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Evolution of Chaotic Domain in the Discrete Lotka-Volterra Model for Predator-Prey Interaction

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Abstract: We undertake a detailed numerical analysis of the discrete version of the Lotka-Volterra model for predator-prey interactions. A complete picture of the long time dynamics of the system is presented including the type of bifurcations, nature of the underlying attractors and the general pattern for the transition to chaos, as each of the control parameter is varied independently. We are able to identify how the domain of chaos evolves in the parameter plane with the help of a dimensional analysis using a recently proposed algorithmic scheme for computing the fractal dimension of a chaotic attractor from time series. Finally, we also report the presence of a small region in the parameter plane with fractal structure where, the asymptotic dynamics depends sensitively on the control parameter values.

Keywords: Discrete Predator-Prey Model, Bifurcations, Chaos, Dimensional Analysis

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1 Introduction

Life in an ecosystem is very complex. One of the essential ingredients of this complex ecosystem is the co-evolution of different species, typically represented by the predatorprey interaction. It has been a long standing effort by the ecologists and mathematicians to understand the interaction and co-existence of predator and prey using simple mathematical models. This is also of interest to biologists trying to understand how different communities are structured and sustained.

The first attempt to this effect was made independently by Alfred Lotka [1] and Vito Volterra [2] who proposed a system of two coupled first order differential equations to understand the mechanism of evolution of the predator and prey. The field of mathematical biology flourished with the introduction of this model and a large number of variants of this model were suggested to capture the predator-prey and host-parasite dynamics. For details, see the excellent reviews by Freeman [3], Murray [4] and Brauer and Chavez [5].

In general, it is difficult to obtain a model that accurately mimics the real behavior in nature. The first goal of most of the models proposed initially was to find a regime where the out of phase periodic oscillations of predator-prey populations existed. Also, these models were two dimensional coupled differential equations where irregular or complex dynamics was not possible. The scenerio changed drastically after the seminal work by May [6, 7] who used discrete mathematical models to study the evolution of population of species and showed the presence of a wider range of dynamical behavior including chaos.

The original model proposed by Lotka-Volterra (L-V) had a few simplifying assumptions:

i) Prey population grows exponentially in the absence of predator

ii) Predator population starve to death in the absence of prey

iii) There is no environmental complexity; both populations are moving randomly through a homogeneous environment.

But in the last two decades, numerous modifications to the original model, both continuous and discrete, have been proposed and analysed to reveal various aspects of predator-prey dynamics. For example, some authors have addressed the effect of periodically changing environment and delay in the predator-prey dynamics [8, 9, 10, 11], while some others have focussed on models with functional response and group defense for predator-prey interactions [12, 13, 14]. Some studies have been phenomenological where results obtained from theoretical models are compared with real data sets [15, 16, 17].

Even with all these modifications, the discrete version of the original L-V model is considered to be the prototype for the study of predator-prey dynamics with nonoverlapping populations, which we discuss in some detail. For a single species with limited resources, the simplest model that can be used to study the evolution of population is the standard logistic map [7]:

$$x_{n+1} = ax_n(1 - x_n)$$
(1)

The expansion phase of the population is represented by the term ax_n , with a being the constant growth rate. To avoid over population with limited resources, there should be a contracting phase represented by the term $(1 - x_n)$. The parameter a should vary in the range 0 < a < 4 for x_n to be limited in the interval [0, 1]. The L-V system for predator-prey interactions with limited resources for prey can be written in the general

form:

$$\frac{dx}{dt} = rx(t)(1 - x(t)) - bkx(t)y(t)$$

$$\frac{dy}{dt} = -cy(t) + dkx(t)y(t)$$
(2)

where x(t) and y(t) represent the population of prey and predator respectively and r, b, c, dand k are positive parameters. The rescaled discrete version of the above model which comes under the family of discrete canonical models can be written in general as (see [8]):

$$x_{n+1} = ax_n(1 - x_n) - p(y_n)x_n$$

$$y_{n+1} = -cy_n + q(x_n)y_n$$

For the model to represent the predator-prey interaction in a region, x_n corresponds to the normalised fraction of the population of prey, while y_n corresponds to the population density of predator over the region at a discrete time step n. The parameter a represents the intrinsic growth rate of prey and c the natural death rate of predator and both are positive. The terms $(-p(y_n)x_n)$ and $(+q(x_n)y_n)$ describe the predator-prey interactions which are favourable for the predator and fatal for prey.

