

On the Integrability and Chaotic behaviour of an ecological model

M. P. Joy*

Materials Research Centre, Indian Institute of Science
Bangalore - 560 012, India.

Abstract

A three species food chain model is studied analytically as well as numerically. Integrability of the model is studied using Painlevé analysis while chaotic behaviour is studied using numerical techniques, such as calculation of Lyapunov exponents, plotting the bifurcation diagram and phase plots. We correct and critically comment on the wrong results reported recently on this ecological model, in a paper by Rai ([1995] “Modelling ecological systems”, Int. J. Bifurcation and Chaos **5**, 537-543).

Short Title : Chaos in an ecological model

*email : joy@mrc.iisc.ernet.in

1 Introduction

Several studies on chaos in continuous as well as discrete ecological models are available in the literature [May, 1976; Gilpin, 1979; Schaffer, 1985; Schaffer & Kot, 1985; Hastings & Powell, 1991]. Recently Rai [1995] has presented some studies on an ecological model, where he has used mainly Painlevé analysis for studying the integrability and has given results of some numerical calculations also. The calculations given in that paper is completely wrong and the claims he is making based on these wrong results are misleading and confusing. Almost all results presented in that paper have been published in another paper by Rai et al. [1993]. They claim that they could identify the key parameters controlling the dynamics of the system, using Painlevé property (PP) analysis. They used singular manifold analysis of Weiss, Tabor and Carnevale (WTC) [Weiss et al., 1983] which was originally developed for testing necessary conditions for Painlevé property of partial differential equations and it is a direct extension of Ablowitz, Ramani and Segur (ARS) algorithm [Ablowitz et al., 1980] for ordinary differential equations. Here we give the correct P-test results for the model. Numerical evidence given in that paper is also inconclusive and wrong. Here we present results of some extensive numerical calculations and show the irrelevance of their claims. We also mention some aspects of the importance of studies on chaos in ecological models.

2 The Model

The three species food chain model is given by the following set of ordinary differential equations.

$$\begin{aligned}\frac{dX}{dt} &= AX\left(1 - \frac{X}{K}\right) - \frac{BXY}{(X + D_1)} \\ \frac{dY}{dt} &= -CY + DXY - \frac{EYZ}{(Y + D_2)} \\ \frac{dZ}{dt} &= -FZ + GYZ,\end{aligned}\tag{1}$$

where $A, B, C, D, E, F, G, D_1, D_2$ and K are model parameters assuming only positive values. The model describes a prey population X and two predator populations Y and Z . The predator Y preys on X and the predator Z preys on Y . Here Holling type functional response [Murdoch & Oaten, 1975] for the predator population is used. Chaos in a similar model has been studied earlier [Hastings & Powell, 1991].

By the following scaling transformations,

$$X \rightarrow Kx, Y \rightarrow \frac{KA}{B}y, Z \rightarrow \frac{KA^2}{EB}z, t \rightarrow \frac{T}{A},\tag{2}$$

system (1) becomes

$$\frac{dx}{dT} = x(1 - x) - \frac{xy}{(x + a)}$$

$$\begin{aligned}\frac{dy}{dT} &= -by + cxy - \frac{yz}{(y+d)} \\ \frac{dz}{dT} &= -ez + fyz,\end{aligned}\tag{3}$$

where $a = \frac{D_1}{K}$, $b = \frac{C}{A}$, $c = \frac{KD}{A}$, $d = \frac{BD_2}{KA}$, $e = \frac{F}{A}$ and $f = \frac{GK}{B}$. This scaling reduces the number of parameters in the system from ten to six. The interesting fact is that, here, K (carrying capacity of the environment) and A (growth rate of X) are absent. Since this is a continuous system, it can be easily seen that K is just a scaling parameter of the maximum size of population X , which can be arbitrarily fixed at some value. By fixing other parameters, K or A may be used as a control parameter, which is the case with most of the parameters. Parameter E does not have any effect on the dynamics of the system.

3 Painlevé Test

Painlevé test (P-test) is a widely used technique to find the integrability of a dynamical system. It is conjectured that if the complex time solutions of a system of equations are free from movable singularities other than poles (Painlevé property), then it is integrable. Several papers and reviews are available on this technique [Ramani et al., 1989; Lakshmanan & Sahadevan, 1993].

