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Deterministic and Stochastic Analysis of a Ratio-Dependent Predator-Prey System with Delay

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Abstract. Recently ratio-dependent predator-prey models have become the focus of considerable attention in theoretical ecology in their own right. In this paper, we have studied the deterministic and stochastic dynamical aspects of stability of a Michaelis-Menten type ratio-dependent predator-prey system that includes discrete time-delay. Computer simulations are carried out to explain the analytical findings in deterministic environment. The biological implications of our analytical and numerical findings are discussed critically.

Keywords: predator-prey model, ratio-dependence, time-delay, stability, bifurcation, white noise.

1 Introduction

Simple predator-prey models often predict extreme instability in interactions where the prey are depressed well below the carrying capacity – a phenomenon called the "paradox of enrichment" (introduced by Hairston et al. [1] and Rosenzweig [2]) because such depression is more likely in nutrient rich systems. Another similar paradox is the so called "biological control paradox", which was brought into discussion by Luck [3], stating that according to the classic predator-prey theory, you can not have both a low and stable prey equilibrium density. It has long been recognized that a milestone progress in the study of predator-prey interactions is the discovery of these paradoxes. However, in reality, there are numerous examples of successful biological control where the prey are maintained at densities less than 2 % of their carrying capacities [4]. This clearly indicates that the paradox of the biological control is not intrinsic to predator-prey interactions.

In recent years there is a growing explicit biological and physiological evidences [4–9] that in many situations, especially when predators have to search for food (and therefore have to search or compete for food), a more suitable functional response depending on the densities of both prey and predator should be introduced. Such a functional response is called a ratio-dependent functional response. Arditi and Ginzburg [10] introduced a Michaelis-Menten type ratio-dependent functional response of the form

$$p(x/y) = \frac{c(x/y)}{m + (x/y)} = \frac{cx}{my + x}, \tag{1}$$

where x, y stand for densities of prey and predator respectively. The positive constants c and m are the capturing rate and the half capturing saturation constant, respectively. Predator-prey models with such ratio-dependent functional response are strongly supported by numerous field and laboratory experiments [5, 6, 10, 11] and their deterministic dynamics have been studied extensively in ecological literature [9, 12–16].

It is now well understood that many of the processes, both natural and manmade, in biology, medicine etc. involve time-delays. Time-delays occur so often, in almost every situation, that to ignore them is to ignore reality (see references [17–20] and references there in). Samanta [20] argued that in an improved analysis, the effect of time-delay due to the time required in going from egg stage to the adult stage, gestation period etc. has to be taken into account. Kuang [18] mentioned that animals must take time to digest their food before further activities and responses take place and hence any model of species dynamics without delays is an approximation at best. Although various aspects of ratio-dependent predator-prey models have been studied in ecological literature, the effect of time-delay on such models has not yet been addressed considerably. From this viewpoint, we have considered the following Michaelis-Menten type ratio-dependent predator-prey system involving discrete time-delay:

$$\begin{aligned} &\frac{dx}{dt} = x(a - bx) - \frac{cxy}{my + x}, \\ &\frac{dy}{dt} = y\left(- d + \frac{fx(t-\tau)}{my(t-\tau) + x(t-\tau)}\right), \\ &x(0) > 0,\ \ y(0) > 0 \quad \text{and} \quad \frac{dx}{dt} = \frac{dy}{dt} = 0 \ \text{ for } \ (x, y) = (0, 0), \end{aligned} \tag{2}$$

where $x(t)$ and $y(t)$ respectively denote population densities of prey and predator at time t. Here $a/b > 0$ is the carrying capacity of the prey, $d > 0$ is the death rate of the predator and a, c, m and f are positive constants that stand for prey intrinsic growth rate, capturing rate, half capturing saturation constant and conversion rate respectively. The delay τ in (2) can be regarded as the gestation period or reaction time of the predator y.