The function $p(y_n)$ is called the *predator response function* and represents the effectiveness of predation which is a measure of the death rate of prey. In each time step, a fraction $p(y_n)x_n$ of prey density is lost by prey due to predation. Similarly, the function $q(x_n)$ called the *predator transfer function*, is a measure of how much the predator can transfer the advantage of predation for increasing its population. Its population increases by a factor $q(x_n)$ from one generation to the next. Note that both $p(y_n)$ and $q(x_n)$ depend on the particular predator-prey system and also on several factors, such as, environment or seasonal change, search time for predation, maturity time for predator, etc. and can, in general, be nonlinear functons. Several authors [8, 9, 10, 11, 12] have used nonlinear functions which are specific to the predator-prey interactions in particular contexts. But in a general context, one usually employs simple linear functions for $p(y_n)$ and $q(x_n)$ as a first approximation. We show that even the simplest linear case is very rich in dynamical behavior. Taking $p(y_n) = by_n$ and $q(x_n) = dx_n$, where b and d are positive parameters, the model can be written as:

$$x_{n+1} = ax_n(1 - x_n) - bx_n y_n$$

$$y_{n+1} = -cy_n + dx_n y_n$$
(3)

Note that we use two different parameters b and d since the two functions $p(y_n)$ and $q(x_n)$ are, in general, different. While b has to be very small since the successful predation rate is usually small, the parameter d is very crucial and has to be much larger than b, as it corresponds to what fraction of the prey population is consumed by predator to enhance its population. Details regarding the selection of all the parameter values are discussed in §3.

It is clear that the model can be regarded as a coupling perturbation of model (1) in \mathbb{R}^2 and in the absence of predator, the model reduces to the logistic map. Apart from the

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ecological relavance, our focus in this study will also be the richness in dynamics shown by this simple discrete model. Many authors have studied this model in detail analytically and numerically. For example, the above model for c = 0 has been analysed by Danca et al. [18] and showed the presence of chaotic attractors for certain range of parameter values. The case $c \neq 0$ has been studied analytically and numerically by Liu and Xiao [19] and Elsadany et al. [20]. They have shown that both a and d can independently act as control parameters and as the parameters are tuned, the asymptotic state can be periodic or chaotic with underlying strange attractors. Some variants of this model have also been proposed and analysed in the past. Examples are discrete models with nonlinear response functions [21, 22], models with both prey and predator having logistic evolution [23] and titrophic food chain models involving 3 species [24, 25, 26, 27, 28].

However, in most of the cases, studies have mainly been confined either to locating the stable regimes using linear stability analysis, or to bifurcation analysis searching for chaos and underlying strange attractors for selected range of parameter values. On the other hand, a detailed understanding of the dynamical behavior over the entire parameter plane is still lacking in most of the cases, which requires a comprehensive numerical analysis of the parameter plane. For example, regarding model (3), it is still not clear what the exact sequence and type of bifurcations is, as the system turns chaotic. Another point of interest is to locate the various domains of dynamics in the parameter plane, especially that of chaos, and to understand how these domains evolve as the control parameters are tuned. Note that in order to locate the domain of chaos in the parameter plane, one has to scan the entire plane and also use a quantifying measure to distinguish chaotic from periodic behavior. Here we use the dimension of the underlying attractor as the quantifying measure. Dimension is computed from the time series for each parameter value using an algorithmic scheme recently proposed by one of us [30, 31]. While doing this analysis, we have come across an interesting result which is also reported here. We find that over a small range of d values in the parameter plane, the asymptotic state shows "sensitive dependence" on the value of d. In other words, the asymptotic state switches between two stable attractors for an infinitesimal change in the parameter and the set of d values leading to any one attractor is a *fractal*.

Our paper is organised as follows: In the next section, we discuss the linear stability analysis and the periodic regime of the map. Results of numerical analysis are presented in §3. This section is divided into two subsections for c = 0 and c > 0. For each case, bifurcation diagrams, parameter plane analysis and the corresponding state space dynamics showing the nature of attractors are shown. Our numerical analysis gives a complete understanding regarding the dynamics of the system in the 3D parameter space (a, d, c). The details of the dimensional analysis for identifying the chaotic domain for each value of c is presented in §4 and the discussion and conclusions are drawn in §5.

2 Stability Analysis and Periodic Regime

In this section, we present some analytical results related to fixed points and periodic cycles of the map which are essential for a proper understanding of our numerical results. More details can be found elsewhere [18, 19, 20]. There are two stable fixed points for the

map (3) given by

$$(x_1^*, y_1^*) = (\frac{a-1}{a}, 0), (x_2^*, y_2^*) = (\frac{1+c}{d}, \frac{a}{b}(1 - \frac{1+c}{d}) - \frac{1}{b})$$

apart from the trivial fixed point $(x^*, y^*) = (0, 0)$. Taking the linearised Jacobian matrix J, the stability of a fixed point can be established by calculating the eigen values λ of J corresponding to the fixed point using the characteristic equation

$$|J - \lambda I| = 0 \tag{4}$$

For the trivial fixed point (x^*, y^*) , one can easily show that the eigen values are given by $\lambda_1 = a, \lambda_2 = -c$. Thus, the fixed point (0, 0) is asymptotically stable only if both a, c < 1, otherwise it is unstable. As discussed in §3, since here we consider c to be in the interval [0, 1], the fixed point (0, 0) is stable for a < 1 irrespective of the values of b and d and both prey and predator vanish asymptotically.

