Ratio-dependent predator–prey model: effect of environmental fluctuation and stability

M Bandyopadhyay[1] **and J Chattopadhyay**[2,3]

[1] Department of Mathematics, Scottish Church College, Kolkata 700006, India
[2] Embryology Research Unit, Indian Statistical Institute, Kolkata 700108, India

E-mail: malay_ban@rediffmail.com and joydev@isical.ac.in

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Abstract
This paper deals with the problem of a ratio-dependent predator–prey model. The deterministic and stochastic behaviour of the model system around biologically feasible equilibria are studied. Conditions for which the deterministic model enter into Hopf-bifurcation are worked out. Stochastic stability of the system around positive interior equilibrium is studied. To substantiate our analytical findings numerical simulations are carried out for a hypothetical set of parameter values.

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1. Introduction

The dynamical relationship between prey and their predators has long been and will continue to be one of the dominant themes in ecology due to its universal existence and importance [16, 18]. The dynamical problems involved with mathematical modelling of predator–prey systems may appear to be simple at first sight; however, the detailed analysis of these model systems often leads to very complicated as well as challenging problems. The most important part of modelling the population ecosystem is to make sure that the concerned mathematical model can exhibit well-known system behaviour for the system under consideration. Dynamical modelling of ecological systems is a frequently evolving process. A systematic mathematical approach can lead to a better understanding of the plausible models and the exposed discrepancies in turn lead to the necessary modifications [43].

After the pioneering work of Alfred Lotka and Vito Volterra in the middle of 1920 for predator–prey interactions, prey-dependent predator–prey models were studied extensively

[26, 31, 49, 50]. In population dynamics, a functional response of the predator to prey density refers to the change in the density of prey per unit time per predator as a function of the prey density. Quite a good number of works have already been performed in ecological systems [7, 10, 14, 21, 23, 33, 62] where the model systems are based on prey-dependent model systems. The classical prey–predator models with prey-dependent functional response take the form (or some equivalent form)

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - p(N)P, \qquad \frac{dP}{dt} = cp(N)P - eP, \tag{1.1}$$

where $p(N)$ is the so-called prey-dependent functional response ($N(t)$ and $P(t)$ denote prey and predator population density at any instant of time 't', respectively, and other parameters have the usual meaning). In most cases prey-dependent functional response $p(N)$ is given by $p(N) = aN/(b + N)$ or $p(N) = aN^2/(b + N^2)$ or $p(N) = aN^2/(b + N + \alpha N^2)$ or $p(N) = aN^\theta/(b + N^\theta)$ or some equivalent form. These types of classical predator–prey model systems exhibit not only the well known 'paradox of enrichment' formulated by Hairston *et al* [34] and Rosenzweig [56] but also the so-called 'biological control paradox', which was introduced by Luck [47]. The 'paradox of enrichment' states that enriching a predator–prey system (by increasing the carrying capacity) will cause an increment in equilibrium density of predator but not of prey population which in turn destabilizes the interior equilibrium. As a result it increases the chance of stochastic extinction of the predator population. However, in nature, it is observed that enriching the system increases the prey density which is not a factor responsible for destabilizing a stable equilibrium and fails to increase the amplitude of oscillations in systems that already cycles [1].

The so-called 'biological control paradox' states that we cannot have a low and stable prey equilibrium density, which is in contradiction with many examples of successful biological controls where the prey population is maintained at low densities compared to its environmental carrying capacity [4, 6]. A further example is, cactoblastis–opuntia in Australia, where the crucial factor seems to be pseudo-interference (see, May [49]), and where biological control has worked and resulted in low and stable pest densities. So this paradox is a pure artefact, created by simplifying assumptions on functional response. For the rest, the paradox of enrichment exists, but only in systems where one predator–prey pair exists in isolation and the predictions radically change when they are embedded in a simple food chain model [52]. Most of the natural systems are indeed very complex with the predators being exposed to various degrees of facultative secondary carnivory and interacting with many other subsystems in various ways. This indicates the fact that the paradox of biological control is not intrinsic for most predator–prey systems.

There are some good data on simple as well as fairly isolated predator–prey systems, like Mary Power's catfish–alga system in the Panamian streams [54] where one can find the interesting phenomenon that some increment in the resource for prey population at equilibrium increases the predator density in place of prey abundance. In some predator–prey systems where the Holling disc is a reasonable assumption for predators (e.g. the weasel–vole system found in boreal Europe, where voles have a hiding place and weasels have no alternative resources), we observe large amplitude oscillations of population distribution like carnivore–herbivore systems [52, 53]. According to the 'paradox of enrichment' these types of large amplitude oscillations are expected in relatively productive areas and in the most reproductive parts of tundra, while voles inhabiting less productive tundra areas are relatively stable [55]. High amplitude oscillations were the basic characteristics in high alpine barrens where the density of predator is low, but at present, rodent time trajectories indicate the fingerprints of predators [60]. The change in dynamic position of herbivores along productivity

gradients thus indicates the necessity of reasonable alteration or corrections of simple as well as traditional food chain models [52]. Recently, predator–prey models with prey-dependent response function have been facing a great challenge from biological and physiological researchers [3–5, 32]. At present it is clear that predator abundance also has the ability to influence the functional response. Arditi and Ginzburg [5] have suggested that, in situations characterized by strong space and time heterogeneities, the functional response can be approximated by a function of the prey-to-predator ratio. Several biologists have been able to establish the fact that functional responses over typical ecological timescales ought to depend on the densities of both prey and predators, especially when predators have to search for food and therefore have to share or compete for food. Actually prey-dependent and ratio-dependent models are extremes or limiting cases; prey-dependent models are based on the daily energy balance of predators, on the other hand ratio-dependent models presuppose that prey are easy to find and that predator dynamics are, in essence, governed by direct density dependence, with prey densities determining the sizes of defended territories. Within the natural environment both aspects have the ability to influence predator–prey dynamics, and the issue of which of the two extremes is closer to reality in which system is wide open. Moreover, the pursuit of the prey-dependent approach has proved more fertile since its 'paradoxes' seem to be quite realistic where the premises for their existence are found, but here opinions may differ and there is no strong evidence to close one door or another.

Arditi and Ginzburg [5] first proposed the following Michaelis–Menten–Holling type, ratio-dependent predator–prey system

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) - \frac{\alpha NP}{k_1 P + N}, \qquad \frac{\mathrm{d}P}{\mathrm{d}t} = \frac{c\alpha NP}{k_1 P + N} - eP. \tag{1.2}$$

The dynamics of this type of ratio-dependent predator–prey model has been studied by many researchers (see, e.g., Kuang and Beretta [44], Jost *et al* [39], Hsu *et al* [38]).

Major parts of the work in this direction are based on deterministic models of differential and difference equations. The deterministic approach has, however, some limitations in biology: it is always difficult to predict the future of the system accurately. Deterministic models in ecology do not usually incorporate environmental fluctuations based on the idea that in the case of large populations, stochastic deviations (or the effect of random environmental fluctuations) are small enough to be ignored. A stochastic model provides a more realistic picture of a natural system than its deterministic counterpart. A central obstacle in the stochastic modelling of an ecosystem is the lack of mathematical machinery available to analyse nonlinear multi-dimensional stochastic models [28, 40, 41]. A quantum leap in the mathematical sophistication of ecological modelling occurred when May [49] introduced stochastic differential equations (SDEs) to investigate limits to niche overlap in a randomly fluctuating environment. Well-known deterministic population models (such as the Lotka–Volterra model, Gauss type prey–predator model, etc) are the starting points of stochastic multi-species models which include demographic or environmental stochasticity. The resulting stochastic models involve nonlinear SDEs whose solutions pose great difficulties. Different techniques of linearization of nonlinear SDEs giving rise to a set of deterministic moment equations have been receiving a great deal of attention in different fields of science and technology [8, 11, 12, 28, 29, 40, 41, 51, 57].

The main objective of this paper is to consider a ratio-dependent predator–prey model and its stability behaviour around different equilibrium points with special emphasis on the controversial equilibrium point (0, 0) for the ratio-dependent model. Our next objective is to develop a stochastic dynamic model for the ratio-dependent predator–prey model and to examine the stability of the model system under random environmental fluctuations. We make

a comparative analysis of the stability of the model system within deterministic and stochastic environments.

2. Deterministic model

The classical model for predator–prey systems can be written in its classical form by a system of first order nonlinear ordinary differential equations as

$$\frac{dN}{dt} = Nf(N) - g(N, P)P, \qquad \frac{dP}{dt} = h(N, P)P - \gamma P \tag{2.1}$$

with prey abundance $N(t)$ and predator abundance $P(t)$ at any given instant of time 't'. $f(N)$ is the per capita rate of increase of the prey in the absence of predation and 'γ' is the food-independent mortality rate of the predator, assumed to be constant. The amount of prey biomass consumed by each predator per unit of time is described by the function $g(N, P)$, while $h(N, P)$ describes per capita production rate of the predator. There is a considerable amount of evidence to show that predator production rate can be modelled as simply proportional to food intake (up to a very good approximation)

$$h(N, P) = eg(N, P), \tag{2.2}$$

where the constant 'e' is interpreted as conversion efficiency and satisfies the condition $0 < e < 1$. Specific examples are given by Slobodkin [58] for hydras, by Beddington *et al* [13] for numerous arthropods and by Coe *et al* [24] for large African herbivores in support of previous assumptions. The trophic function $g(N, P)$ is the sole link between prey–predator dynamics [5]. In this paper we will consider the usual logistic form of the growth function for prey in the absence of predator as

$$f(N) = r\left(1 - \frac{N}{K}\right),$$

where 'r' is the intrinsic growth rate of prey and 'K' is the environmental carrying capacity. For the traditional prey-dependent predator–prey models (e.g. (1.1)), the functional response $g(N, P)$ depends only on the density of prey population 'N' as we have remarked in the introduction of this paper. According to Berryman [18], credible and consistent predator–prey models must be able to satisfy the minimum biological property that 'when resources are low relative to population density, the predator per-capita growth rate should decline with its density'. However, the prey-dependent predator–prey models are unable to satisfy this criterion due to the fact that the predator per-capita growth rate becomes a function of prey population 'N' only, which is independent of the density of predators 'P'. To overcome this situation, Arditi and Ginzburg [5] have suggested that for situations characterized by strong space and time heterogeneities, the functional response can be approximated by a function of the prey-(N)-to-predator-(P) ratio (N/P) and this leads to the ratio-dependent functional response $g(N, P)$ as follows:

$$g := g\left(\frac{N}{P}\right) = \frac{\alpha(N/P)}{1 + \alpha\beta(N/P)} = \frac{\alpha N}{P + \alpha\beta N},$$

where 'α' represents the total attack-rate for predator and 'β' is the handling time and the functional response is known as the Michaelis–Menten–Holling type functional response [17, 39, 43]. Under these assumptions the dynamics of the ratio-dependent predator–prey system is governed by the following system of first order nonlinear ordinary differential equations:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{\alpha NP}{P + \alpha\beta N}, \qquad \frac{dP}{dt} = \frac{e\alpha NP}{P + \alpha\beta N} - \gamma P. \tag{2.3}$$