After Lorenz [21] and May [22,23], theoretical ecologists have undoubtedly accepted the fact that deterministic approach has some limitations in biology. In deterministic situation, it is always difficult to predict the future of the system accurately. This difficulty increases as we move outside the tightly controlled biochemical and physiological systems to the more complex behaviour of whole organism system or to the dynamics of population ecosystems or global environmental systems. One reason to this difficulty is that biological systems are subject to apparently random fluctuations. That is, either the state variables themselves or the parameters are perturbed at random times and by random events. In 1995, Renshaw [24] mentioned that the most natural phenomena do not follow strictly deterministic laws but rather oscillate randomly about some average so that the deterministic equilibrium is not an absolutely fixed state; instead it is a “fuzzy” value around which the biological system fluctuates. In fact, randomness or stochasticity plays a vital role in the structure and function of biological systems. The environmental factors are time-dependent, randomly varying and should be taken as stochastic. In ecology, we have two types of stochasticity – namely the demographic stochasticity and the environmental stochasticity [25, 26]. Both types of stochasticity play a significant part in the realistic dynamical modelling of ecosystems. A central obstacle in the stochastic modelling of an ecosystem is the lack of mathematical machinery available to analyze non-linear multi-dimensional stochastic process [22, 27]. A quantum leap in the mathematical sophistication of ecological modelling occurred when May [22] introduced stochastic differential equations to investigate limits to niche overlap in randomly fluctuating environment. Subsequently, the sensibility of stochastic models in comparison with deterministic models is established by many researchers [20, 28–33]. Recently, Bandyopadhyay and Chattopadhyay [34] and Mankin et al. [35] have studied the effect of fluctuating environment on ratio-dependent predator-prey model. These definitely indicate that researchers are increasingly realizing the necessity of such considerations. But, unfortunately, the effect of environmental fluctuation on time-delayed ratio-dependent predator-prey model has not yet been investigated in theoretical ecology. Our endeavour may accomplish such a necessity.

The objective of this paper is to study the dynamical behaviours of the model (2) in deterministic and stochastic environment.

The paper is structured as follows. In Section 2, we present the deterministic analysis of the system (2). Our study includes boundedness, stability and bifurcation of the system (2). Numerical simulation of a variety of solutions of this system is also presented in this section. In Section 3, we have formulated the stochastic version of the model (2) by superimposing Gaussian white noises. Then a rigorous analysis of the resulting stochastic model (10) is presented following Nisbet and Gurney [26]. Section 4 contains the general discussions of the paper and biological implications of our mathematical findings.

2 Deterministic scenarios

In this section, we discuss the dynamical behaviours of the deterministic system (2) when $\tau = 0$ and $\tau \neq 0$.

Case 1: $\tau = 0$. We first discuss the boundedness of the system (2).

Theorem 1. *When* $\tau = 0$ *, the system* (2) *is dissipative.*

For proof, see [34].

The system (2) always have the boundary equilibrium points $E_0(0, 0)$ and $E_1((a/b), 0)$. The interior equilibrium point $E^*(x^*, y^*)$ exists uniquely if and only if any one of the following two conditions is true:

$$\text{(i)}\quad d < f < \frac{cd}{c - ma}, \quad \text{when } \; c > ma$$

$$\text{(ii)}\quad f > d, \quad \text{when } \; c \le ma.$$

In both the cases x^* and y^* are given by

$$x^* = \frac{f(am - c) + cd}{bmf}, \quad y^* = \frac{(f - d)\{f(am - c) + cd\}}{bdfm^2}.$$

Kuang and Beretta [9] derived a blend of dynamical behaviours for the system (2). We mention below some of their results.

Theorem 2. *If* $f > d$ *and* $am > c$ *then the system is permanent.*

Theorem 3. *If* $c > am + dm$*, then the system is not persistent.*

On deterministic extinction, Kuang and Beretta [9] have derived the following results.

Theorem 4. *If* $c > am + dm$*, then there exist positive solutions* $(x(t), y(t))$ *of the system such that* $\lim_{t\to\infty}(x(t), y(t)) = (0, 0)$.

Theorem 5. *If* $c \le am$ *and* $f \le d$*, then* E_1 *is globally asymptotically stable.*

Theorem 6. *If* $f \ge cd/(c - am)$ *and* $c > am$ *then* E_0 *is globally asymptotically stable.*

For proofs of Theorems 2–6, see [9].

Theorem 7. *If* E^* *exists, then it is locally asymptotically stable or unstable according as* $\Delta = (c - am - dm)f^2 + (mf - c)d^2 <$ *or* > 0.