We now consider the stability of (x_1^*, y_1^*) and (x_2^*, y_2^*) . The eigen values $\lambda_{1,2}$ corresponding to (x_1^*, y_1^*) are

$$\lambda_1 = 2 - a \tag{5}$$

and

$$\lambda_2 = \frac{d(a-1)}{a} - c \tag{6}$$

Thus, (x_1^*, y_1^*) is stable if

$$1 < a < 3 \tag{7}$$

and

$$d < \frac{a(1+c)}{(a-1)} \tag{8}$$

for c restricted in the interval [0, 1].

For the fixed point (x_2^*, y_2^*) , note that while x_2^* is always positive, y_2^* is not. For y_2^* to be positive, $a(1 - \frac{1+c}{d}) > 1$. This gives the condition

$$d > \frac{a(1+c)}{(a-1)} \tag{9}$$

with a > 1 for $y_2^* > 0$. This implies that for a given value of c, if we draw a curve given by

$$d = \frac{a(1+c)}{(a-1)}$$
(10)

in the parameter plane a - d, the predator population tends to zero asymptotically below this curve and the dynamics of prey is governed by the logistic map with period doubling and chaos as a increases.

We now consider the case $y_2^* > 0$ and check the domain of stability of (x_2^*, y_2^*) . For this, we calculate the eigen values $\lambda_{1,2}$ corresponding to (x_2^*, y_2^*) which are

$$\lambda_{1,2} = \left(1 - \frac{a(1+c)}{2d}\right) \pm \sqrt{\left(1 - \frac{a(1+c)}{2d}\right)^2 - a(1+c)\left(1 - \frac{c}{d}\right) + c} \tag{11}$$

One can check that the condition $\lambda_{1,2} < 1$ is satisfied for exactly the same condition (11) as above. Hence, the fixed point (x_2^*, y_2^*) becomes stable as the parameter values make a transition above this curve and one expects a stable fixed point with co-existence of prey and predator.

The domain of stability for the fixed point (x_2^*, y_2^*) can be determined by looking at the characteristic equation for the Jacobian J at the fixed point, which can be shown to be of the form

$$P(\lambda) = \lambda^2 - Tr\lambda + Det = 0 \tag{12}$$

where Tr is the trace and Det is the determinant of the Jacobian matrix $J(x_2^*, y_2^*)$ and are given by

$$Tr = 2 - \frac{a(1+c)}{d} \tag{13}$$

$$Det = a(1+c)(1 - \frac{(2-c)}{d}) - c$$
(14)

If the eigen values λ_i for $J(x_2^*, y_2^*)$ are inside the unit circle in the complex plane, then the fixed point (x_2^*, y_2^*) is locally stable. The necessary and sufficient condition for this are given by

- i. P(1) = 1 Tr + Det > 0
- ii. P(-1) = 1 + Tr + Det > 0
- iii. P(0) = Det < 1

By substituting the values of Tr and Det, the above 3 conditions can be shown to be equivalent to

$$d > \frac{a(1+c)}{(a-1)}$$
(15)

$$d > \frac{a(1+c)(3+c)}{a(1+c)-c+3} \tag{16}$$

$$d < \frac{a(2+c)}{(a-1)} \tag{17}$$

Thus, the region of stability for the fixed point (x_2^*, y_2^*) is determined by the condition

$$d \in \left(\frac{a(1+c)}{(a-1)}, \frac{a(2+c)}{(a-1)}\right)$$
(18)

As d increases beyond the limiting value, the fixed point becomes unstable through a Hopf bifurcation producing a limit cycle. Thus, the curve of Hopf bifurcation in the parameter plane is given by the condition

$$d = \frac{a(2+c)}{(a-1)}$$
(19)

The domain of limit cycle attractor and what happens beyond that can only be determined numerically. As a and d increase further, the system shows more complex behavior including chaos. We now explore this region of the parameter plane numerically in detail and show that the asymptotic state passes through different stages, such as, inverse Hopf bifurcation, period doubling and finally chaos. We also identify the domain of chaos exactly in the parameter plane using a dimensional analysis recently proposed.



Figure 1: The bifurcation structure of the predator-prey model (3) with a as the control parameter for c = 0 and d fixed at 3.56. The upper panel shows the variation of prey population and the lower panel the corresponding values of predator. The asymptotic state passes through different phases as discussed in the text, starting from fixed point. Moreover, the nature of the attractor for both prey and predator are always identical and synchronised. Note that while the long time behaviour of prey is always confined to the unit interval, that of predator varies over a much wider range. Beyond a = 4, the trajectories escape to ∞ .

3 Numerical Analysis of the Parameter Plane

In this section, we undertake a detailed numerical analysis of map (3). For that, one has to fix the set of parameter values (a, b, c, d) and the range of initial condition for the population densities x_n and y_n of the prey and the predator. As the growth rate of prey is governed by the logistic dynamics, the value of x_n should always be confined within the unit interval [0, 1], where as, no such restrictions are required for y_n . For this, the value of the parameter a is to be confined to the interval [0, 4] and for a > 4, the trajectory will eventually escape to ∞ . In our numerical simulations, we have used different initial conditions (x_0, y_0) within the unit interval [0, 1] and we have found that the asymptotic state is independent of the initial condition. While x_n is confined in the unit interval, y_n varies over a much wider range, as can be readily seen from our figures.

