Modelling The Host-Parasite Interaction

Hemant Dixit, Ganesh Bagler and Somdatta Sinha

Abstract—**Discrete reproduction occurs in organisms whose generations do not overlap and are modelled using discrete equations or "maps". The simplest model for a single species population follows the logistic map where the population size shows a variety of stable and unstable dynamics, including chaos, with increasing intrinsic growth rate. Most organisms in nature exist in a trophic network, and their population sizes are dependent on the activity and abundance of the other species. Here we study the dynamics of a discrete host-parasite population and show, both analytically and numerically, that the presence of parasite affects the logistic growth dynamics of the host in a major way that depends on the infection properties of the parasite. The population dynamics of the host is stabilised irrespective of its intrinsic growth rate in presence of parasites with small infection rate. There is also a threshold infection rate below which the host population is not affected by parasites.**

Keywords— **Logistic Map, Bifurcation Diagram, Host-Parasite System, Population Dynamics.**

I. Introduction

THERE are two major types of reproduction (termed "growth" here) that occur in biological organisms. (i) Continuous growth, where generations overlap and successive generations can exist at the same time. These are modelled using differential equations. An example of a continuously growing organism is human. (ii) Discrete growth, where either (a) generations do not overlap, or, (b) there is age and stage structure of birth. These are modelled using discrete equations or "maps". Insects and annual plants are good examples of species exhibiting discrete growth. Many insects (butterflies and moths) go through different stages in their life-cycle by moulting from one stage to the other. The two stages do not co-exist in the same individual. Similarly the annual plants die once the seeds attain maturity.

A model for discrete growth with non-overlapping generations is given by the one-dimensional map $N_{t+1} = F(N_t)$, where N_{t+1} and N_t are the population sizes in the $(t+1)^{th}$ and t^{th} generations. Thus the population size in a generation is dependent only on its size at the previous generation. The function F depends on parameters such as growth and death rates of the organism, the carrying capacity of the environment and other processes such as predation pressure, migration.

When growth is density-dependent, i.e., population size decreases at higher density due to crowding effects, the simplest discrete model is given by the logistic equation

$$N_{t+1} = [1 + r'(1 - N_t/K)]N_t$$

On scaling N and r', the standard form of the logistic map is obtained as,

$$X_{t+1} = r\ X_t\ (1 - X_t)$$

where $X = [r'/(r'+1)](N/K)$ and $r' = (1+r)$. This form of F has a convex "single-hump" shape. There are many other formulations of F in discrete single population models which have similar shape decided by one or more parameters [1].

Most organisms in nature interact with other organisms in a trophic network. The well-known example is the prey-predator interaction where the population sizes of both the prey and predator is dependent on each other's activity and abundance. These are interacting species populations and are modelled using multi-dimensional coupled discrete maps [2]. A very important interaction for mankind is the host-parasite interaction, which contributes to the spread of disease and epidemic in both animal and plant resources. The general form of the discrete model used to describe host-parasite interactions in ecology is:

$$H_{n+1} = F(H_n, P_n)$$
$$P_{n+1} = G(H_n, P_n)$$

where H_{n+1} and H_n are the host and P_{n+1} and P_n are the parasite populations at $(n+1)^{th}$ and n^{th} generations. The functions F and G model the details of the host-parasite interactions. There are many different ways this interaction may occur in ecology [3].

In this paper we first study single population dynamics following the logistic map, and then study the host-parasite model where the logistically growing host is infected with the parasite. We study how the dynamics of the host is altered, when compared to its single population dynamics, due to presence of another species, which has some trophic interaction with it. The results indicate that the observed population dynamics of host species is more critically dependent on the infectivity of the parasite and the growth rate of the host plays a less significant role.