The proof of the theorem is given in the Appendix.

On global stability of E^*, we have the following theorems:

Theorem 8. *If* $\Delta < 0$ *and* $c \le am$ *then* E^* *is globally asymptotically stable.*

For proof, see [9].

Theorem 9. *If* $f > dm$ *and* $\frac{c}{a} < \min\{\frac{f}{am}, \frac{f}{f-dm}, \frac{f}{f-dm}(\frac{d}{a} + \frac{f}{d-am})\}$*, then* E^* *is globally asymptotically stable.*

For proof, see [34].

The following theorem gives a criterion for the existence of a Hopf bifurcation near E^*.

Theorem 10. *If* E^* *exists, then Hopf bifurcation occurs at* $c = c^* = \frac{mf\{f(a+d)-d^2\}}{f^2-d^2}$.

Following the same line as in [34], the theorem can easily be proved.

Case 2: $\tau \neq 0$. In this case the equilibrium points of the system (2) are the same as that of the system when $\tau = 0$ with the same conditions of existence. Beretta and Kuang [36] derived some important behaviour of the time-delayed system (2). Some of them are mentioned below.

Theorem 11. *If $f > d$, then the time-delayed system is dissipative.*

Theorem 12. *Theorem* 2 *and* 3 *also hold good for $\tau \neq 0$.*

On deterministic extinction of the time-delayed system (2), Beretta and Kuang [36] derived the following results.

Theorem 13. *If $c > am + dm$ and $f < cd/(c - am - dm)$, then there exist positive solutions $(x(t), y(t))$ of the system such that $\lim_{t\to\infty}(x(t), y(t)) = (0, 0)$.*

Theorem 14. *If $c < am$ and $f < d$, then E_1 is globally asymptotically stable.*

We now study the stability behaviour of interior equilibrium point $E^*(x^*, y^*)$ of the system (2) when $\tau \neq 0$. We linearize the system (2) by using the following transformations: $x' = \ln x$, $y' = \ln y$ and $x' = x'^* + u$, $y' = y'^* + v$. Then the linear system is given by

$$\frac{dU}{dt} = AU(t) + BU(t - \tau), \tag{3}$$

where

$$U = [u, v]^T, \quad A = (a_{ij})_{2\times 2}, \quad B = (b_{ij})_{2\times 2}$$

and

$$\begin{aligned} a_{11} &= -bx^* + \frac{cx^*y^*}{(my^* + x^*)^2}, & a_{12} &= -\frac{cx^*y^*}{(my^* + x^*)^2}, \\ b_{21} &= \frac{mfx^*y^*}{(my^* + x^*)^2}, & b_{22} &= -\frac{mfx^*y^*}{(my^* + x^*)^2} \end{aligned}$$

and all other $a_{ij} = b_{ij} = 0$.

We look for solution of the model (2) of the form $U(t) = \rho e^{\lambda t}$, $0 \neq \rho \in \mathbb{R}^2$. This leads to the following characteristic equation:

$$\lambda^2 - a_1\lambda + (a_2\lambda + a_3)e^{-\lambda\tau} = 0, \tag{4}$$

where $a_1 = -a_{11}$, $a_2 = -b_{22}$ and $a_3 = a_{11}b_{22} - a_{12}b_{21}$.

It is well known that the signs of the real parts of the solutions of (4) characterize the stability behaviour of E^*. Therefore, substituting $\lambda = \xi + i\eta$ in (4) we obtain real and imaginary parts, respectively, as

$$\xi^2 - \eta^2 + a_1\xi + \{(a_2\xi + a_3)\cos\eta\tau + a_2\eta\sin\eta\tau\}e^{-\xi\tau} = 0 \tag{5}$$

and

$$2\xi\eta + a_1\eta + \{a_2\eta\cos\eta\tau - (a_2\xi + a_3)\sin\eta\tau\}e^{-\xi\tau} = 0. \tag{6}$$

A necessary condition for a stability change of E^* is that the characteristic equation (4) has purely imaginary solutions. Hence to obtain the stability criterion, we set $\xi = 0$ in (5) and (6) to obtain

$$\eta^2 = a_3\cos\eta\tau + a_2\eta\sin\eta\tau \tag{7}$$

$$a_1\eta = a_3\sin\eta\tau - a_2\eta\cos\eta\tau. \tag{8}$$

Eliminating τ between (7) and (8) by squaring and adding, we get the equation for determining η as

$$\sigma^2 + d_1\sigma + d_2 = 0, \tag{9}$$

where $\sigma = \eta^2$, $d_1 = a_1^2 - a_2^2$, $d_2 = -a_3^2 < 0$.