From the results obtained from the stability analysis in §2, it is clear that only the three parameters a, c, d are important in deciding the asymptotic dynamics of the system. The effect of the parameter b is only to fix the position of the attractor in the state space and by changing b, the attractor only gets shifted, but the nature of the attractor is not changed. Moreover, both b and c represent the measures by which the prey and the predator population get decreased, the former due to interaction with predator and the latter due to natural causes. For a physically meaningful model, both these terms should



Figure 2: Same as the previous figure, but with d as the control parameter and a fixed at 3.56.

be small. Since b cannot be a control parameter, we fix b = 0.2 throughout in all our numerical calculations in this paper while the value of c is varied in the interval [0, 1].

The value of the parameter d quantify the increase in the predator population as a result of predation. It depends on many factors, such as, population density of prey, the efficiency of predation, etc. We find that, to sustain the predator population, sufficient amount of prey bio mass $(q(x_n) \equiv dx_n)$ has to be consumed which, in turn, implies that the value of d should be fairly large for the predator to survive. Hence, d has to vary over a wider range. Though the model may not be ecologically relevant as d becomes large, we use a wider range of values of d to explore the richness in the dynamical behavior of the system. Since a and d represent the growth rates of prey and predator, we take a and d as the primary set of parameters and numerically analyse the bifurcations, nature of attractors, onset of chaos, etc. in the a - d parameter plane for different fixed values of c increasing it from 0 to 1. Obviously, c has to be a small fraction since it represents the eath rate of predator due to natural causes. Here we vary c upto 1 only to explore the rich dynamics of the model. We have numerically found that the range of d values where the system shows rich dynamics is [0, 4] for small c, beyond which the trajectories mostly escape to ∞ .

3.1 Case I: c = 0

We first fix the value of c as 0 which implies that the natural death rate of the predator is zero. From the results in §2, the predator population becomes extinct and the dynamics of prey is governed by the logistic map below the curve

$$d = \frac{a}{a-1} \tag{20}$$



Figure 3: Bifurcation structure of model (3) with c = 0 and a as the control parameter for a fixed value of d = 4.5. Only the asymptotic values of prey (x) are shown as that of predator are identical. The richness in the dynamics is evident. Also, the domain of escape starts much earlier at $a \sim 2.8$ and keeps on advancing as d increases shrinking the chaotic phase.

in the a - d plane. As d crosses this curve, the population of predator and prey get stabilized asymptotically as a stable fixed point until the fixed point becomes unstable along the curve

$$d = \frac{2a}{a-1} \tag{21}$$

Along this curve, the system undergoes a Hopf bifurcation and the fixed point is converted into a limit cycle with stable oscillations for predator and prey. We now explore numerically as to what happens beyond this curve by varying both a and d.

For this, we first fix the value of d starting from 2 and increase it in steps of 0.01 and for each d value, the bifurcation structure for both prey and predator are computed with a as the control parameter, increasing a in steps of 0.001. The analysis is repeated with das the control parameter increasing in steps of 0.001 for different fixed values of a in the range [1, 4]. Typical bifurcation structure in bothcases are shown in Fig.1 and Fig.2, for both prey and predator. In Fig.1, a is the control parameter with d = 3.56 and vice versa in Fig.2. It is clear that the asymptotic state passes through different phases, in both cases. For example, in Fig.1, the fixed point is first converted to a limit cycle by Hopf bifurcation, which varies in size and shape as a increases. The limit cycle then undergoes an inverse Hopf bifurcation and gets converted into a *period* – n orbit. This appears as a periodic window in the bifurcations and finally gets converted into a chaotic attractor at a critical value of a. There are also several periodic windows, large and small, within the chaotic regime.



Figure 4: A part of the bifurcation structure for predator with d as the control parameter for c = 0 and the value of a as indicated. There is a small region shown within the two vertical lines where the dynamics sensitively depends on the value of d. The asymptotic state switches between zero and a stable state for an infinitesimal change in the control parameter d.

The general sequence of bifurcation pattern is more or less the same in Fig.2 also and at a critical value of d, the system turns chaotic. An interesting observation is that the bifurcation structure for prey and predator are exactly identical in both cases. In other words, the asymptotic states of prey and predator are always synchronised. We have found that this is generally true for all parameter values, except when the predator becomes extinct asymptotically.