We apply here the P-test as devised by WTC [Weiss et al., 1983] on system (1). For testing PP in the case of ordinary differential equations, one can use ARS algorithm [Ablowitz et al., 1980] which can be considered as a special case of WTC method. Here we try to expand the solutions about an arbitrary singular manifold determined by $\phi(t) = 0$, in power series.

$$\begin{aligned}X &= \sum_{j=0}^{\infty} x_j \phi^{j+\alpha} \\ Y &= \sum_{j=0}^{\infty} y_j \phi^{j+\beta} \\ Z &= \sum_{j=0}^{\infty} z_j \phi^{j+n},\end{aligned}\tag{4}$$

where x_j, y_j, z_j and ϕ are time dependent quantities. If we replace ϕ by $\tau \equiv t - t_0$, (t_0 is position of the singular point), and consider time independent coefficients, we obtain ARS P-test, which is easier to do. But WTC method is useful in finding Bäcklund transformations, Lax Pairs, special solutions, etc.

Mainly there are three steps in P-test, viz, finding the dominant behaviour, finding the resonance values and checking whether there exist arbitrary expansion coefficients at the resonance values. Substituting the $j = 0$ terms of (4) in (1) and equating dominant terms we obtain, $\alpha = \beta = -1$ and $n = -2$. Using this and inserting the full expansion in (1) we obtain the following recursion relations.

$$D_1[x_{j-2,t} + (j-2)x_{j-1,t}\phi_t] + \sum_{k=0}^j x_{j-k}[x_{k-1,t} + x_k(k-1)\phi_t]$$

$$\begin{aligned}
& - A(1 - \frac{D_1}{K}) \sum_{k=0}^j x_{j-k} x_{k-1} - AD_1 x_{j-2} + B \sum_{k=0}^j x_{j-k} y_{k-1} \\
& + \frac{A}{K} \sum_{k=0}^j \sum_{l=0}^k x_{j-k} x_{k-l} x_l = 0,
\end{aligned} \tag{5}$$

$$\begin{aligned}
D_2[y_{j-2,t}] & + y_{j-1}(j-2)\phi_t] + \sum_{k=0}^j y_{j-k}[y_{k-1,t} + y_k(k-1)\phi_t + Cy_{k-1} + Ez_k] \\
& + CD_2 y_{j-2} - DD_2 \sum_{k=0}^j x_{j-k} y_{k-1} - D \sum_{k=0}^j \sum_{l=0}^k x_{j-k} y_{k-l} y_l = 0,
\end{aligned} \tag{6}$$

$$z_{j-1,t} + (j-2)z_j\phi_t + Fz_{j-1} - G \sum_{k=0}^j y_{j-k} z_k = 0. \tag{7}$$

On collecting terms of x_r, y_r and z_r we obtain the matrix equation,

$$\mathbf{M} \begin{pmatrix} x_r \\ y_r \\ z_r \end{pmatrix} = \mathbf{R}_r, \tag{8}$$

where

$$\mathbf{M} = \begin{pmatrix} (r-2)x_0\phi_t + \frac{3A}{K}x_0^2 & 0 & 0 \\ -Dy_0^2 & (r-2)y_0\phi_t - 2Dx_0y_0 + Ez_0 & Ey_0 \\ 0 & -Gz_0 & (r-2)\phi_t - Gy_0 \end{pmatrix}, \tag{9}$$

and elements of \mathbf{R}_r are functions of $x_i, y_i, z_i, (i < r)$ and ϕ and their derivatives. When the determinant of the matrix \mathbf{M} becomes zero, arbitrary coefficients, x_r, y_r , or z_r can exist. Those values of r are called resonances. In [Rai, 1995] this step is wrong and hence they got wrong values for the resonances. They have only one resonance $r = 2$, which is wrong because in a 3-d system there will be three resonances corresponding to a generic leading order behaviour. The actual resonance values are -1 and $\frac{1+(KD/A)\pm\sqrt{K^2D^2/A^2+10KD/A+9}}{2}$. Resonance value -1 corresponds to the arbitrariness of ϕ . $r = 2$ is a resonance only when $KD/A = 0$, and resonances are not integers when $KD/A > 0$. Hence the system is nonintegrable. In the case of weak PP we can allow certain rational resonance values also but here it is not valid because the dominant powers are integers [Ramani et al., 1982, Joy & Sabir, 1988]. When $D = 0$, the equations for Y and Z are decoupled from that of X , and there is an integer resonance $r = 2$. This special case also does not have PP because there is only one positive resonance value; others are negative.