By Descartes' rule, the quadratic equation (9) always have a unique positive root. Consequently the stability criteria of the system (2) for $\tau = 0$ will not necessarily ensure the stability of the system for $\tau \neq 0$. In the following theorem, we have given a criterion for switching the stability behaviour of E^*. The proof of the theorem is deferred to the Appendix.

Theorem 15. *Let E^* exists with $(c - am - dm)f^2 + (mf - c)d^2 < 0$. Also let $\sigma_0 = \eta_0^2$ be the unique positive root of the equation* (8)*. Then there exists a $\tau = \tau^*$ such that E^* is locally asymptotically stable for $0 \leq \tau < \tau^*$ and unstable for $\tau > \tau^*$, provided*

$$f(\eta_0) = 2\eta_0^2 + a_1^2 - a_2^2 > 0,$$

where τ^* is given by $\tau^* = \frac{1}{\eta_0}\arccos[\frac{\eta_0^2(a_3 - a_1a_2)}{a_2^2\eta_0^2 + a_3^2}]$.

On global stability of E^*, we have the following theorems [36]:

Theorem 16. *If $fm > c$ and $\tau < \min\{\frac{2b}{cf}, \frac{2m(fm-c)}{f\{bm+(fm+c)(1+m^2)\}}\}$, then E^* is globally asymptotically stable in $\mathbb{R}_+^2$.*

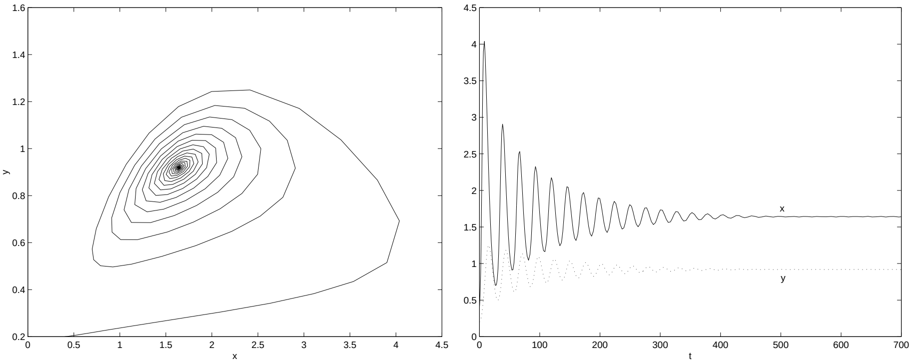
Theorem 17. *If $fm > c$ and $\tau < \frac{2(fm-c)}{f\{1+c^2+f(1+m^2)\}}$, then E^* is globally asymptotically stable in $\mathbb{R}_+^2$.*

For proofs of Theorems 16 and 17, see [36].

2.1 Numerical simulation

Analytical studies always remain incomplete without numerical verification of the results. Here we present computer simulation of some solutions of the system (2).

We take the parameters of the system as $a = 1.1,\ b = 0.2,\ c = 2.15,\ m = 1,$ $d = 0.5,\ f = 0.78,\ \tau = 0$ and $(x(0), y(0)) = (0.4, 0.2)$. Then $E^*(x^*, y^*) = (1.641, 0.919)$ and $\Delta = -0.0079 < 0$. Therefore, by Theorem 7, E^* is locally asymptotically stable. The corresponding phase portrait is shown in Fig. 1(a). In this case, the prey and predator populations approach to their equilibrium values x^* and y^* respectively in finite time (see Fig. 1(b)).