Initial conditions for the system of equation (2.2) are given by $N(t=0)=N_0 \geqslant 0$ and $P(t=0)=P_0 \geqslant 0$. It is typical for predator–prey systems: positive N-axis, positive P-axis and the interior of the first quadrant invariant under system (2.3) and the solutions with positive initial condition continue to be positive for all time 't'. As observed by Freedman and Mathsen [27], Jost *et al* [39], Kuang and Beretta [44] and Kuang [43], system (2.3) is not well-defined at the origin $(0, 0)$ and hence the model is unable to capture the idea that the growth rate of both the populations are zero in the absence of prey as well as predator population. To overcome this situation, Xiao and Ruan [63] have modified the model system (2.3) by redefining it as follows:

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - \frac{\alpha NP}{P+\alpha\beta N}, \quad \frac{dP}{dt} = \frac{e\alpha NP}{P+\alpha\beta N} - \gamma P \qquad \text{when } (N, P) \neq (0, 0), \tag{2.4a}$$

$$\frac{dN}{dt} = 0 = \frac{dP}{dt} \qquad \text{when } (N, P) = (0, 0). \tag{2.4b}$$

For the sake of simplicity it is convenient to scale the variables as $x = N/K$, $y = P/K\alpha\beta$ and consider the dimensionless time $\tau = tr$. The dimensionless equations are then given by

$$\frac{dx}{d\tau} = x(1-x) - \frac{axy}{x+y} \equiv F_1(x, y), \qquad \frac{dy}{d\tau} = \frac{bxy}{x+y} - cy \equiv F_2(x, y), \tag{2.5a}$$

$$F_1(0, 0) = F_2(0, 0) = 0, \tag{2.5b}$$

where $a = \alpha/r, b = e/\beta r$ and $c = \gamma/r$. For convenience, in the following, time τ is replaced by t as the dimensionless time. The initial conditions for the system of equations (2.5) are given by $x(0) = x_0 \geqslant 0$ and $y(0) = y_0 \geqslant 0$ which is also biologically meaningful.

2.1. Boundedness

Due to the boundedness of the functional responses, we see that

$$\lim_{(x,y)\to(0,0)} F_1(x, y) = \lim_{(x,y)\to(0,0)} F_2(x, y) = 0.$$

Using equation (2.5*b*) we can conclude that the functions $F_1(x, y)$ and $F_2(x, y)$ are continuous functions on $\mathbb{R}^2_+ = [(x, y) : x \geqslant 0, y \geqslant 0]$. Straightforward computation shows that they are Lipschizian on $\mathbb{R}^2_+$. Hence a solution of (2.5) with non-negative initial condition exists and is unique. It is also easy to see that these solutions exist for all $t > 0$ and stay non-negative. In fact, if $x(0) = x_0 > 0$, then $x(t) > 0$ for all $t > 0$. The same argument is true for the y-component. Hence, the interior of $\mathbb{R}^2_+$ is invariant under model system (2.5). Our next task is to consider the boundedness for the solutions of the model system (2.5).

Lemma 1. *All the solutions of the system (2.5) with the positive initial condition (x_0, y_0) are uniformly bounded within a region Ω, where,*

$$\Omega = \left\{(x, y) : 0 \leqslant x \leqslant 1, 0 \leqslant x + \frac{a}{b}y \leqslant \frac{L}{c}\right\}$$

with $L = c + 1/4$.

Proof. From the first equation of (2.5) we get,

$$\frac{dx}{dt} = x(1-x) - \frac{axy}{x+y} \leqslant x(1-x).$$

So, $x(t) \leqslant 1$, as $t \to +\infty$.

Let us define the function

$$W(t) = x(t) + \frac{a}{b}y(t).$$

Calculating the time derivative of $W(t)$ along the trajectories of equations (2.5), we get

$$\frac{\mathrm{d}}{\mathrm{d}t}W(t) = \frac{\mathrm{d}x}{\mathrm{d}t} + \frac{a}{b}\frac{\mathrm{d}y}{\mathrm{d}t} = x(1-x) - \frac{ac}{b}y.$$

Clearly, the maximum value of $x(1-x)$ is $1/4$, whenever $0 \leqslant x \leqslant 1$. Then,

$$\frac{\mathrm{d}}{\mathrm{d}t}W(t) + cW(t) = x(1-x) + cx \leqslant c + \frac{1}{4} = L \qquad \text{(say)}.$$

Thus, as $t \to +\infty$, $0 \leqslant W(t) \leqslant L/c$ [19]. Hence system (2.5) is dissipative with the asymptotic bound L/c. This ensures the existence of a compact neighbourhood Ω which is a proper subset of $\boldsymbol{R}_+^2$ such that for sufficiently large initial conditions (x_0, y_0) the trajectories of the system of equations (2.5) will always be within the set Ω.

Hence we have shown that the model system (2.5) is dissipative.

2.2. *Equilibria*

For population models in deterministic environments, with the environmental parameters being well-defined constants, it is natural curiosity to find the community equilibria where all the species' populations have time independent values, that is, where all net growth rates are zero. Classical two species predator–prey models always possess at least three equilibrium points: (i) trivial equilibrium, (ii) axial equilibrium and (iii) positive interior equilibrium [45]. Earlier works on ratio-dependent predator–prey models (e.g. [27, 39, 43, 44]) have mentioned that the model system (2.3) cannot be linearized at $(0, 0)$ and consistent dynamical analysis for the model system in the vicinity of the origin reveals the rich and complicated dynamics. Based on the redefined ratio-dependent predator–prey model (2.4) and its non-dimensionalized version (2.5) we are able to mention that the system of equations (2.5) has two equilibria, $E_0(0, 0)$ and $E_1(1, 0)$ on the x-axis for all possible as well as admissible values of the parameters involved with the model system (2.5). The third and most interesting equilibrium point (from a biological point of view) is $E_*(x^*, y^*)$ where x^* and y^* are non-zero positive solutions of the equations $F_1(x, y) = 0 = F_2(x, y)$ and are given by

$$x^* = 1 - \left[\frac{a(b-c)}{b}\right] \qquad \text{and} \qquad y^* = \left[\frac{(b-c)x^*}{c}\right]. \tag{2.6}$$

Simple mathematical argument shows that x^* is positive for all $a < b/(b-c)$ and positivity of y^* demands an extra condition $b > c$.

2.3. *Behaviour around* $E_0(0, 0)$

The study of stability plays a significant role in understanding the structure and functions of ecological systems. A variety of ecologically interesting interpretations are involved with the term '*stability*'. The most common meaning corresponds to *neighbourhood stability* which means stability in the vicinity of an equilibrium point associated with the deterministic model system. An equilibrium point is called a stable equilibrium point if, when the populations are perturbed they will return to the equilibrium point with the advancement of time. The return may be achieved either as damped oscillations or monotonically. It is common practice to find the linearized system of equations around the equilibrium point and the sign of eigenvalues associated with the corresponding Jacobian matrix determines the stability around the equilibrium point. Before studying the stability of controversial equilibrium point $E_0(0, 0)$

we would like to remark that mathematical investigation of the nature of the solution for the model system in the vicinity of origin reveals some interesting dynamical behaviour depending on the parametric restrictions. This type of dynamical behaviour has never been observed in classical prey-dependent predator–prey models. Based on the outcome of stability analysis around $E_0(0, 0)$, one can obtain a clear idea of the possibility of extinction of population at low population density of both prey and predators. In the case of the ratio-dependent predator–prey model it is not possible to linearize the model system around $E_0(0, 0)$. To study the behaviour of the model system around E_0 we follow the technique developed by Arino *et al* [7]. (For rigorous calculations and mathematical justification of the said technique, interested readers may consult the work of Arino *et al* [7] and the references therein.) For this purpose the model system (2.5) can be written as

$$\frac{\mathrm{d}X}{\mathrm{d}t} = H(X(t)) + Q(X(t)), \tag{2.7}$$

where $H(.)$ is C^1 except at the origin, is a continuous and homogeneous function of degree one, i.e. $H(sX) = sH(X)$ for all scalar $s \geqslant 0$, $X(t) = (x_1, x_2) \in \mathbb{R}^2_+$ and Q is a C^1 function and satisfies the condition $Q(X) = \circ(X)$ in the vicinity of the origin. The functions $H(.)$ and $Q(.)$ are defined by

$$H(X) \equiv (H_1(X), H_2(X)), \qquad Q(X) \equiv (Q_1(X), Q_2(X)), \tag{2.8}$$

$$H_1(X) = x_1 - \frac{ax_1x_2}{x_1 + x_2}, \qquad H_2(X) = \frac{bx_1x_2}{x_1 + x_2} - cx_2, \tag{2.9}$$

$$Q_1(X) = -x_1^2, \qquad Q_2(X) = 0. \tag{2.10}$$

Let us assume that $X(t)$ is a solution of (2.7), is bounded such that $\liminf_{t\to\infty} \|X(t)\| = 0$. For this situation it is possible to find a sequence $X(t_n + .) \to 0$ uniformly as $t_n \to \infty$. Define

$$y_n(s) = \frac{X(t_n + s)}{\|X(t_n + s)\|}. \tag{2.11}$$

Clearly, Y_n is a sequence with $\|y_n\| = 1$. Applying the Ascoli–Arzela theorem [20], it is possible to find a subsequence corresponding to y_n which converges towards some function $y(t)$ and the limiting function satisfies the equation

$$\frac{\mathrm{d}y}{\mathrm{d}t} = H(y(t)) - (y(t), H(y(t)))y(t). \tag{2.12}$$

In equation (2.12), $(.,.)$ stands for the standard inner-product in $\mathbb{R}^2$. The steady states of (2.12) are vectors V satisfying $H(V) = (V, H(V))V$ which are solutions of the nonlinear eigenvalue problem, $H(V) = \mu V$ with $\mu = (V, H(V))$. These stationary solutions correspond to the fixed directions along which the trajectories of (2.12) may converge asymptotically. Using (2.9), the nonlinear eigenvalue problem becomes

$$[(1 - \mu)v_1 + (1 - a)v_2]v_1, \qquad [(b - c)v_1 - (c + \mu)v_2]v_2 = 0. \tag{2.13}$$

Now we are in a position to discuss in detail the possibility of reaching the origin following fixed directions.