As mentioned earlier, eventhough the value of a is to be restricted to a maximum of 4, d is varied over a wider range. But it is found that as d increases beyond 4, there is a particular point (a, d) in the parameter plane for a < 4 at which the attractor suddenly disappears through a phenomenon called *crisis* [29] and the trajectory escapes to infinity. In the present case, it is the boundary crisis. For a = 4, the escape occurs at d = 4. As d increases beyond 4, the value of a decreases correspondingly and the domain of escape grows to values for a within the interval [0, 4] and into the regime of stable dynamics in the parameter plane. It also encroaches into the domain of chaos as d increases, which keeps on depleting and finally gets fully swamped out by the region of escape for a value of d close to 4.7. To show this, we present the bifurcation for prey in Fig.3 for a value of d = 4.5. The bifurcation structure of predator is not shown as it is identical. Note that the chaotic domain gets depleted and the trajectories escape to ∞ beyond $a \approx 2.8$. This value keeps on decreasing as d increases.

Thus, in the parameter plane, small values of a or d leads to logistic dynamics for prey and extinction for predator. As a or d increases, the successive domains are that of fixed point, limit cycle, chaos and finally escape of the trajectories. One important result



Figure 5: The figure shows self similar fractal structure for the control parameter d. Top panel shows the magnified view of the region bounded by the two vertical lines in the previous figure. Each panel is a blow up of the segment bounded by the vertical lines in the panel above it.

that we report in this work is the identification of the domain of chaos exactly in the parameter plane for different values of c and we show how the domain of chaos varies as c increases. This is achieved using a dimensional analysis, whose details are presented in §4. We now discuss another result which, we think is unique for this model and has not been reported elsewhere. In Fig.4, we show part of the bifurcation structure for predator with d as the control parameter for a fixed value of a. Note that for a small range of d values, indicated by two vertical lines, the asymptotic state is sensitively dependent on the value of d. In other words, the asymptotic state switches between zero and the fixed point for an infinitesimal change in the value of d. Corresponding to this, the long time steady state of prey switches between logistic chaos and fixed point. A fractal structure for d is evident if we give a blow up of this small region as shown in Fig.5. This happens for a range of a values. From a physical point of view, this may be considered as a result of competition between predator and prey for survival as it occurs on the doundary between predator extinction and stability.

To ensure that this is not a numerical artifact, we have checked the result with 10 different initial conditions in the interval [0, 1], all showing the same result. The only change is that the range of d values showing this sensitive dependance fluctuates depending on the initial conditions. There is always a finite set of d values leading to stability (extinction) of predator population which is fractal. In other words, this is a sort of bistability in the parameter plane. An infinitesimal perturbation to the value of d can flip the asymptotic state of the system from stability to extinction and vice versa. Interestingly, no such sensitivity occurs if d is fixed in the sensitive region and a is varied. We have verified this numerically. A more detailed numerical investigation is currently going on to

understand this result.

We now combine all our results so far for c = 0 in Fig.6, where the complete parameter plane for the model is shown. Different domains of dynamics are indicated. The dotted line represents the theoretical curve, as obtained in $\S 2$, above which the nontrivial fixed point becomes stable and prey and predator co-exist. The dashed curve is the one obtained numerically below which the predator becomes extinct. Obviously, the two lines deviate at a = 3. The reason is that at a = 3, the logistic map undergoes period doubling and the asymptotic values of prev starts fluctuating rather than staving fixed. For d small (d < 2) and a > 3, the dynamics of the total system is dominated by that of the logistic map, forcing the predator to extinction. Thus, numerically we find a small domain in the parameter plane for values of a in the range [3, 4] and values of d small where, y_n asymptotically $\rightarrow 0$. This domain is indicated by a *star* in the parameter plane. We see below that this domain gets widened and shifted to larger values of d as the value of c increases since a non-zero natural death rate further increases the chance of predator extinction. On the boundary between this domain and the domain of fixed point, there is a small region indicated by scattered points where, the dynamics is sensitively dependent on the value of d switching between extinction and stability for the predator as discussed above.

3.2 Case II: c > 0

In the previous section, we assumed that the natural death rate of the predator is zero. Here we will see how the dynamics changes for c > 0. We have analysed the system numerically by incrementing the value of c in steps of 0.2 upto c = 1. The broad pattern of dynamical regimes in the parameter plane is identical to Case I, but our aim is to find out how the finer details of various domains change as c increases. Note that when the natural death rate of predator is > 0, the possibility for predator extinction enhances shifting all the domains upwards. The domains for the fixed point and limit cycle can be obtained using the equations derived in §2, whereas the domain of chaos, escape and the region of sensitivity are obtained for each value of c using the numerical and dimensional analysis as in the case c = 0.

We first fix c = 0.2. As in the previous case, the bifurcation structure is computed first using a as the control parameter fixing d and vice versa with d as the control parameter fixing a. In Fig.7, we show the bifurcation structure for prey for both cases. The corresponding bifurcation structure for predator are not shown as they are identical. Though the bifurcation structure is different in finer details in both cases, the different stages in the transition of attractors from fixed point to chaos are broadly identical as shown in Fig.8. The fixed point first gets transformed into a limit cycle through Hopf bifurcation whose shape changes with the increase in the parameter. The limit cycle then changes into a periodic attractor of period n that is seen as a periodic window in the bifurcation structure. The periodic attractor then period doubles into a chaotic attractor with several pieces which finally combine to form a single chaotic attractor. We also find that the region of sensitive dependence is extended to a wider range of d values as c increases to 0.2, as can be seen from Fig.9.