II. The Logistic Model

The one parameter (r, here) discrete logistic map given below, is the simplest of the one dimensional, non-linear discrete single population models [4].

$$F(X_n) = r\ X_n\ (1 - X_n) \qquad X_n \in [0,1], \quad r \in (1,4]$$

Though it may not be the most realistic model for population growth, it is analytically tractable. The steady states of this model are

$$X^* = 0 \quad \text{and} \quad X^* = 1 - \frac{1}{r}$$

The stability conditions of the two steady states are as follows: For the steady state $X^* = 0$,

$$\left.\frac{dF}{dX}\right|_{X^*=0} = r$$

Thus, for $0 < r < 1$ this steady state is stable and the population size always goes to zero. For $r \geq 1$, this steady state is unstable.

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For the steady state $X^* = 1 - \dfrac{1}{r}$,

$$\left.\frac{dF}{dX}\right|_{X^*=1-\frac{1}{r}} = 2 - r$$

$$\Rightarrow |2 - r| < 1$$

$$\Rightarrow 1 < r < 3 \qquad \text{for } X^* = \left(1 - \frac{1}{r}\right) \text{ to be stable}$$

Thus for $1 < r < 3$ this steady state is stable, and becomes unstable from $r \geq 3$. Since the steady state $X^* = 0$ is unstable from $r \geq 1$, the population stabilizes to $X^* = 1 - \frac{1}{r}$ for $1 < r < 3$, beyond which the logistic map shows unstable dynamics. This is also seen from the bifurcation diagram that summarises the dynamics of the logistic map for different values of the parameter r. Fig. 1 shows the bifurcation diagram of logistic map with increasing r.

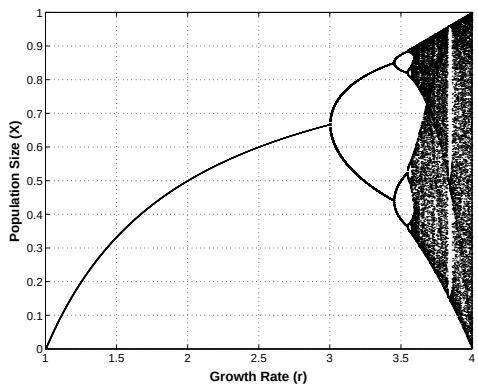

Fig. 1. Bifurcation Diagram for Logistic Map.

As shown in the stability analysis, the population size attains non-zero steady state for $1 < r < 3$. For a range of $r > 3$, (say, for r=3.2) the population size X_n oscillates about the steady state, alternating between a maximum and minimum size in successive generations repeating every two generations in this range of r. This type of oscillation is called period-2 cycle. As r is increased, further period-doubling bifurcation takes place and the population repeats every four generations giving rise to a period-4 cycle. This period doubling continues with increasing r and ultimately the cycle takes infinite time to repeat. It is found that infinite number of bifurcations occur at r=3.56994... and the dynamics become chaotic with population size attaining values between 0 and 1 by $r = 4$ [5].

III. The Host-Parasite (HP) Model

The Host-Parasite (HP) model system [6] is described by

$$\begin{aligned} H_{n+1} &= r\, H_n\,(1 - H_n)\, e^{-\beta P_n} \\ P_{n+1} &= H_n\,(1 - e^{-\beta P_n}) \end{aligned} \tag{1}$$

where H_{n+1} and H_n are the host and P_{n+1} and P_n the parasite populations at $(n+1)^{th}$ and n^{th} generation respectively, r is the intrinsic growth rate of host and β is the searching efficiency of the parasite, indicating its infectivity.

The assumptions underlying this model are:
1. The host population grows according to discrete logistic map with growth rate r and hence, in absence of parasite, can show a variety of dynamics depending on its growth rate (see Fig. 1).
2. The parasite can grow only in the presence of the host. The effect of parasite is to reduce the size of the host population.
3. Host-Parasite interaction is through the independent and random search by the parasite with constant searching efficiency. This interaction function is given by $e^{-\beta P_n}$, where β is searching efficiency of the parasite.