Case 1. $v_1 = 0$ and $v_2 \neq 0$

In this case, there is a possibility of reaching the origin along the y-axis, with $\mu = -c$.

Case 2. $v_1 \neq 0$ and $v_2 = 0$

In this case, it is possible to reach the origin along the x-axis, with $\mu = 1$.

Case 3. $v_1 \neq 0$ and $v_2 \neq 0$

In this case, the possibility of reaching the origin along some fixed direction from the interior of the first quadrant depends on the existence of a real root of the quadratic equation

$$\mu^2 + \mu(c-1) + ab - b - bc = 0. \tag{2.14}$$

The existence of a real root of the quadratic equation (2.14) demands

$$c < b < \frac{1}{a-1}\left[\frac{(c-1)^2}{4} + ac\right]. \tag{2.15}$$

Again the upper bound for the parameter b will be biologically feasible if and only if $a > 1$ or equivalently $\alpha > r$. This result has the biological significance that if the prey-catching capacity is higher than the intrinsic growth rate of predator then both the populations approach total extinction.

Under the three conditions discussed above, it is possible to reach the trivial equilibrium point $E_0(0, 0)$ and hence E_0 is an attractor for the model system (2.5).

2.4. Behaviour around E_1 and E_*

The Jacobian matrix $J(x, y)$ for the system (2.5) at any point of the first quadrant (x, y), except at the origin, is given by

$$J(x, y) = \begin{bmatrix} -x + \dfrac{axy}{(x+y)^2} & -\dfrac{a(x)^2}{(x+y)^2} \\ \dfrac{b(y)^2}{(x+y)^2} & -\dfrac{bxy}{(x+y)^2} \end{bmatrix}. \tag{2.16}$$

The Jacobian matrix evaluated at the boundary equilibrium point $E_1(1, 0)$ takes the form

$$J_1 = [J(x, y)]_{E_1} = \begin{bmatrix} -1 & -a \\ 0 & b-c \end{bmatrix} \tag{2.17}$$

and therefore, if the positive interior equilibrium point exists (i.e. $b > c$), $E_1(1, 0)$ is always stable along the x-direction and unstable along the y-direction and consequently, $E_1(1, 0)$ is a saddle point.

At the interior equilibrium point $E_*(x^*, y^*)$ the Jacobian matrix J_* is given by

$$J_* = [J(x, y)]_{E_*} = \begin{bmatrix} -x^* + \dfrac{ax^*y^*}{(x^*+y^*)^2} & -\dfrac{a(x^*)^2}{(x^*+y^*)^2} \\ \dfrac{b(y^*)^2}{(x^*+y^*)^2} & -\dfrac{bx^*y^*}{(x^*+y^*)^2} \end{bmatrix}. \tag{2.18}$$

The characteristic equation for the Jacobian matrix J_* is given by

$$\lambda^2 + A_1\lambda + A_2 = 0, \qquad \text{where } A_1 = -\mathrm{Tr}(J_*) \quad \text{and} \quad A_2 = \det(J_*). \tag{2.19}$$

As $\det(J_*) = ab(x^*)^2y^*/(x^*+y^*)^2 > 0$ the stability of the equilibrium point E_* solely depends on the sign of $\mathrm{Tr}(J_*)$ and hence E_* is stable if $\mathrm{Tr}(J_*) < 0$ and unstable if $\mathrm{Tr}(J_*) > 0$. It is easy to verify that both the situations are possible for the model system under some appropriate parameter values. In terms of the parameters the stability condition of positive interior equilibrium point E_* is $a < b[c + b/(b-c)]/(b+c)$. We have noted earlier that $a < b/(b-c)$ and $b > c$ are the necessary conditions for the positivity of E_*. Hence the stability of equilibrium point E_* demands the following condition

$$a < \bar{a} \equiv \min\left[\frac{b}{b-c}, \frac{b}{b+c}\left(c + \frac{b}{b-c}\right)\right] \qquad \text{with } b > c. \tag{2.20}$$

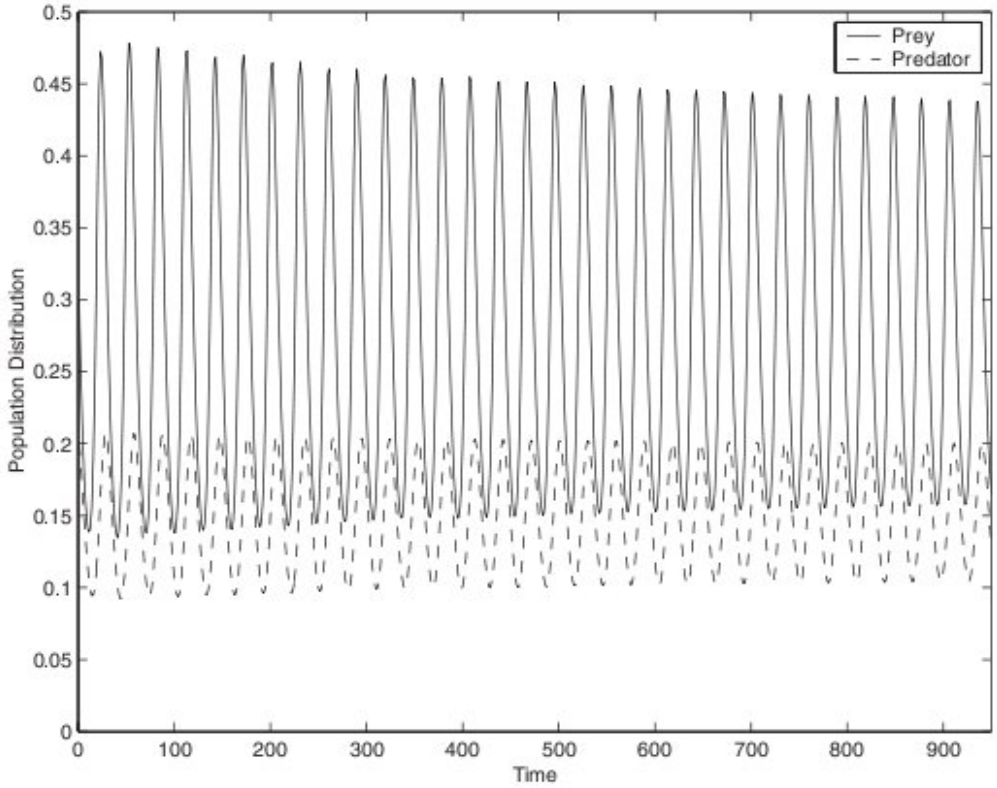

Figure 1. The Hopf-bifurcating periodic solution of the model system (2.5) for parametric values $a = 2.0, b = 0.7808$ and $c = 0.5$.

If we increase the value of 'a' further such that $a > b[c + b/(b - c)]/(b + c)$ with the restriction $b > c$ then E_* becomes locally unstable. Hence by the Poincaré criteria [11] there exists at least one limit cycle around E_* within the positive (x, y)-plane. We now deduce the condition for the existence of a Hopf-bifurcating small amplitude periodic solution.

Lemma. *If $a = a^* = b[c + b/(b - c)]/(b + c)$ with $b > c$, then the system (2.5) exhibits Hopf-bifurcation near E_*.*

Proof. At the parametric value $a = a^* = b[c+b/(b-c)]/(b+c)$, $\mathrm{Tr}(J_*) = 0$ and $\det(J_*) > 0$. When a takes the value $a = a^*$, the roots of the characteristic equation (2.19) are purely imaginary. Also we can verify that the result $(\mathrm{d}/\mathrm{d}a)[\mathrm{Tr}(J_*)]_{a=a^*} \neq 0$. Hence both the conditions for Hopf-bifurcation [9, 22, 36, 48] are satisfied (see figure 1). □

