the basins of attraction are fractals.

seven-piece quasiperiodic and chaotic attractors at $a = 0.06492$; for $r = 2.8$: four-piece chaos and four-cycle at $a = 0.044$. The reason why in some cases the attractor is composed of, e.g. six-piece chaos or seven invariant circles is related to the fact that the attractor has a strong periodic component in the dynamics. An n -piece chaos means a chaotic attractor which is divided into n distinct subsets (e.g. Testa & Held, 1983; Kaitala & Heino, 1996).

The basins of attraction are defined as the set of the initial conditions whose trajectories asymptotically approach that attractor as time

increases (e.g. Grebogi *et al.*, 1983). Figure 7 illustrates the basins of attraction for two alternative attractors—the black and white areas are the basins of attraction for the period-four and period-16 attractors, respectively. The fractal properties of the basins of attraction—self-similarity and fractal basin boundaries—can be clearly seen from two enlargements of the basins of attraction.

One very interesting aspect of non-uniqueness observed in this model is the non-uniqueness of the area of coexistence (Fig. 1). For some parameter values complex coexistence prevails or

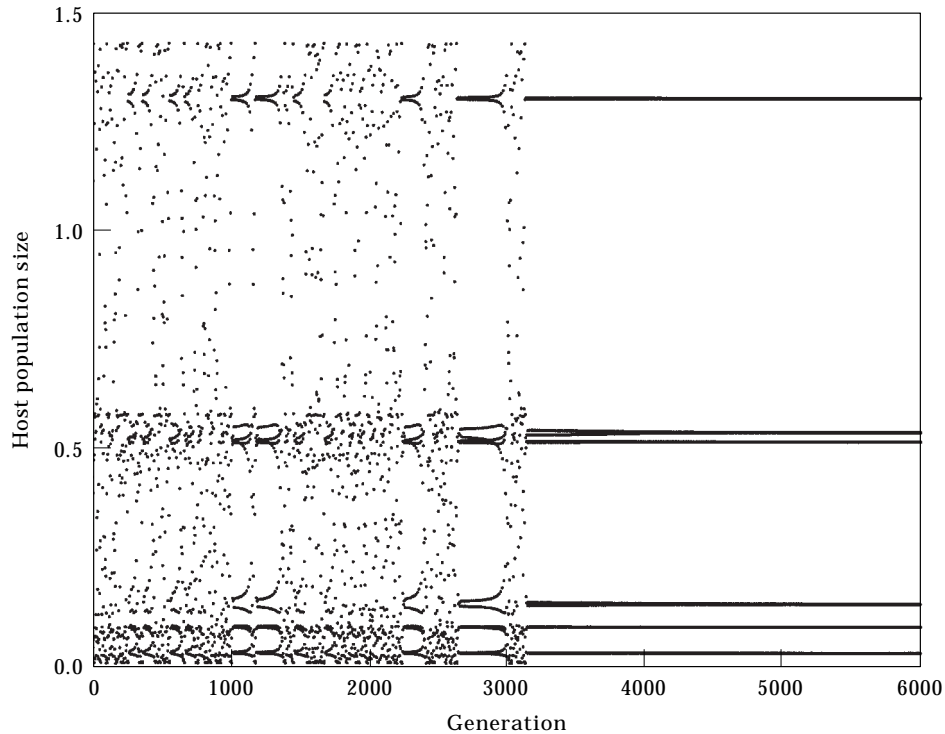


FIG. 8. Supertransient for $r = 2.1$, $a = 0.0716$ and initial conditions $N_0 = 0.5$, $P_0 = 0.5$.

parasitoids go extinct, depending on the initial conditions.

5. Supertransients and Chaos-like Transients

We conclude the analysis by studying some observations related to supertransients, chaos-like transients and chaotic attractors in the host-parasitoid interactions. Supertransients are used to denote an unusually long convergence to an attractor. These transient dynamics are considerably longer than the time-scale of significant environmental perturbations (Hastings & Higgins, 1994). The time-scale of ecological interest is tens or hundreds of generations, while supertransients can persist thousands of generations or even longer. Figure 8 shows an example of a supertransient. In this example, the host population size suddenly stabilizes into a period-six attractor after 3000 generations of complicated fluctuations resembling an intermittent trajectory. This indicates that transient chaos (e.g. Gavrillets & Hastings, 1995) can be observed also in a supertransient. Thus, chaos-like behavior is potential even when

the ultimate attractors do not suggest the presence of chaos in the dynamics.