At the resonance values arbitrary expansion constants should enter in the expansion for integrability. But here we can find all the expansion coefficients using the recursion relations.

For $j = 0$:

$$x_0 = \frac{K\phi_t}{A}, \quad y_0 = -\frac{2\phi_t}{G} \text{ and } z_0 = -\frac{2\phi_t^2}{GE}\left(1 + \frac{KD}{A}\right). \tag{10}$$

In [Rai, 1995] these solutions are given incorrectly and the expressions they obtained for other x_j, y_j , and z_j are also wrong.

For $j = 1$:

$$x_1 = -\frac{K}{2A} \frac{\phi_{tt}}{\phi_t} + \frac{K}{2} + \frac{B}{G} \quad (11)$$

$$y_1 = \frac{\phi_{tt}}{G\phi_t} - \frac{[D_2 + \frac{2C}{G} - \frac{2F}{G}(1 + \frac{KD}{A}) + \frac{KDD_2}{A} - \frac{KD}{G} - \frac{2BD}{G^2}]}{(2 + \frac{3KD}{A})} \quad (12)$$

$$z_1 = (1 + \frac{KD}{A}) \left(\frac{4\phi_{tt}}{GE} - \frac{2F\phi_t}{GE} - \frac{2\phi_t y_1}{E} \right) \quad (13)$$

Similarly all x_j , y_j and z_j for higher values of j can also be determined using the recursion relations. For a general solution of the system, we need 3 arbitrary coefficients, which do not exist in this case. Thus the nonintegrability of the system is confirmed.

According to the expressions in [Rai, 1995, Eq. (25)], x_1 is determined and their assertion that X is indeterminate and hence it is non Painlevé type is misleading. They are getting y_2 and z_2 in terms of x_2 , and claiming that they are arbitrary because x_2 is arbitrary! Moreover they are asserting that the system is nonintegrable because these coefficients are arbitrary; but for PP we actually need arbitrary coefficients at the resonance values. They claim that X is the variable contributing chaotic dynamics to this system which is otherwise completely integrable [Rai, 1995, last sentence of the first paragraph in page 540]. Since the system is a coupled set of 3 differential equations, only one of the variables cannot be chaotic. When we speak about chaos we describe the phase trajectories. It is obvious from basic dynamical systems theory that there cannot be chaos in a 2-dimensional system. They have gone to the extent of saying that since x_0 contains the parameters A and K , the indeterministic nature depends on them and they are the key parameters controlling the dynamics of the system; and that is their main result! Though the authors did wrong analysis they could give the correct answer to the question regarding the integrability of the system in negative. This happened to be correct because most of the dynamical systems are nonintegrable.

4 Numerical Results

For studying the chaotic behaviour we have plotted the bifurcation diagram and calculated the maximal Lyapunov exponents (LE) for various values of the parameters. Fig. 1 gives the bifurcation diagram for the parameter values $B = 1$, $C = 1$, $D = 0.05$, $E = 1$, $F = 1$, $G = 0.05$, $D_1 = 10$, $D_2 = 10$, $K = 50$, when A is varied from 1.0 to 10.0. These are the same parameter values which has been used in the paper [Rai, 1995]. To construct the bifurcation diagram we integrated the system using the above parameter values and after reaching the attractor (discarded large number of initial points), we plotted successive maxima (local maxima) of the Z variable, as a function of A . The bifurcation diagram indicates a period doubling route to chaos in the system. For higher values of A , sequences of periodic windows and chaos repeat. Though the details are different, period doubling is observed in each sequence. It is clear from the bifurcation diagram that chaotic behaviour starts before $A = 4.0$ and it is confirmed by the Lyapunov exponent calculation. We have checked our calculations with different initial conditions also.