The above result establishes the existence of a small amplitude periodic solution near the interior equilibrium point E_*. Our next task is to find the condition for stability of the Hopf-bifurcating periodic solution and for this we have to calculate the first Lyapunov coefficient at the critical parametric value $a = a^*$. For this purpose we follow the procedure and standard notation as introduced by Kuznetsov [46]. First we translate the origin to the equilibrium point E_* using the change of variables $x = x^* + h_1$ and $y = y^* + h_2$. Substituting this transformation in (2.5a) and expanding in Taylor series at the critical parametric condition $a = a^*$

we get

$$\frac{dh_1}{d\tau} = a_{10}h_1 + a_{01}h_2 + a_{20}h_1^2 + a_{11}h_1h_2 + a_{02}h_2^2 + a_{30}h_1^3 + a_{21}h_1^2h_2 + a_{12}h_1h_2^2 + a_{03}h_2^3 + \cdots, \tag{2.21a}$$

$$\frac{dh_2}{d\tau} = b_{10}h_1 + b_{01}h_2 + b_{20}h_1^2 + b_{11}h_1h_2 + b_{02}h_2^2 + b_{30}h_1^3 + b_{21}h_1^2h_2 + b_{12}h_1h_2^2 + b_{03}h_2^3 + \cdots, \tag{2.21b}$$

where the a_{ij} and b_{ij} are given by

$$a_{ij} = \left[\frac{\partial^{i+j}F_1(x,y)}{\partial x^i \partial y^j}\right]_{a=a^*}, \qquad b_{ij} = \left[\frac{\partial^{i+j}F_2(x,y)}{\partial x^i \partial y^j}\right]_{a=a^*}. \tag{2.22}$$

In the above expansion we are not interested in the coefficients of fourth and higher order terms as they make no contribution to the calculation of the first Lyapunov coefficient. In order to make the coefficients of h_1 in $dh_1/d\tau$ and of h_2 in $dh_2/d\tau$ equal to zero we introduce the non-singular transformation of variables as $h_1 = (a_{10}/b_{10})u_1 + u_2$, $h_2 = u_1$ in the above expansion to get the transformed system as

$$\frac{du_1}{d\tau} = \alpha_{01}u_2 + \alpha_{20}u_1^2 + \alpha_{11}u_1u_2 + \alpha_{02}u_2^2 + \alpha_{30}u_1^3 + \alpha_{21}u_1^2u_2 + \alpha_{12}u_1u_2^2 + \alpha_{03}u_2^3 + \cdots, \tag{2.23a}$$

$$\frac{du_2}{d\tau} = \beta_{10}u_1 + \beta_{20}u_1^2 + \beta_{11}u_1u_2 + \beta_{02}u_2^2 + \beta_{30}u_1^3 + \beta_{21}u_1^2u_2 + \beta_{12}u_1u_2^2 + \beta_{03}u_2^3 + \cdots. \tag{2.23b}$$

The above system can be written in the following form

$$\frac{d}{d\tau}\boldsymbol{u} = A\boldsymbol{u} + \frac{1}{2}B(\boldsymbol{u},\boldsymbol{u}) + \frac{1}{6}C(\boldsymbol{u},\boldsymbol{u},\boldsymbol{u}) + \cdots, \tag{2.24}$$

where A denotes the coefficient matrix of linear part with zero as the main diagonal elements; $B(\boldsymbol{u},\boldsymbol{v})$, $C(\boldsymbol{u},\boldsymbol{v},\boldsymbol{w})$ are symmetric multi-linear vector functions of $\boldsymbol{u} = (u_1, u_2)$, $\boldsymbol{v} = (v_1, v_2)$, $\boldsymbol{w} = (w_1, w_2) \in \boldsymbol{R}^2$ and take the following forms:

$$B(\boldsymbol{u},\boldsymbol{v}) = \begin{bmatrix} 2\alpha_{20}u_1v_1 + \alpha_{11}(u_1v_2 + u_2v_1) + 2\alpha_{02}u_2v_2 \\ 2\beta_{20}u_1v_1 + \beta_{11}(u_1v_2 + u_2v_1) + 2\beta_{02}u_2v_2 \end{bmatrix}, \tag{2.25}$$

$$C(\boldsymbol{u},\boldsymbol{v},\boldsymbol{w}) = \begin{bmatrix} c_{11} + c_{12} + c_{13} + c_{14} \\ c_{21} + c_{22} + c_{23} + c_{24} \end{bmatrix}, \tag{2.26}$$

where the c_{ij} $(i = 1, 2;\ j = 1, 2, 3, 4)$ are given by

$$c_{11} = 6\alpha_{30}u_1v_1w_1, \qquad c_{12} = 2\alpha_{21}(u_1v_1w_2 + u_1v_2w_1 + u_2v_1w_1),$$
$$c_{13} = 2\alpha_{12}(u_1v_2w_2 + u_2v_1w_2 + u_2v_2w_1), \qquad c_{14} = 6\alpha_{03}u_2v_2w_2,$$
$$c_{21} = 6\beta_{30}u_1v_1w_1, \qquad c_{22} = 2\beta_{21}(u_1v_1w_2 + u_1v_2w_1 + u_2v_1w_1),$$
$$c_{23} = 2\beta_{12}(u_1v_2w_2 + u_2v_1w_2 + u_2v_2w_1), \qquad c_{24} = 6\beta_{03}u_2v_2w_2.$$

Let $\lambda_{1,2} = \pm i\omega$ be the eigenvalues of the matrix A and $\boldsymbol{p}, \boldsymbol{q}$ proper eigenvectors satisfying the relations

$$A\boldsymbol{q} = i\omega\boldsymbol{q}, \qquad A^T\boldsymbol{p} = -i\omega\boldsymbol{p} \qquad \text{and} \qquad \langle \boldsymbol{p}, \boldsymbol{q}\rangle = 1, \tag{2.27}$$

where $\langle .,. \rangle$ means the standard scalar product in $\mathbb{C}^2$: $\langle \boldsymbol{p}, \boldsymbol{q} \rangle = \bar{p}_1 q_1 + \bar{p}_2 q_2$. The first Lyapunov coefficient determining the stability of the Hopf-bifurcating periodic solution is given by [46]

$$l_1 = \frac{1}{2\omega^2} \mathrm{Re}(\mathrm{i} g_{20} g_{11} + \omega g_{21}). \tag{2.28}$$

The quantities g_{20}, g_{11} and g_{21} are given by

$$g_{20} = \langle \boldsymbol{p}, B(\boldsymbol{q}, \boldsymbol{q}) \rangle, \qquad g_{11} = \langle \boldsymbol{p}, B(\boldsymbol{q}, \bar{\boldsymbol{q}}) \rangle, \qquad g_{21} = \langle \boldsymbol{p}, C(\boldsymbol{q}, \boldsymbol{q}, \bar{\boldsymbol{q}}) \rangle. \tag{2.29}$$

The stability of the Hopf-bifurcating periodic solution depends on the sign of first Lyapunov coefficient. The limit cycle is called stable if $l_1 < 0$ and is unstable for $l_1 > 0$. The explicit expression for g_{20}, g_{11}, g_{21} and hence that of the Lyapunov coefficient l_1 in terms of the system parameters is too lengthy and would take at least two printed pages. Furthermore, it is quite difficult to conclude about the sign of l_1 due to its complicated algebraic expression. For this reason we present here a numerical example to illustrate the method of calculation for l_1. For numerical calculation of the first Lyapunov coefficient l_1, we consider the following model

$$\frac{\mathrm{d}x}{\mathrm{d}\tau} = x(1-x) - \frac{2xy}{x+y} \equiv F_1(x, y), \qquad \frac{\mathrm{d}y}{\mathrm{d}\tau} = \frac{0.780\,776\,4064xy}{x+y} - 0.5y \equiv F_2(x, y). \tag{2.30}$$

From the previous analysis, one can easily verify that the positive equilibrium point is $E_* = (0.280\,776\,4064, 0.157\,670\,7808)$ and the system exhibits limit cycle oscillation at the critical parametric value $a^* = 2$. Let $x = 0.280\,776\,4064 + h$, $y = 0.157\,670\,7808 + k$, then system (2.30) becomes

$$\begin{aligned}\frac{\mathrm{d}h}{\mathrm{d}\tau} &= 0.179\,805\,8984h - 0.820\,194\,1014k - 0.410\,097\,0509h^2 - 2.100\,970\,508hk \\ &\quad + 1.870\,679\,355k^2 - 1.345\,436\,728h^3 + 3.446\,407\,236kh^2 \\ &\quad + 0.525\,242\,6287k^2h - 4.266\,601\,336k^3, \end{aligned} \tag{2.31a}$$

$$\begin{aligned}\frac{\mathrm{d}k}{\mathrm{d}\tau} &= 0.100\,970\,5080h - 0.179\,805\,8985k - 0.230\,291\,1524h^2 + 0.820\,194\,1016hk \\ &\quad - 0.730\,291\,1521k^2 + 0.525\,242\,6269h^3 - 1.345\,436\,728kh^2 \\ &\quad - 0.205\,048\,5261k^2h + 1.665\,630\,829k^3. \end{aligned} \tag{2.31b}$$

Making the non-singular transformation $h = (0.179\,805\,8983/0.100\,970\,5080)u + v$, $k = u$, we see that system (2.31) becomes

$$\begin{aligned}\frac{\mathrm{d}u}{\mathrm{d}\tau} &= 0.100\,970\,5080v - 0.000\,000\,001u^2 + 0.000\,000\,002vu - 0.230\,291\,1524v^2 \\ &\quad - 0.000\,000\,01u^3 - 0.000\,000\,11vu^2 + 1.460\,582\,304v^2u + 0.525\,242\,6269v^3, \end{aligned} \tag{2.32a}$$

$$\begin{aligned}\frac{\mathrm{d}v}{\mathrm{d}\tau} &= -0.499\,999\,9995u - 3.171\,164\,609u^2 - 3.561\,552\,813vu - 0.000\,000\,002v^2 \\ &\quad + 0.000\,0013u^3 + 0.000\,0161vu^2 - 6.342\,329\,213v^2u - 2.280\,776\,405v^3. \end{aligned} \tag{2.32b}$$

$\lambda_{1,2} = \pm \mathrm{i}\omega = \pm 0.224\,689\,2386\mathrm{i}$ are the eigenvalues of the coefficient matrix corresponding to the linear part of (2.32) where the matrix A is given by,

$$A = \begin{bmatrix} 0 & 0.100\,970\,5080 \\ -0.499\,999\,9995 & 0 \end{bmatrix}.$$

The eigenvectors as defined in (2.27) are given by $\boldsymbol{p} = (0.175\,432\,0563, 0.078\,835\,390\,39\mathrm{i})$ and $\boldsymbol{q} = (0.078\,835\,390\,39, 0.175\,432\,0563\mathrm{i})$. Now one can calculate the quantities g_{20}, g_{11}, g_{21}