6. Concluding Remarks

We have analysed in this paper the dynamic complexities in a basic discrete-time model of a host-parasitoid interaction. There are many forms of complexities in the interspecific interactions. Some complexities are related to the long-term behavior of population dynamics, characterized either by well-behaving relatively simple or very complicated strange attractors. Some complexities are related to the “non-equilibrium” transient dynamics towards the attractors, and the rest of the complexities reported here are related to the non-uniqueness of the dynamics, or attractors. The latter problem also leads us to study the patterns in the basins of attraction with fractal patterns. All the phenomena discussed in this paper are commonly observed in the model for $r > 1.7$ and $a > 0.03$.

The dynamic complexities are caused by nonlinearities in the population dynamics. These nonlinearities arise as abstractions of basic intra- and interspecific interactions, such as

cannibalism on larvae (Moran–Ricker-type of density dependence) and saturation of predation rate (Holling type II and III functional responses). Although many simplifying assumptions are necessary when modelling these interactions, dynamic complexities predicted by population dynamics models can be observed at least in laboratory populations (e.g. Costantino *et al.*, 1995, 1997).

The dynamic behavior of a population may dramatically be affected by small changes in the values of the parameters (e.g. periodic windows, frequency-locking) or in the values of the initial conditions as seen in the case of basins of attraction. Even if the parameter values and initial conditions remain the same, the trajectory can change significantly as time passes (e.g. intermittency and long transient behavior). This shows that if the time series is too short, only a part of the dynamic structure will be detected. Unfortunately, as the existence of supertransients imply, it may be difficult to determine the appropriate and reliable length for a time series.

Although the analysis has been conducted with constant parameter values for the handling time, T_h and total time initially available for searching, T , we have looked at the dynamic complexities for other values of T and T_h as well (for example, $T = 150$ and $T_h = 0.12$; $T = 96$ and $T_h = 0.24$). The results of these studies showed similar patterns as the case studied here. We also examined other forms of functional response (Holling types I and III; Holling, 1959b, 1966), which all produced complex dynamics. Thus, a certain type of functional response seems not to be necessary for the results observed in this paper.

Complex dynamic patterns have been observed in spatial logistic models in which local populations are connected by migration (e.g. Adler, 1993; Hastings, 1993; Lloyd, 1995). Beddington *et al.* (1975) showed that in discrete-time host–parasitoid models the dynamics can produce high period cycles and chaos. Dynamic complexities can also be observed in two-species interactions of hosts and parasites (Kaitala & Heino, 1996) and in predator–prey models (Rohani & Miramontes, 1995). Elsewhere, predators have been proposed to cause chaos-like oscillations in the dynamics of small

rodents (Hanski *et al.*, 1993). Nevertheless, identifying complicated, possibly chaotic dynamics in population data has remained a major challenge in ecological studies (Sugihara & May, 1990; Cazelles & Ferrière, 1992; Hastings *et al.*, 1993; Stone, 1993; Cohen, 1995; Kaitala & Ranta, 1996). The increasing number of potential complexities predicted by the theory does not seem to make this task any easier.

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APPENDIX

Local Stability Analysis

Let

$$B = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}$$

denote the linear approximation matrix of the system (2)–(3) at the non-trivial steady state (4)–(5). Then B is given as

$$b_{11} = 1 - rN^* + \frac{a^2 T T_h N^* P^*}{(1 + a T_h N^*)^2}, \quad (\text{A.1})$$

$$b_{12} = \frac{-a T N^*}{1 + a T_h N^*}, \quad (\text{A.2})$$

$$b_{21} = 1 - \left[1 + \frac{a^2 T T_h N^* P^*}{(1 + a T_h N^*)^2} \exp\left(\frac{-a T P^*}{1 + a T_h N^*}\right) \right], \quad (\text{A.3})$$

$$b_{22} = \frac{a T N^*}{1 + a T_h N^*} \exp\left(\frac{-a T P^*}{1 + a T_h N^*}\right). \quad (\text{A.4})$$

In a special case $(N^*, P^*) = (1, 0)$,

$$B = \begin{pmatrix} 1 - r & \frac{-a T}{1 + a T_h} \\ 0 & \frac{a T}{1 + a T_h} \end{pmatrix}$$

and the steady state is locally asymptotically stable (e.g. Caswell, 1989) when $|1 - r| < 1$ and $|a T / (1 + a T_h)| < 1$.