We calculated the LE directly from the equations using the same parameter values. For calculating the Lyapunov exponents we have to solve the system alongwith the corresponding linearised variational system. The method is available in any book on nonlinear dynamics. (See for example [Lichtenberg & Lieberman, 1992]). Rai [1995] used Wolf's code for extracting the LE from a time series, by taking the X variable as the time series, though Wolf et al. [1985] lists a FORTRAN code for calculating the Lyapunov spectrum from a system of equations also! Methods of calculating LE from a time series are not used when there are equations known for describing the system, but it is used when there is only an experimental time series available. Finding LE from a time series is not at all reliable and it is always approximate. In the calculation of invariants such as LE from time series there are a lot of details to be considered such as the number of data points, time delay used for reconstruction, the selection of proper embedding dimension, time used for sampling the data, etc. There is a large literature available on this topic of time series analysis. (See for example a review on this topic by Abarbanel et al. [1993]). In Fig. 2 we give maximal Lyapunov exponent of the system as a function of the parameter A from 3.0 to 10.0, keeping all other parameters constant.

Our numerical calculations show that K and A are not the only parameters determining the dynamics of the system but most of them have got some relevance. Detailed studies of such models in general, will be reported elsewhere. Rai et al. [1993] claim that they did not observe chaotic behaviour by varying other parameters.

In Fig. 3 we have plotted $X - Y$ projection of the attractor for $A = 4.0$, with all other parameters are kept the same as that given above. This is entirely different from the Fig. 2 of [Rai, 1995]. Here we may note that they have gone wrong somewhere in the calculation, because in their Fig. 2 of $X - Y$ plot at $A = 4$ the X variable reaches values more than the maximum it can attain which is equal to the value of $K (= 50.)$; but it goes upto ~ 200 . It is interesting to note that the maximal LE we got is one order less than that is given in [Rai, 1995]. We have done the calculations very accurately in double precision for different initial conditions and for different variations and verified our results.

5 Conclusion

We have done P-test of the model food chain and found it to be nonintegrable. We have explored numerically the chaotic behaviour of the system by calculating the maximal Lyapunov exponents, plotting the bifurcation diagram and phase plots. We have shown the fallacies of the work and irrelevance of the claim that P-test can be used to identify the key parameters determining the dynamics of the system by Rai [1995]. In well known models like Lorenz, Rossler, etc., also P-test does not give any idea about the key parameters. In any system, usually all parameters have some effect on the dynamical behaviour. Usually relevant parameters are chosen by their physical importance. In many systems, dimensions of the parameter space can be reduced by proper transformations, using symmetries, physical considerations, etc. Singularity structure in the complex time plane is very much related to the chaotic dynamics of the system, but to my knowledge no paper has appeared in which P-test is used to identify directly or indirectly the key parameters controlling the dynamics of the system.

Selection of biologically realistic parameter values for the numerical simulation of ecological models is a difficult problem. Biologically relevant parameter values can be found by proper identification of the system and its parameters with natural system for which the model is applicable. Studies on chaos such as time series analysis, prediction techniques, and modelling the system using the nonlinear dynamical data are useful in this regard. With biologically realistic parameters, we can have not only chaotic behaviour but also simple fixed point behaviour, limit cycles, etc, depending upon the natural system which is studied.

Many people misunderstand the importance and the meaning of chaos in deterministic dynamical systems; they consider the terminology *chaos* of dynamical systems theory for its literary meaning of total disorder or confusion. We can study chaos and even characterize it; moreover there is a possibility of checking it with the original natural system. There is a kind of order in chaos that is what we are interested in and of course the possibility of short term prediction is always there since it is a deterministic system [Schaffer 1985]. Modelling of ecological systems and comparing it with actual ecological data help us to understand, control, predict, etc., such systems. It helps us to understand how the ecology is going to be affected by various external factors also.

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Figure Captions

Fig. 1 Bifurcation diagram for the model. Here the local maxima of Z vs A is plotted. Other parameters are kept fixed at the values given in the text.

Fig. 2 Maximal Lyapunov exponent vs model parameter A . Other parameter values are the same as that of Fig. 1.

Fig. 3 Projection of the attractor at $A = 4.0$ on to the $X - Y$ plane