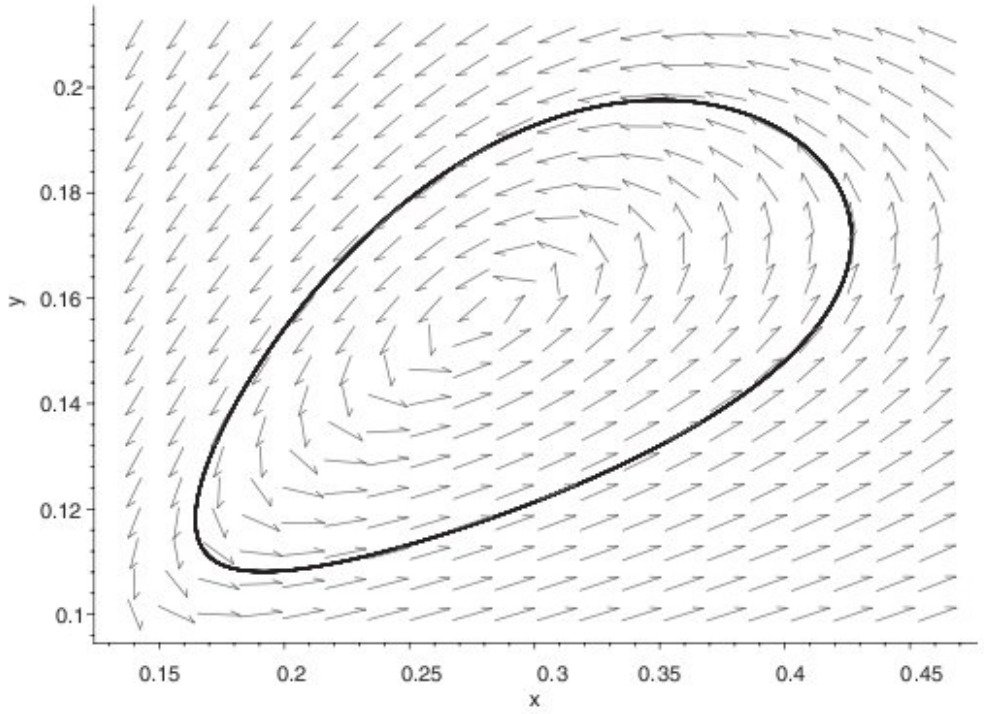

Figure 2. Stable limit cycle around the positive interior equilibrium point for the model system (2.30).

easily by using any mathematical software (e.g. MAPLE) as

$$g_{20} = -0.005\,279\,657\,042 + 0.003\,107\,509\,389\mathrm{i},$$
$$g_{11} = 0.005\,279\,657\,042 + 0.003\,107\,509\,388\mathrm{i},$$
$$g_{21} = -0.004\,581\,433\,107 + 0.005\,411\,288\,533\mathrm{i}.$$

Hence the first Lyapunov coefficient l_1 is given by

$$l_1 = -0.201\,941\,0159.$$

Thus the Hopf-bifurcating periodic solution is stable and all other trajectories around the limit cycle ultimately approach it (see figure 2).

2.5. Global stability

In the previous section we have obtained the conditions for the existence of positive equilibrium and its local asymptotic stability conditions. We have observed that instability of the boundary equilibrium E_1 gives support for the existence of positive interior equilibrium point E_*. The parametric conditions for local asymptotic stability of E_* are $a < \bar{a}$ and $b > c$. Now we try to find the condition under which system (2.5) will have no non-trivial periodic solutions around E_*. For this purpose we recall the divergence criterion for the stability of a periodic solution for planner systems [35, 37].

Let us construct the function $h(x, y) = 1/(xy)$ such that $h(x, y) > 0$ for all $x > 0$, $y > 0$. Using the definition of $F_1(x, y)$ and $F_2(x, y)$ from equation (2.2) we get

$$\frac{\partial}{\partial x}(F_1 h) + \frac{\partial}{\partial y}(F_2 h) = -\frac{1}{y} - \frac{(b-a)}{(x+y)^2}.$$

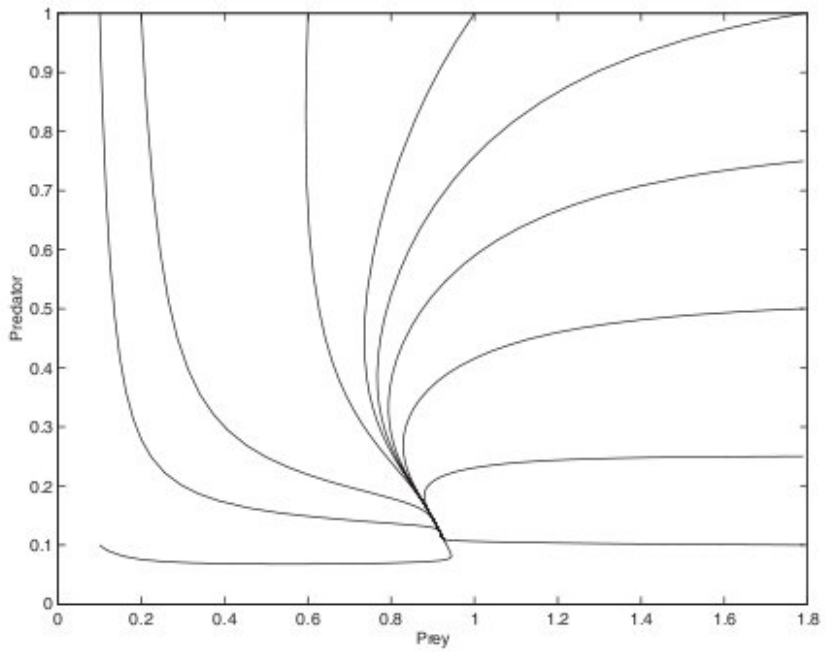

Figure 3. The phase portrait of the system (2.5) created by MATLAB. E_* is a global attractor, where $a = 0.7$, $b = 0.9$ and $c = 0.8$.

Clearly

$$\triangle(x, y) \equiv \frac{\partial}{\partial x}(F_1 h) + \frac{\partial}{\partial y}(F_2 h) < 0 \qquad \text{for } a < b.$$

According to the Bendixon–Dulac criterion, there will be no limit cycle in the positive quadrant of the xy-plane. Now we can state the following lemma.

Lemma. *The existence of interior equilibrium point E_* along with its local stability and the restriction $a < b$ eliminates the chance of existence of a non-trivial periodic solution around E_*.*

Now we are in a position to prove the global stability of the model system (2.5).

Lemma. *If $a < a_*$ $[a_* = min\ (b, \bar{a})]$ and $b > c$ then E_* is globally asymptotically stable.*

Proof. The system (2.5) has no positive periodic solution around E_* for $a < a^*$ and $b > c$. The boundedness of the solution together with the saddle nature of boundary equilibrium point E_1 and local asymptoticality of E_* leads to the conclusion that all the trajectories will approach E_* with increasing time 't'. Hence E_* is a global attractor and the system is globally asymptotically stable (see figure 3).

3. The stochastic model

The above discussion rests on the assumption that the environmental parameters involved with the model system are all constants irrespective of time and environmental fluctuations. In reality all such parameters exhibit random variations to a greater or lesser extent. In previous discussions we have dealt with the equilibrium populations and their stability with regard to the imposition of small disturbances. In this section we consider the effect of environmental

fluctuations on the model system and the stochastic stability of the coexisting equilibrium point associated with the model system.

Environmental fluctuations are important components in an ecosystem. Most natural phenomena do not follow strictly deterministic laws but rather oscillate randomly about some average value so that the deterministic equilibrium is no longer an absolutely fixed state [5, 9]. May [49] pointed out the fact that due to environmental fluctuations, the birth rates, carrying capacity, competition coefficients and other parameters involved with the model system exhibit random fluctuations to a greater or lesser extent. Consequently the equilibrium population distribution fluctuates randomly around some average value. Elton [25] observed that 'the chief cause of fluctuations in animal numbers is the instability of the environment'. Within a deterministic environment we seek the constant equilibrium population and then investigate its stability which follows from the dynamics of the interactions between and within the species. For systems which are driven by environmental stochasticity, it is impossible to find a time-independent equilibrium point as a solution of the governing SDEs. In this situation it is reasonable to find a probabilistic 'smoke cloud', described by the equilibrium probability distribution. For the model systems described by the system of SDEs, there is a continuous spectrum of disturbances generated by the environmental stochasticity, and the system is in tension between two countervailing tendencies. On the one hand, random environmental fluctuations are responsible for spreading the cloud and making the probability distribution move diffusively, while on the other hand, the dynamics of stabilizing population interactions tend to restore the populations to their mean value in order to compact the cloud [49]. Model systems with this type of compact cloud of population distribution are called stochastically stable systems. To study the effect of random environmental fluctuations we have to construct the stochastic counterpart of the deterministic model system by incorporating environmental fluctuations.

There are two ways of developing the stochastic model corresponding to an existing deterministic one to study the effect of fluctuating environment. First, one can replace the environmental parameters involved with the deterministic model system by some random parameters (e.g. the growth rate parameter 'r' can be replaced by $r_0 + \epsilon\gamma(t)$, where r_0 is the average growth rate, $\gamma(t)$ is the noise function and ϵ is the intensity of fluctuation). Second, one can add a randomly fluctuating driving force directly to the deterministic growth equations of prey and predator populations without altering any particular parameter [8, 11, 59].