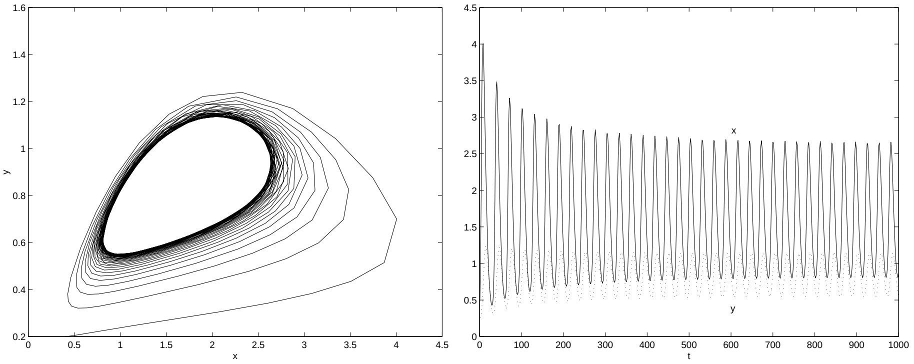
(a) (b)

Fig. 1. Here $x(0) = 0.4,\ y(0) = 0.2$ and $a = 1.1,\ b = 0.2,\ c = 2.15,\ m = 1,$ $d = 0.5,\ f = 0.78,\ \tau = 0$. (a) Phase portrait of the system (2) showing that $E^*(x^*, y^*) = (1.641, 0.919)$ is locally asymptotically stable; (b) the solid curve depicts the prey population and the dotted one the predator population. Both the populations converge to their equilibrium-state values in finite time.

If we gradually increase the value of c, keeping other parameters fixed, then following Theorem 10, we have a critical value $c^* = 2.172$ such that E^* loses its stability as c passes through c^*. For $c = 2.18 > c^*$, we verify that $E^*(1.5872, 0.8888)$ is unstable ($\Delta = 0.0029 > 0$) and there is a periodic orbit near E^* (see Fig. 2(a)). The oscillations of prey and predator populations in time are shown in Fig. 2(b).

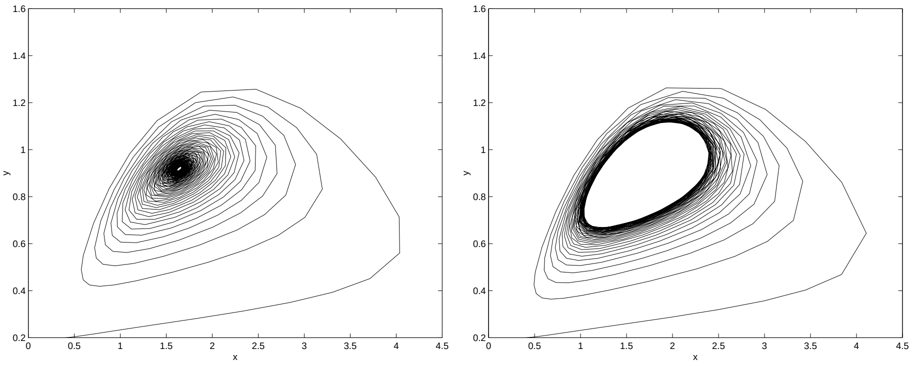
It is mentioned before that the stability criteria in the absence of delay ($\tau = 0$) will not necessarily guarantee the stability of the system in presence of delay ($\tau \neq 0$). Let us choose the parameters of the system as $a = 1.1,\ b = 0.2,\ c = 2.15,\ m = 1,\ d = 0.5,$ $f = 0.78$ and $(x(0), y(0)) = (0.4, 0.2)$. It is already seen that for such choices of parameters $E^*(x^*, y^*) = (1.641, 0.919)$ is locally asymptotically stable in the absence of delay. Now for such choices of parameters, it is seen from Theorem 15 that there is a unique positive root of the equation (9) given by $\sigma_0 = \eta_0^2 = 0.2474$ for which $f(\eta_0) = 0.1179 > 0$ and Hopf bifurcation occurs at $\tau = \tau^* = 0.2156$. We verify that for $\tau = 0.15 < \tau^*$, E^* is locally asymptotically stable and the corresponding phase portrait (Fig. 3(a)) is a stable spiral converging to E^*. For $\tau = 0.24 > \tau^*$, we see that E^* is unstable and there is a bifurcating periodic solution near E^* (see the phase portrait depicted in Fig. 3(b)).