The complete parameter plane for c = 0.2 explicitly showing different domains of

dynamics is given in Fig.10. The changes in the finer details of the domain structure is evident on comparison with Fig.6. Note that the region of forced predator extinction, indicated by *star*, has been extended to larger values of d and even encroached in to the limit cycle regime while the domain of chaos has shifted upwards and shrinked. The analysis is repeated by increasing c in steps of 0.2. We find that, as c increases, the domain of chaos keeps on depleting and the regime where the predator is forced into extinction (for a in the range [3, 4]) keeps on expanding. As an example, we show the parameter plane for c = 0.8 in Fig.11.

To get a better idea of the change in the domain structure, we show in Fig.12, the variation of the projection of different domains along the vertical line a = 4 of the parameter plane as c varies from 0 to 1. The depletion in the chaotic domain and the expansion of the domain of predator extinction as c increases is evident from this figure. One may expect that for sufficiently large value of c, the chaotic domain may disappear altogether.

4 Dimensional Analysis

In this section, we present the details of the dimensional analysis used to identify the chaotic domain in the parameter plane. The quantifying measure used to identify chaos is the correlation dimension D_2 of the underlying attractor. We use the nonsubjective algorithmic scheme proposed [30, 31] and implemented [32] recently to compute D_2 from the time series, which is based on the delay embedding algorithm [33]. To apply this, one has to generate the time series of the underlying attractor for each set of parameters (a, d, c).

To show the details, we fix c = 0.2. For a constant value of d, we scan the region of the parameter plane starting from the Hopf bifurcation value of a and increasing it in steps of 0.01. For each pair of values (a, d), we generate 10000 data points of the attractor after discarding the transients. Each time series is then subjected to the dimensional analysis using the non subjective algorithmic scheme, computing D_2 as a function of the embedding dimension M. The saturated value of D_2 is taken as the dimension of the underlying attractor as shown in Fig.13 for a typical time series. We label the attractor as chaotic if the saturated $D_2 > 1$. We mark the point (a, d) in the parameter plane where D_2 first crosses 1. The analysis is repeated by incrementing d in steps of 0.01. We are thus able to identify the curve the (a, d) plane within an accuracy of 0.01 where the attractor first turns chaotic. The region in the parameter plane between this curve and the curve joining the points of escape for each (a, d) is taken as the domain of chaos. Note that within the domain of chaos, there are innumerable periodic windows as well.

Typical chaotic attractors of the predator-prey model (3) for four different sets of parameter values are shown in Fig.14. In Fig.15, we show the variation of the saturated D_2 as a function of the parameter *a* for two different fixed values of *d*. As the attractor becomes chaotic at a critical value of *a*, D_2 makes a transition to a value > 1. We have found that the value of D_2 can vary up to a maximum of ~ 1.94. Dimension is a measure of the geometric complexity of the attractor. Our results imply that the underlying chaotic attractors of the model vary significantly in geometric complexity and also formed as a disjoint set initially. It is interesting that even the simplest model shows such a varied range of complexity in the predator-prey interaction.

5 Discussion and Conclusion

The problem of competition between two species is an old one and different mathematical models have been proposed to understand its mechanism. The predator-prey models are probably the most studied ones in the context of deterministic chaos. In this study, we consider the simplest of the predator-prey models and undertake a detailed numerical analysis of the entire parameter plane of the model. We also present some basic results on periodic regimes using the stability analysis. We take the natural growth rate of prey (a) and the growth rate of predator (d) as the primary set of parameters and clearly unravel the different types of bifurcations and asymptotic dynamics leading to chaos as these two control parameters are changed. With the help of a dimensional analysis, we are able to locate the domain of chaos exactly in the parameter plane and also determine how the domain evolves as the natural death rate of predator (c) increases from zero. We find that the domain of chaos is maximum when c = 0 which shrinks and also get shifted to higher values of d as c is increased. Another novel result, which we find numerically and not reported elsewhere, is the identification of a sensitive region in the parameter plane with a fractal structure where the asymptotic state of the system switches between two stable states with an infinitesimal perturbation in the control parameter.

One general conclusion that we can arrive at from our analysis is that the asymptotic states of prey and predator are mostly synchronised except for sufficiently low value of d when the dynamics is dominated by the logistic map and the predator is forced into extinction. The synchronisation in the predator-prey dynamics is already a known result and has been discussed by some authors previously [34, 35]. When the natural growth rate a of prey is small and < 1, the predator population inevitably becomes extinct along with prey. However, when a is close to its maximum possible value 4, we still find that the prev population forces the predator to extinction if d is small. The region 3.5 < a < 4in the parameter plane is where the dynamics becomes most interesting. As the value of d increases, there is a competition between predator and prey for survival. For a small range of d values on the boundary between stability and extinction, the asymptotic state depends sensitively on the value of d as well as initial condition and can even flip between two stable states as d varies infinitesimally. As d increases further, the predator and prey populations get synchronised into a stable limit cycle or chaos. The stable co-existence of predator and prev mostly occurs when the range of values of a and d are intermediate. Note that even for a < 3 (corresponding to stable one cycle of logistic map), the system can settle into chaotic oscillations for sufficiently large value of d for c = 0, as can be seen from Fig.6. Different asymptotic states are possible for the intermediate range of adepending on the value of d, such as, fixed point, limit cycle, periodic orbit or chaos. But in all cases, the asymptotic states of prey and predator are always synchronised.