Model (2.2) was just a first attempt towards the modelling of predator–prey interaction with ratio-dependent functional response. In this study we introduce stochastic perturbation terms into the growth equations of both prey and predator populations to incorporate the effect of randomly fluctuating environment. We assume that stochastic perturbations of the state variables around their steady-state values E_* are of Gaussian white noise type which are proportional to the distances of x, y from their steady-state values x^*, y^*, respectively [15]. Gaussian white noise is extremely useful to model rapidly fluctuating phenomena [11, 59]. So the deterministic model system (2.2) results in the following stochastic model system:

$$\mathrm{d}x = F_1(x, y)\mathrm{d}t + \sigma_1(x - x^*)\mathrm{d}\xi_t^1, \qquad \mathrm{d}y = F_2(x, y)\mathrm{d}t + \sigma_2(y - y^*)\mathrm{d}\xi_t^2, \tag{3.1}$$

where σ_1, σ_2 are real constants and known as the intensity of environmental fluctuations, $\xi_t^i = \xi_i(t)$, $i = 1, 2$ are standard Wiener processes independent of each other [30]. In the rest of this work we consider (3.1) as an Ito stochastic differential system of the type

$$\mathrm{d}X_t = f(t, X_t)\mathrm{d}t + g(t, X_t)\mathrm{d}\xi_t, \qquad X_{t0} = X_0, \tag{3.2}$$

where the solution $(X_t, t > 0)$ is an Ito process, 'f' is a slowly varying continuous component or *drift coefficient*, 'g' is the rapidly varying continuous random component or diffusion coefficient and ξ_t is a two-dimensional stochastic process having scalar Wiener process

components with increments $\Delta\xi_t^j = \xi_j(t+\Delta t) - \xi_j(t)$ that are independent Gaussian random variables $N(0, \Delta t)$. In the case of system (3.1),

$$X_t = (x, y)^{\mathrm{T}}, \qquad \xi_t = (\xi_t^1, \xi_t^2)^{\mathrm{T}}, \qquad f = \begin{bmatrix} F_1(x, y) \\ F_2(x, y) \end{bmatrix},$$
$$g = \begin{bmatrix} \sigma_1(x - x^*) & 0 \\ 0 & \sigma_2(y - y^*) \end{bmatrix}. \tag{3.3}$$

Since the diffusion matrix 'g' depends on the solution X_t, system (3.1) is said to have multiplicative noise.

3.1. Stochastic stability of interior equilibrium

The stochastic differential system (3.1) can be centred at its positive equilibrium point $E_*(x^*, y^*)$ by introducing the variables $u_1 = x - x^*$ and $u_2 = y - y^*$. It looks a very hard problem to derive asymptotic stability in the mean square sense by the Lyapunov function method working on the complete nonlinear equations (3.1). For simplicity of mathematical calculations we deal with the SDEs obtained by linearizing the vector function 'f' in (3.3) about the positive equilibrium point E_*. The linearized version of (3.2) around E_* is given by

$$\mathrm{d}U(t) = F(U(t))\mathrm{d}t + g(U(t))\mathrm{d}\xi(t), \tag{3.4}$$

where $U(t) = \mathrm{col}(u_1(t), u_2(t))$ and

$$F(U(t)) = \begin{bmatrix} -a_{11}u_1 - a_{12}u_2 \\ a_{21}u_1 - a_{22}u_2 \end{bmatrix}, \qquad g(U(t)) = \begin{bmatrix} \sigma_1 u_1 & 0 \\ 0 & \sigma_2 u_2 \end{bmatrix} \tag{3.5}$$

with

$$a_{11} = x^* - \frac{ax^*y^*}{(x^* + y^*)^2}, \qquad a_{12} = \frac{a(x^*)^2}{(x^* + y^*)^2},$$
$$a_{21} = \frac{b(y^*)^2}{(x^* + y^*)^2}, \qquad a_{22} = \frac{bx^*y^*}{(x^* + y^*)^2}. \tag{3.6}$$

Note that, in (3.4) the positive equilibrium E_* corresponds to the trivial solution $(u_1, u_2) = (0, 0)$. Let Ω be the set defined by $\Omega = [(t \geqslant t_0) \times \mathbb{R}^2, t_0 \in \mathbb{R}^+]$. Let $V \in C_2(\Omega)$ be a twice differentiable function of time t. We define the following theorem due to Afanas'ev *et al* [2].

Theorem. *Suppose there exists a function $V(U, t) \in C_2(\Omega)$ satisfying the inequalities*

$$K_1|U|^\alpha \leqslant V(U, t) \leqslant K_2|U|^\alpha, \tag{3.7}$$

$$LV(U, t) \leqslant -K_3|U|^\alpha, \qquad K_i > 0, \quad i = 1, 2, 3, \quad \alpha > 0. \tag{3.8}$$

Then the trivial solution of (3.4) is exponentially α-stable for all time $t \geqslant 0$.

With reference to (3.8) the expression for $LV(U, t)$ is defined by

$$LV(U, t) = \frac{\partial V(U, t)}{\partial t} + F^{\mathrm{T}}(U)\frac{\partial V(U, t)}{\partial U} + \frac{1}{2}\mathrm{Tr}\left[g^{\mathrm{T}}(U)\frac{\partial^2 V(U, t)}{\partial U^2}g(U)\right], \tag{3.9}$$

where

$$\frac{\partial V(U, t)}{\partial U} = \mathrm{col}\left(\frac{\partial V}{\partial u_1}, \frac{\partial V}{\partial u_2}\right), \qquad \frac{\partial^2 V(U, t)}{\partial U^2} = \left[\left(\frac{\partial^2 V}{\partial u_i \partial u_j}\right)_{i,j=1,2}\right]. \tag{3.10}$$

Let us consider the Lyapunov function

$$V(U(t), t) = \tfrac{1}{2}[u_1^2 + \omega_1 u_2^2], \tag{3.11}$$

where ω_1 is a positive real constant to be chosen later. It can be easily checked that (3.7) holds for the Lyapunov function defined in (3.11) with $\alpha = 2$. Now,

$$LV(U,t) = (-a_{11}u_1 - a_{12}u_2)u_1 + (a_{21}u_1 - a_{22}u_2)\omega_1 u_2 + \frac{1}{2}\mathrm{Tr}\left[g^{\mathrm{T}}(U)\frac{\partial^2 V(U,t)}{\partial U^2}g(U)\right]. \tag{3.12}$$

From (3.5), (3.10) and (3.11) we get,

$$\frac{\partial^2 V}{\partial u^2} = \begin{bmatrix} 1 & 0 \\ 0 & \omega_1 \end{bmatrix}, \qquad g^{\mathrm{T}}(U)\frac{\partial^2 V(U,t)}{\partial U^2}g(U) = \begin{bmatrix} \sigma_1^2 u_1^2 & 0 \\ 0 & \omega_1 \sigma_2^2 u_2^2 \end{bmatrix}. \tag{3.13}$$

Hence from (3.12) we get,

$$LV(U,t) = -\left(2a_{11} - \frac{\sigma_1^2}{2}\right)u_1^2 + 2(a_{21}\omega_1 - a_{12})u_1u_2 - \left(2a_{22} - \frac{\omega_1\sigma_2^2}{2}\right)u_2^2.$$

If we choose $\omega_1 = (a_{12}/a_{21}) > 0$, then from the above result we get,

$$LV(U,t) = -\left(2a_{11} - \frac{\sigma_1^2}{2}\right)u_1^2 - \left(2a_{22} - \frac{a_{12}\sigma_2^2}{2a_{21}}\right)u_2^2 = -U^{\mathrm{T}}QU, \tag{3.14}$$

where $Q = \mathrm{diag}[(2a_{11} - \sigma_1^2/2), (2a_{22} - a_{12}\sigma_2^2/2a_{21})]$ and the diagonal matrix Q will be a real symmetric positive definite matrix and hence its eigenvalues λ_1 and λ_2 will be positive real quantities if and only if the following conditions hold:

$$\sigma_1^2 < 4a_{11} \qquad \text{with } a_{11} > 0 \quad \text{and} \quad \sigma_2^2 < \frac{4a_{22}a_{21}}{a_{12}}. \tag{3.15}$$

If λ_{m} stands for the minimum of two positive eigenvalues λ_1 and λ_2 for the diagonal matrix Q then from (3.14) we get the following result:

$$LV(U,t) \leqslant -\lambda_{\mathrm{m}}|U|^2. \tag{3.16}$$

This leads us to the following theorem.

Theorem. *Assume that for some positive real value of $\omega_1 = a_{12}/a_{21}$ and the inequalities in (3.15) hold then the zero solution of system (3.4) is asymptotically mean square stable.*

Recall that $a < \bar{a}$ and $b > c$ are the conditions for deterministic stability of the interior equilibrium point E_*. Conditions for deterministic stability of interior equilibrium point along with the inequalities (3.15) are the necessary conditions for stochastic stability of the model system under environmental fluctuation. Inequalities (3.15) defines the upper threshold values for the intensities of the environmental fluctuations 'σ_1' and 'σ_2' determined by the system parameters (i.e. a, b and c) as

$$\sigma_1^2 < \bar{\sigma}_1^2 = 4\left[\frac{b^2 - a(b-c)^2}{b^2}\right] \qquad \text{and} \qquad \sigma_2^2 < \bar{\sigma}_2^2 = \frac{4(b-c)^3}{ac}. \tag{3.17}$$

Thus the internal parameters of the model system and the intensities of environmental fluctuation have the ability to maintain the stability of the stochastic model system and exhibit a balanced dynamics at any future time within a bounded domain of $(a, b, c, \sigma_1, \sigma_2)$-parametric space. The boundaries of the bounded set in $(a, b, c, \sigma_1, \sigma_2)$-parametric space are defined by the following inequalities (which are some implicit functional relations):

$$a < \bar{a}, \qquad b > c, \qquad \sigma_1^2 < \bar{\sigma}_1^2, \qquad \sigma_2^2 < \bar{\sigma}_2^2, \tag{3.18}$$

where the expressions for $\bar{a}$, $\bar{\sigma}_1^2$ and $\bar{\sigma}_2^2$ are given in (2.20) and (3.17), respectively. The inequalities in (3.17) can be put into an alternative form as

$$a < \left[\frac{b}{b-c}\right]^2\left[1 - \frac{\sigma_1^2}{4}\right] \qquad \text{and} \qquad a < \frac{4(b-c)^3}{c\sigma_2^2}. \tag{3.19}$$

For a given set of values for b, c, σ_1 and σ_2 with $b > c$ we can find an estimate for the parameter 'a' which will ensure the deterministic stability as well as stochastic stability of interior equilibrium point E_* for the model system (2.5). Defining the upper threshold limit 'a' for 'a' as

$$A = \min\left[\frac{b}{b-c}, \frac{b}{b+c}\left(c + \frac{b}{b-c}\right), \left[\frac{b}{b-c}\right]^2\left[1 - \frac{\sigma_1^2}{4}\right], \frac{4(b-c)^3}{c\sigma_2^2}\right] \tag{3.20}$$

we can conclude that $a < A$ and $b > c$ are the necessary and sufficient conditions for the stochastic stability of interior equilibrium point E_* for the model system under consideration.