The numerical study presented here shows that, using the time-delay as control, it is possible to break the stable behaviour of the system (2) and drive it to an unstable state. Also it is possible to keep the population levels at a required state using the above control.



(a) (b)

Fig. 2. Here all the parameters are same as in Fig. 1 except $c = 2.18 > c^*$. (a) Phase portrait of the system (2) showing a periodic orbit near $E^*(1.5872, 0.8888)$; (b) oscillations of the prey and predator populations in time. The solid curve represents the population density of the prey and the dotted one the population density of the predator.



(a) (b)

Fig. 3. Here $x(0) = 0.4$, $y(0) = 0.2$, $a = 1.1$, $b = 0.2$, $c = 2.15$, $m = 1$, $d = 0.5$, $f = 0.78$. (a) Phase portrait of the system (2) when $\tau = 0.15 < \tau^*$; (b) phase portrait when $\tau = 0.24 > \tau^*$.

3 The stochastic model

The basic mechanism and factors of population growth like the resources and vital rates-birth, death etc. change non-deterministically due to random environment and they are the main parameters subject to coupling of the system with its environment [32, 33, 37, 38]. From this viewpoint, we assume that fluctuations in the environment will manifest themselves mainly as fluctuations in the intrinsic growth rate a of the prey and in the mortality rate d of the predator. Thus the behaviour of the system in a random environment will be considered within the framework of the following stochastic model with discrete time-delay:

$$\begin{aligned} \frac{dx}{dt} &= x\{a + \eta_1(t) - bx\} - \frac{cxy}{my + x}, \\ \frac{dy}{dt} &= y\{-d + \eta_2(t)\} + \frac{fx(t-\tau)y}{my(t-\tau) + x(t-\tau)}, \end{aligned} \tag{10}$$

where the perturbed terms $\eta_1(t)$ and $\eta_2(t)$ are uncorrelated Gaussian white noises characterized by

$$\langle \eta_j(t) \rangle = 0 \quad \text{and} \quad \langle \eta_j(t)\eta_j(t') \rangle = \delta_j \delta(t - t') \quad \text{for } \ j = 1, 2.$$

Here δ_j $(j = 1, 2)$ are the intensities or strengths of the random perturbations, δ, the Dirac delta function and $\langle \cdot \rangle$ represents the ensemble average.

Now we are concerned with stochastic differential equations (10) which are driven by Gaussian white noises. Gaussian white noise, which is a delta-correlated random process, is very irregular and as such it is to be treated with care. In spite of this, it is an immensely useful concept to model rapidly fluctuating phenomenon. Of course, true white noise does not occur in nature. However, as can be seen by studying their spectra, thermal noise in electrical resistance, the force acting on a Brownian particle and climate fluctuations, disregarding the periodicities of astronomical origin etc. are white to a very good approximation. These examples support the usefulness of the white-noise idealization in applications to natural systems. Furthermore, it can be proved that the process (x, y), a solution of (10), is Markovian if and only if the external noises are white. These results explain the importance and appeal of the white noise idealization [39]. Here we have assumed the Stratonovich interpretation of stochastic differential equations, which conserves the ordinary rule of calculus and in this case the stochastic differential equations can be considered as an ensemble of ordinary differential equations [20].

Again using the transformations: $x' = \ln x$, $y' = \ln y$; $x' = x'^* + u$, $y' = y'^* + v$ and assuming the delay to be very small, the system (10) (to a first approximation) can be written as

$$\begin{aligned} \frac{du}{dt} &= \alpha_1 u + \beta_1 v + \eta_1, \\ \frac{dv}{dt} &= \alpha_2 u(t-\tau) + \beta_2 v(t-\tau) + \eta_2, \end{aligned} \tag{11}$$

where

$$\begin{aligned} \alpha_1 &= -bx^* + \frac{cx^*y^*}{(my^* + x^*)^2}, & \beta_1 &= -\frac{cx^*y^*}{(my^* + x^*)^2}, \\ \alpha_2 &= \frac{mfx^*y^*}{(my^* + x^*)^2}, & \beta_2 &= -\frac{mfx^*y^*}{(my^* + x^*)^2}. \end{aligned}$$