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References

- [1] Lotka, A. J., *Elements of Physical Biology*, (Williams and Wilkins, USA, 1925).
- [2] Volterra, V., Variazioni e fluttuazioni del numero in specie animali conventi, Mem. Acad. Lincei. 2, 31–113, (1926).
- [3] Freedman, H. I., Deterministic Mathematical Models in Population Ecology, (Marcel Dekker, New York, 1980).
- [4] Murray, J. D., *Mathematical Biology*, (Springer, New York, 1993).
- Brauer, F., Chavez, C., Mathematical Models in Population Biology and Epidemology, (Springer, New York, 2001).
- [6] May, R. M., Biological populations obeying difference equations, stable points, stable cycles and chaos, J. Theor. Biology, 51(2), 511–524, (1975).
- [7] May, R. M., Simple mathematical models with very complicated dynamics, Nature, 261, 459–467, (1976).
- [8] Kuznetzov, Y. A., Muratori, S., Rinaldi, S., Bifurcations and chaos in a periodic predator-prey model, Int. J. Bif. and Chaos, 2, 117–128, (1992).
- [9] Dodd, R. R., Periodic effects arising from Hopf bifurcations in predator-prey model, J. Math. Biology, 35, 432–452, (1997).
- [10] Krise, S., Choudhury, S. R., Bifurcations and chaos in predator-prey model with delay and laser diode system with self sustained pulsations, Chaos, Solitons & Fractals, 16, 59–77, (2003).
- [11] Yan, X. P., Chu, Y. D., Stability and bifurcation analysis for a delayed Lotka-Volterra predator-prey system, J. Comp. Appl. Math., 196, 198–210, (2006).
- [12] Kazarinoff, N. D., Driessche, P. vanden, A model predator-prey system with functional response, Math. Bioscience, 39, 125–134, (1978).
- [13] Ruan, S., Xiao, D., Global analysis in a predator-prey system with non-monotonic functional response, SIAM J. Appl. Math., 61, 1445–1472, (2001).
- [14] Walkowicz, G. S. K., Bifurcation analysis of a predator-prey system involving group defense, SIAM J. Appl. Math., 48, 592–606, (1988).
- [15] Berryman, A. A., On choosing models for describing and analysing ecological time series, Ecology, 73, 694–698, (1992).
- [16] Berryman, A. A., Population cycles: a critique of maternal effects and allometric hypothesis, J. Animal Ecology, 64, 290–298, (1995).

- [17] Tonnang, H., Nedorezov, L. V., Owino, J., Host-parasitoid population density prediction using artificial neural networks: diamondback moth and its natural enimies, Agricultural and Forest Entomology, 12(3), 233-242, (2010).
- [18] Danca, M., Codreanu, S., Bako, B., Detailed analysis of a nonlinear prey-predator model, J. Biological Phys., 23, 11–20, (1997).
- [19] Liu, X., Xiao, D., Complex dynamic behaviors of a discrete time predator-prey system, Chaos, Solitons & Fractals, 32, 80–94, (2007).
- [20] Elsadany, A. A., Metwally, H. A. E., Elabbasy, E. M., Agiza, H. N., Chaos and bifurcation of a nonlinear discrete prey-predator system, Comp. Ecology and Software, 2(3), 169–180, (2012).
- [21] Huang, J. C., Xiao, D. M., Analysis of bifurcation and stability in a predator-prey system with Holling type functional response, Acta. Math. Appl. Sinica, 20(1), 167– 178, (2004).
- [22] Jing, Z., Yang, J., Bifurcations and chaos in discrete time predator-prey system, Chaos, Solitons & Fractals, 27, 259–277, (2006).
- [23] Ruiz, L., Prunaret, F., Complex patterns on the plane: different types of basin fractalization in a two dimensional mapping, Int. J. Bif. and Chaos, 13, 287–310, (2003).
- [24] Arneodo, A., Coullet, P., Tresser, C., Occurence of strange attractors in three dimensional Volterra equations, Phys. Letters A, 79, 259–263, (1980).
- [25] Arneodo, A., Coullet, P., Peyraud, J., Strange attractors in Volterra equations for three species competition, J. Math. Biol., 14, 153–157, (1982).
- [26] Hastings, A., Powell, T., Chaos in three species food chain, Ecology, 72, 8956–8960, (1991).
- [27] Kuznetzov, Y. A., De Fer, O., Rinaldi, S., Belyakov homoclinic bifurcations in a titrophic food chain, SIAM J. Appl. Math., 62(2), 462–487, (2001).
- [28] Elsadany, Abd. E. A., Dynamical complexities in a discrete time food chain, Comp. Ecology and Software, 2(2), 124–130, (2012).
- [29] Grebogi, C., Ott, E., Yorke, J. A., Chaotic attractors in crisis, Phys. Rev. Lett., 48, 1507–1511, (1982).
- [30] Harikrishnan, K. P., Misra, R., Ambika, G., Kembhavi, A. K., A non-subjective approach to the GP algorithm for analysing noisy time series, Physica D, 215, 137– 145, (2006).
- [31] Harikrishnan, K. P., Ambika, G., Misra, R., An algorithmic computation of correlation dimension from time series, Modern Phys. Letters B, 21, 129–138, (2007).