The steady states for the HP system in (1) is obtained from

$$e^{-\beta H^*\left(1-\frac{1}{(r(1-H^*))}\right)} = \left[1 - \frac{1}{(r(1-H^*))}\right] \tag{2}$$

$$P^* = H^*\left[1 - \frac{1}{(r(1-H^*))}\right] \tag{3}$$

To solve for H^*, we consider the following transcendental equation

$$1 - e^{-\beta H^*\left(1-\frac{1}{(r(1-H^*))}\right)} = 1 - \left[1 - \frac{1}{(r(1-H^*))}\right] \tag{4}$$

The solution of (4) gives the steady state values H^* and then using (3) we can find the corresponding P^*.

We use a graphical approach to solve for H^*. Let us denote

$$f = 1 - \left[1 - \frac{1}{(r(1-H))}\right] \tag{5}$$

$$g = 1 - e^{-\beta H\left(1-\frac{1}{(r(1-H))}\right)} \tag{6}$$

When we plot f and g for $0 < H < 1$, the intersections of these two curves satisfy (4) at $H = H^*$. Using (3) we can find the corresponding P^*. Fig. 2 shows the f, g plot for parameters $r = 2$ and $\beta = 4$. The figure shows that (4) gives two values of H^*, namely 0.50 and 0.29. The corresponding P^* are 0 and 0.09. Thus there are two steady states (H^*, P^*) of the Host-Parasite system. It may be noted that since we are interested in biological populations, we restrict the discussion only to the positive steady states, i.e., when both $H^*, P^* \geq 0$.

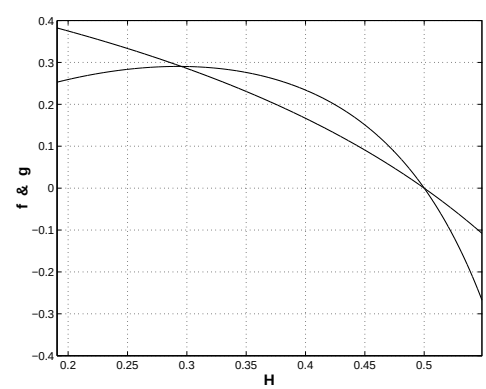

Fig. 2. f, g plot for $r = 2$ and $\beta = 4$.

Linear stability analysis shows that the steady states of HP system will be stable if they satisfy the conditions

$$2 > 1 + \beta H^* \left(1 - \frac{H^*}{r(1-H^*)^2}\right) \tag{7}$$

and

$$1 + \beta H^* \left(1 - \frac{H^*}{r(1-H^*)^2}\right) > \left|\frac{r + (\beta - 2r)H^*}{r(1-H^*)}\right| \tag{8}$$

Because of the presence of the transcendental function none of the relations obtained above can be simplified further. To understand the dynamics of the host and parasite populations for changes in the parameters r and β, we performed computational studies of (1).

IV. Computational analysis of the HP system

From the analysis of the logistic map in II, the population dynamics of the host (in the absence of parasite) is known for different values of r (see Fig. 1). We now show the dynamics of the host in the HP system below, for specific values of r and β.

A. For $r = 2$

The bifurcation diagram in Fig. 3 shows the long term host dynamics for increasing searching efficiency of the parasite (β). It is known that the intrinsic dynamics of the host (in absence of parasite) at $r = 2$ is equilibrium with $H^* = 0.5$. The bifurcation diagram shows that host exhibits a variety of dynamics with increasing β.

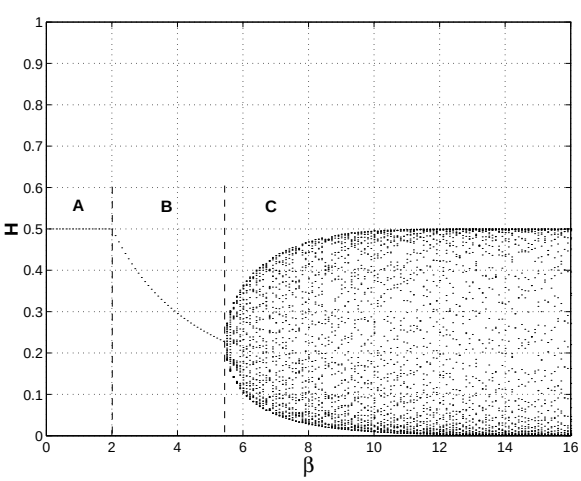

Fig. 3. Bifurcation Diagram with increasing β for $r = 2.0$.