3.2. Numerical simulation

In order to give some support to the stability results of the stochastic model system obtained in the previous section, we numerically simulate the solution of the SDE (3.1). For this purpose we have to keep in mind that approximated sample paths or trajectories of Ito processes obtained from direct simulation must be close to those of the original Ito process and these will lead us to the concept of a strong solution for a system of SDE [21]. To find the approximate strong solution of the Ito system of SDEs (3.1) with given initial condition we use the Euler–Maruyama (EM) and Milstein method.

Consider the discretization of the time interval $[t_0, t_f]$ with

$$t_0 = 0 < t_1 < t_2 < \cdots < t_n < \cdots < t_N < t_{N+1} = t_f$$

and the simplest stochastic numerical scheme for the system under consideration is the EM method

$$u_{k,n+1} = u_{k,n} + f(t_n, u_{k,n})\triangle t_n + g(t_n, u_{k,n})\triangle \xi_n^k$$

with $u_{k,0} = u_{k0}$, $k = 1, 2$ and $\bar{u}_n = [u_{1,n}, u_{2,n}]$ being the numerical solution at time 't_n'. In the above numerical scheme, the increments are given by

$$\triangle t_n = t_{n+1} - t_n,$$

$$\triangle \xi_n^k = \xi_{n+1}^k - \xi_n^k = \xi^k(t_{n+1}) - \xi^k(t_n),$$

where $n = 0, 1, 2, \ldots, N$.

The noise increments $\triangle \xi_n^k$ are $N(0, \triangle t_n)$-distributed independent random variables which can be generated numerically by pseudo-random number generators.

An efficient way to evaluate the increments of the Wiener process $\triangle \xi_n^k$ is to consider

$$\triangle \xi_n^k = \sqrt{I_{nk}}\triangle t_n,$$

where I_{nk} is the nth realization of I_k and I_k is the Gaussian random variable $N(0, 1)$.

Figures 4 and 5 are generated by using the numerical simulation method discussed above with the help of MATLAB software.

4. Conclusion

In classical predator–prey model systems, the consumption rate of a single predator (so-called functional response) is the key component of predation models as it is considered to determine both the prey death rate and the predator rate of increase. In a continuous-time predator–prey model with prey-dependent functional response it is a classical assumption that predators encounter prey at random and that the response function depends solely on prey abundance. This assumption is true for several cases but is not always appropriate [5].

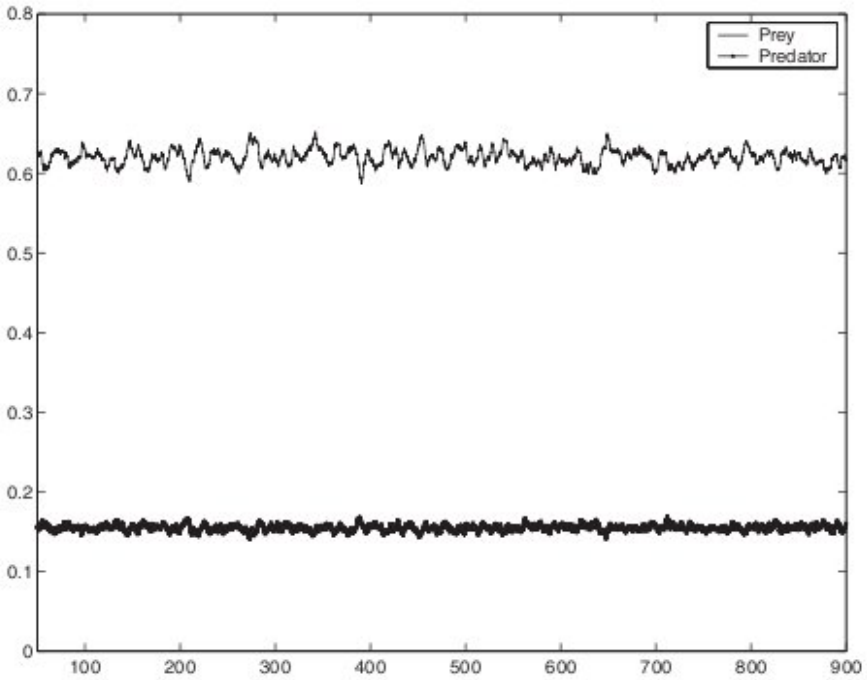

Figure 4. Solution of SDE (3.1) with parametric values $a = 1.9$, $b = 1.5$, $c = 1.2$ and $\sigma_1 = \sigma_2 = 0.2$.

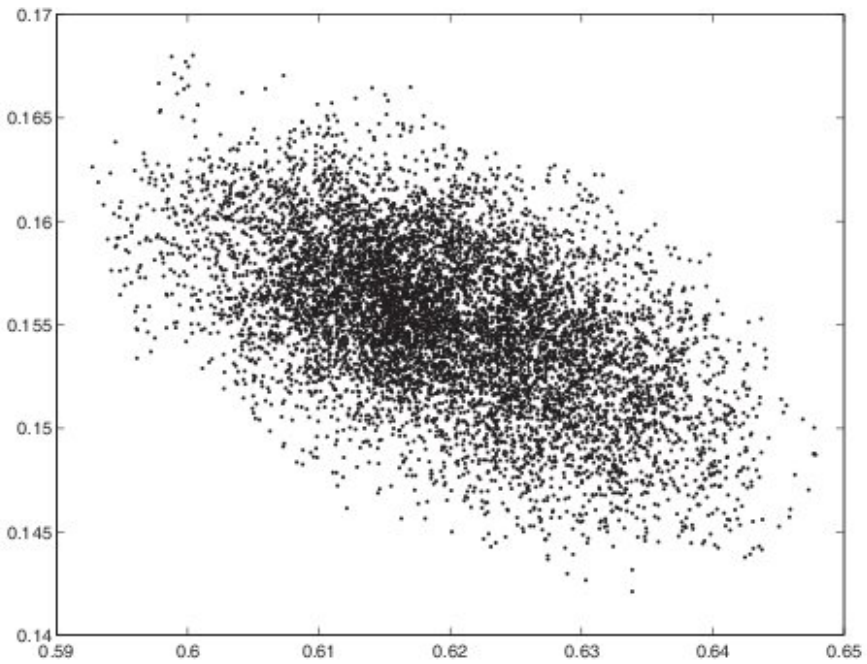

Figure 5. Corresponding population distribution around the equilibrium point $E_* = (0.62, 0.156)$.

In reality, it is reasonable to assume that the response function depends on the ratio of prey to predator abundance. There are several field and laboratory observations in support of ratio-dependent functional response. There is a sharp difference between the two types of response functions with the variations in prey production or abundance. Ratio-dependent models predict proportional increase of both populations while prey-dependent models predict the benefit of predators only from an increase of prey production and abundance.

In this paper we have considered the deterministic analysis of stability for various equilibrium points of a nonlinear predator–prey system with *ratio-dependent* functional response. First we have proved the boundedness of solutions of the model system under consideration. The origin (i.e. $E_0(0,0)$) and $E_1(1,0)$ are two equilibrium points lying on the x-axis for all permissible parameter values. However the model system cannot be linearized at E_0 and hence its local stability analysis is not possible by traditional analysis with a Jacobian matrix. To overcome this situation we have employed the technique introduced by Arino *et al* [7]. Our analysis shows that the trajectories reach the origin and both the populations become extinct. This may happen in two ways. In one case, absence of prey or predator species is responsible for extinction of predator and prey species, respectively. In the other case, over-predation of prey species irrespective of the growth rate of prey drives the system towards total extinction of both prey and predator species. This result agrees well with the result of Kuang [42]. Next we have considered the local asymptotic stability of interior equilibrium point E_* and established the existence of a small-amplitude periodic solution arising from Hopf-bifurcation as the parameter 'a' passes through its critical value '$a = a^*$' from lower to higher. At this position we can conclude that if the consumption ability of the predator is not very high (i.e. $a < a^*$) then both prey and predator populations coexist at their steady-state value E_* and hence the consumption ability and growing ability generate a balanced dynamics for both the populations. Global stability results are obtained from the condition for non-existence of a trivial periodic solution around E_* with the parametric restrictions obtained in the last part of section 2.