- [32] Misra, R., Harikrishnan, K. P., Ambika, G., Kembhavi, A. K., The nonlinear behavior of the black hole system GRS 1915+105, Astrophysical J., 643, 1114–1129, (2006).
- [33] Grassberger, P., Proccacia, I., Characterization of strange attractors, Phys. Rev. Letters. 50, 346–350, (1983).
- [34] Ranta, E., Kaitala, V., Lindstrom, J., Lindew, H., Synchrony in population dynamics, Proc. R. Soc. London B, 262, 113–118, (1995).
- [35] Liebhold, A., Koenig, W. D., Bjomstad, O. N., Spatial synchrony in population dynamics, Annu. Rev. Ecol. Syst., 35, 467–490, (2004).



Figure 6: The complete a-d parameter plane of the predator-prey model showing different domains of dynamics for c = 0. The dotted line represents the boundary above which the second fixed point becomes stable as per the linear stability analysis discussed in §2. The dashed line which coincides with the dotted line for the major part, but deviates from it at a = 3.0, is the one obtained numerically and represents the line of extinction of the predator. In the region below this line, denoted I, $y_n \to 0$ and the model displays logistic dynamics. The region II above this line represents the co-existence of predator and prey with stable one cycle. The solid line represents the transition from stable fixed point to limit cycle attractors by way of Hopf bifurcation and region III is the domain of limit cycle attractors. As the parameters a and d are further increased, the system enters the domain of chaos denoted by IV, for specific range of a and d. Beyond the chaotic domain is the domain of escape denoted by V where the trajectories escape to ∞ . Note that there is a small region in the right bottom of the parameter plane denoted by a *star*, between the dotted line and the dashed line, where the predator is forced into extinction. On the border line between this region and region II, a small region is shown with scattered points where the asymptotic state of the system depends sensitively on the value of d.



Figure 7: Typical bifurcation diagrams for model (3) with c = 0.2. The left panel shows bifurcation diagram with d as the control parameter for a fixed at 3.36 and the right panel with a as the control parameter and d = 3.90. In both cases, only the bifurcation structure of prey are shown as that of predator are identical. The figures are analogous to Fig.1 and Fig.2 top panel for the case c = 0.



Figure 8: Variation in the nature of attractors and transition to chaos in the predatorprey model as the control parameter a is increased. The value of a is shown for each case and the other parameters are fixed as b = 0.2, c = 0.2 and d = 3.5. The top panel shows the Hopf bifurcation starting from a fixed point attractor to form a limit cycle. It then changes into a periodic attractor of period n as shown in the middle panel. As a is increased further, the periodic attractor undergoes period doubling to form a number of chaotic bands which finally merge into a single chaotic attractor.



Figure 9: The figure is analogous to Fig.4 to show that the sensitive region of parameter dependence has extended over a wider range of d values compared to the case c = 0.



Figure 10: Same as Fig.6, but for c = 0.2. Note that the domain of chaotic dynamics has shrinked compared to the case c = 0, while the domain of predator extinction and the regime where the asymptotic dynamics sensitively dependent on the parameter have stretched to larger values of d.



Figure 11: The complete a - d parameter plane of the predator-prey model showing different domains of dynamics for c = 0.8. The domains are labelled as in the earlier cases. Note that the chaotic domain has been displaced upwards and shrunk considerably, while the domain of predator extinction has enlarged and shifted upwards.



Figure 12: The figure shows the variation of different regimes as a function of c along the vertical line of the a - d plane corresponding to a = 4. As c increases, the chaotic domain keeps on decreasing while the domain of predator extinction keeps on increasing.



Figure 13: Variation of the correlation dimension D_2 as a function of the embedding dimension M for two typical time series generated from the predator-prey model corresponding to parameter values a and d as indicated and c = 0.2. The saturated value of D_2 is taken as the dimension of the underlying attractor.



Figure 14: Typical chaotic attractors of the predator-prey model with c = 0.2 and four different sets of parameter values as indicated..0 3



Figure 15: Variation of the dimension of the underlying attractors of model (3) as a function of the control parameter a for two different fixed values of d. Note that D_2 varies from zero for periodic attractors to nearly 1 for limit cycle attractors and between 1 and 2 for chaotic attractors. It is found that the dimension can vary upto a value of 1.94.