For detailed analysis, we divide the bifurcation diagram in Fig. 3 into three regions, **A, B** & **C**. In region **A** and **B** the HP system is stable while in region **C** it shows complex dynamics like quasi-periodic oscillations and chaotic dynamics. We describe these regions using results from the steady state and stability analyses. Fig. 4 shows the plots for the steady states (given by (4)) and their stability (see (7) & (8)). Fig. 4(a - c) show the H^* values (indicated by arrows) for three values of β, (a) $\beta = 1$ (b) $\beta = 4$ and (c) $\beta = 6$, corresponding to the regions **A, B** & **C** respectively. If the parasite population corresponding to one of these H^* is zero, it is called an axial steady state and steady states corresponding to $H^*, P^* > 0$ are called interior steady states.

In region **A** ($0 < \beta < 2$), there is only one positive steady state,

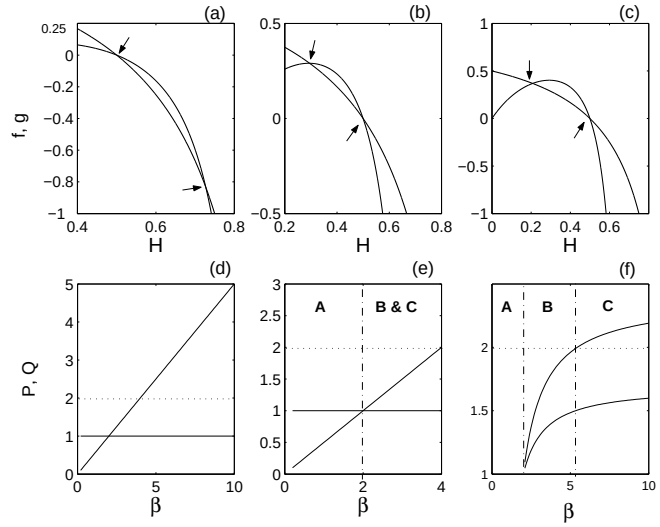

Fig. 4. f, g plots for obtaining H^* for (a) $\beta = 1$, (b) $\beta = 4$ and (c) $\beta = 6$; Stability plots for $r = 2$: (d) & (e) axial steady state and (f) interior steady state.

the axial steady state (Fig. 4 (a)). This implies that the parasite population is zero and host exhibits its intrinsic logistic dynamics in region **A**. We study the stability of the axial steady state by plotting the left (designated as P) and the right (designated as Q) hand side of (8) in Fig. 4(d) for increasing values of β. Fig. 4(e) shows Fig. 4(d) in expanded form. In region **A**, (7) and (8) are satisfied and the axial steady state is stable. Here, the HP system shows dynamics corresponding to the intrinsic growth rate of the host (stable for $r = 2$). In the regions **B** and **C**, the axial steady state is unstable as the stability condition given by (7) and (8) is violated. Thus the steady state analysis shows that the Host-Parasite system follows logistic dynamics in region **A**, as is also seen in the bifurcation diagram.

In region **B**, both the axial and interior steady states exist. The stability analysis (see (7) & (8)) of the interior steady state is shown in Fig. 4(f). It is clear from the figure that the interior steady state is stable for $2 < \beta < 5.4$. The bifurcation diagram (region **B**) also shows this. Here the parasite population increases with increase in searching efficiency β and consequently the host population decreases. Thus in region **B** the parasite grows by affecting the host. The host population decreases from 0.50 to 0.23 and the parasite population increases from 0 to 0.08 in this region.