On the other hand, for the stochastic version of the model system we have obtained the condition for asymptotic stability of equilibrium point E_* in the mean square sense by using a suitable Lyapunov function (3.11). These conditions depend on σ_1, σ_2 and the parameters involved with the model system. For the deterministic environment, the stability of the equilibrium point demands that all eigenvalues of the Jacobian matrix lie in the left-hand half of the complex plane. For the corresponding model within the stochastic environment, this condition is necessary but insufficient, due to the existence of a relatively compact equilibrium probability cloud for the populations around the deterministic equilibrium point. The stochastic stability requires that the stability provided by the interactions (which is measured by the real parts of eigenvalues of Jacobian matrix) be sufficient to counteract the driving arising from random environmental fluctuations [49]. Regarding stability and instability of the stochastic model system, it intuitively seems appropriate to refer to the systems characterized by large fluctuations in the population numbers as 'unstable' and to those with relatively small fluctuations as 'stable'. For stochastic model system (3.1) asymptotic stability of E_* in the mean square sense depends on the restriction of (3.15). Recall that the feasible values of the intensities of environmental fluctuations depend on the system parameters, which in turn decrease with the increase of parameter 'a'. For a given set of values of a, b and c one can easily calculate the upper bounds $\bar{\sigma}_1^2$ and $\bar{\sigma}_2^2$ from the relation (3.17). Within the natural environment it is not possible to control the surroundings in such a way that the intensities of environmental fluctuations cannot exceed the upper bounds settled for them by the system parameters. The restrictions (3.15) or equivalently (3.17) are the boundaries determined by the mathematical methods to obtain a stable population distribution around the equilibrium point

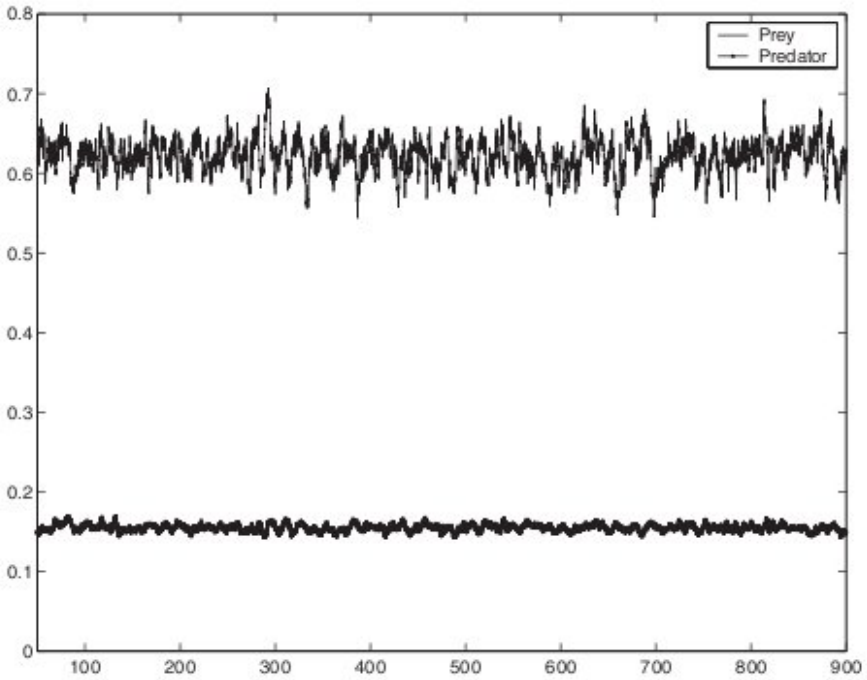

Figure 6. Solution of SDE (3.1) with parametric values $a = 1.9, b = 1.5, c = 1.2$ and $\sigma_1 = 1.2$ and $\sigma_2 = 0.8$.

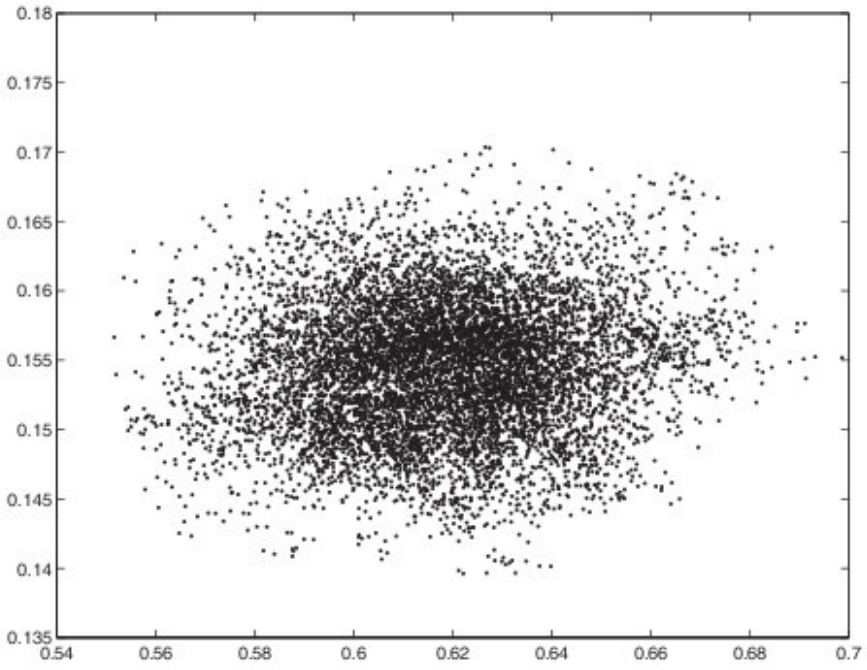

Figure 7. Corresponding population distribution around the equilibrium point $E_* = (0.62, 0.156)$.

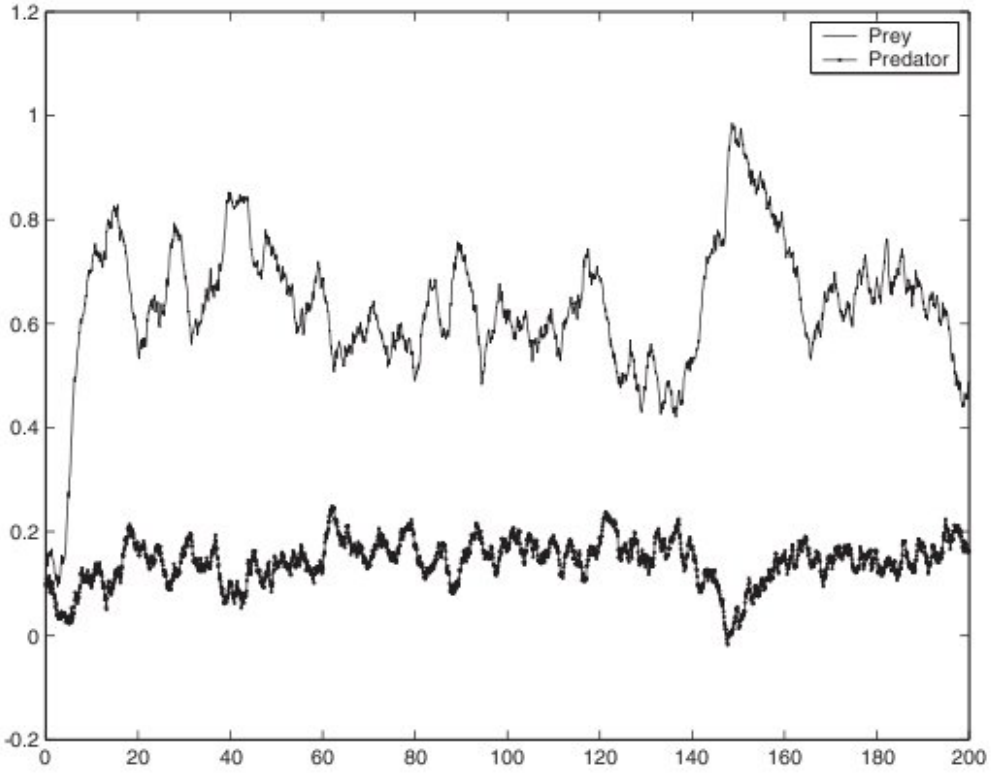

Figure 8. Solution of SDE (3.1) with parametric values $a = 1.9, b = 1.5, c = 1.2$ and $\sigma_1 = 1.9$ and $\sigma_2 = 1.8$.

within a fluctuating environment. Hence we conclude that to preserve the system stochastically stable the above restriction should be maintained.

Now, we are in a position to substantiate the analytical findings for the stochastic model system through numerical experiments. The behaviour of the ecological system depends on the rapidity of environmental fluctuations. This rapidity of fluctuations can be measured through the intensity of fluctuations which act as an environmental driving force. The high amplitude environmental driving force has the ability to change the dynamics of the system from a stable situation to an unstable one. From this viewpoint we have only varied the intensity parameters σ_1 and σ_2, keeping all other parameters unaltered. For the numerical analysis, we choose the hypothetical set of parameter values $a = 1.9$, $b = 1.5$ and $c = 1.2$ and substituting these values in (2.6) we obtain $E_* = E_*(0.62, 0.156)$. Now if we imagine a circular or elliptic neighbourhood around the equilibrium point $E_*(0.62, 0.156)$, we find that 90% or more of the population distribution will lie within the said neighbourhood implying the stochastic stability of the model system (see figure 5). If we increase the intensities of environmental fluctuations from $\sigma_1 = \sigma_2 = 0.2$ to $\sigma_1 = 1.2$ and $\sigma_2 = 0.8$ with the same parameter values for a, b and c, we again find a dense assemblage of probability cloud around $E_*(0.62, 0.156)$ depicting stochastic stability of the model system (see figures 6 and 7). Now, we would like to see how the behaviour of the system changes for increasing fluctuations. If we further increase σ_1 and σ_2 (to $\sigma_1 = 1.9$ and $\sigma_2 = 1.8$) we observe that the amplitude of the fluctuations increases, implying instability of the coexisting equilibrium point within the fluctuating environment (see figure 8). Thus the intensity of the random environmental driving force may be used as

a control parameter. These findings agree well with some earlier works [8, 11, 12, 21, 28, 61]. Numerical simulation establishes the fact that the steady state of the stochastic version is not absolutely fixed but a 'fuzzy' value around which the population fluctuates.

Ecological systems are so complex that environmental fluctuations may not always be controlled. In such a situation, the condition given in (3.20) may provide some feasible way for controlling the species from extinction. It is clear from (3.19) that σ_1 never exceeds the value 2.0 as the parameter a is positive. Hence for a given set of values of b, c, σ_1 and σ_2 (with obvious restrictions $b > c$ and $0 < \sigma_1 < 2$) if we can employ a mechanism to control the predator–prey system such that the parameter value 'a' lies below the numerical value 'A' obtained from (3.20) then the ratio-dependent predator–prey model system will exhibit stable fluctuation of population distribution around its interior equilibrium point E_* embedded within a randomly fluctuating environment.

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