In region **C** ($\beta > 5.4$), as is shown in both Fig. 4(e) and (f), both the axial and interior steady states are unstable as they do not satisfy stability criteria (see (7) & (8)). Hence the HP system shows unstable dynamics in this region. The bifurcation diagram shows quasi-periodic and chaotic dynamics in this range.

B. Other values of r

A similar analysis has been done with other values of r where the logistic map shows intrinsic oscillatory ($r = 3.2$), weak ($r = 3.6$) and strong ($r = 4$) chaotic dynamics. The corresponding bifurcation diagrams are shown in Fig. 5(a,b,c), In all the cases the bifurcation diagrams shows regions where the HP system behaves like logistic map for low values of β and there exist three regions as described in the earlier section.

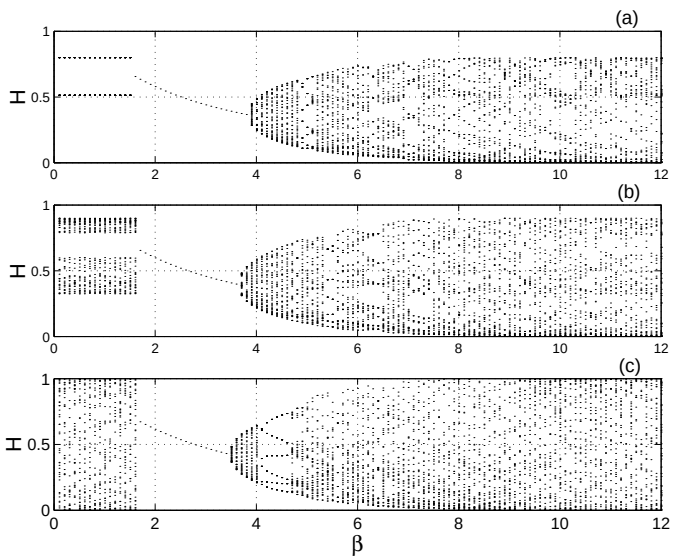

Fig. 5. Bifurcation diagrams for $r = 3.2$, $r = 3.6$ and $r = 4.0$

V. Discussion

In this paper we have discussed the dynamics exhibited by interacting host-parasite populations of discretely growing organisms such as, insects and annual plants. The results clearly show that the host dynamics is modulated by parasites differentially. When the host grows as a single population, its dynamics are solely decided by its intrinsic growth rate, r. In the logistic model the host population shows equilibrium population size at low growth rates and periodic variation as the growth rate is increased. At higher r the growth dynamics become chaotic. Our results show that when a parasite species interacts with the host, the growth of both host and parasite population depends on each others' activity and abundance. The infectivity of the parasite (given by β) has a crucial role to play in deciding the host population dynamics. The bifurcation plots show that there is a threshold value of searching efficiency ($\beta_{threshold}$) of the parasite. Parasites with β value lower than this threshold are unable to affect the host dynamics and the host does not allow parasite population to grow at its expense. They affect the host only if their searching efficiency is greater than the threshold value. The parasite can then exert its effect in modulating the host's intrinsic dynamics also. Following Table enumerates the threshold value of β for different values of r.

r	$\beta_{threshold}$
2	2.0
3.2	1.7
3.6	1.6
4.0	1.6

The Table shows that the threshold values of searching efficiency do not change significantly even when the growth rate of the host is doubled. It is only for $\beta > \beta_{threshold}$, that the Host-Parasite interaction comes into play and the parasite is able to suppress the host's intrinsic dynamics to equilibrium for all values of r. With increasing β the HP dynamics becomes unstable and complex. Thus the interaction between the two populations decides their population size and dynamics. We have shown [7], [8], [9] that it is possible to modulate the dynamics of both the logistic model and the HP system in a meta-population under constant migration of the hosts or parasites to the subpopulations. Thus the dynamics of both single and interacting species populations can be modulated by demographic and ecological processes such as the growth rate r, infectivity β and migration.

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