3.1 Fourier transforms: spectral density

Taking Fourier transform of both sides of each of the equations in (11) and following [20, 26], we obtain

$$\begin{aligned}\widetilde{\eta}_1(s) &= is\widetilde{u}(s) - \alpha_1\widetilde{u}(s) - \beta_1\widetilde{v}(s),\\ \widetilde{\eta}_2(s) &= is\widetilde{v}(s) - \alpha_2\widetilde{u}(s)e^{-is\tau} - \beta_2\widetilde{v}(s)e^{-is\tau},\end{aligned} \tag{12}$$

where $\widetilde{n}(s) = \int_{\infty}^{\infty} n(t)e^{-ist}dt.$

The system of equations (12) can be written in matrix form as

$$AX = B, \tag{13}$$

where

$$A = \begin{bmatrix} -\alpha_1 + is & -\beta_1 \\ -\alpha_2 e^{-is\tau} & -\beta_2 e^{-is\tau} + is \end{bmatrix}, \quad X = \begin{bmatrix} \widetilde{u}(s) \\ \widetilde{v}(s) \end{bmatrix} \quad \text{and} \quad B = \begin{bmatrix} \widetilde{\eta}_1(s) \\ \widetilde{\eta}_2(s) \end{bmatrix}.$$

Now

$$\begin{aligned} M = \det A = &\big\{(\alpha_1\beta_2 - \alpha_2\beta_1)\cos(s\tau) - s\beta_2\sin(s\tau) - s^2\big\}\\ &- i\big\{(\alpha_1\beta_2 - \alpha_2\beta_1)\sin(s\tau) - s\beta_2\cos(s\tau) - \alpha_1 s\big\}\end{aligned}$$

We assume that A^{-1} exists. Then we have $A^{-1} = (a_{ij})_{2\times 2}$, where

$$\begin{aligned} a_{11} &= \frac{-\beta_2\text{cos}(s\tau) + i\{s + \beta_2\text{sin}(s\tau)\}}{M}, & a_{12} &= \frac{\beta_1}{M},\\ a_{21} &= \frac{\alpha_2(\text{cos}(s\tau) - i\text{sin}(s\tau))}{M}, & a_{22} &= \frac{-\alpha_1 + is}{M}.\end{aligned}$$

Then the solution of (13) can be written as

$$\widetilde{u}(s) = \sum_{j=1}^{2} a_{1j}\eta_j, \quad \widetilde{v}(s) = \sum_{j=1}^{2} a_{2j}\eta_j. \tag{14}$$

Now following [20, 26] and using (14), the spectral density of u is given by

$$S_u(\omega) = \lim_{T\to\infty}\frac{1}{T}\int\limits_{-T/2}^{T/2}\int\limits_{-T/2}^{T/2}\langle u(t)u(t')\rangle \exp\{i\omega(t'-t)\}dtdt' = \sum_{j=1}^{2}|a_{1j}|^2 S_{\eta_j}(\omega).$$

Similarly the spectral density of v is given by

$$S_v(\omega) = \sum_{j=1}^{2}|a_{2j}|^2 S_{\eta_j}(\omega).$$

Therefore the fluctuation intensity (variance) of u is given by

$$\sigma_u^2 = \frac{1}{2\pi}\int_{-\infty}^{\infty} S_u(\omega)d\omega = \frac{1}{2\pi}\int_{-\infty}^{\infty}\sum_{j=1}^{2}|a_{1j}|^2 S_{\eta_j}(\omega)d\omega = \frac{1}{2\pi}\int_{-\infty}^{\infty}\sum_{j=1}^{2}|a_{1j}|^2 d\omega,$$

since $S_{\eta_j}(\omega) = 1$.

Similarly the fluctuation intensity of v is given by

$$\sigma_v^2 = \frac{1}{2\pi}\int_{-\infty}^{\infty}\sum_{j=1}^{2}|a_{2j}|^2 d\omega.$$

Let τ be very small and the following two conditions hold

(i) $(\alpha_1\beta_2 - \alpha_2\beta_1) < \min\left\{\dfrac{\beta_1^2+\beta_2^2}{1+\beta_2\tau}, (1+\beta_2\tau)\big(\alpha_1^2+\alpha_2^2\big)\right\}$,

(ii) $4(1+\beta_2\tau)(\alpha_1\beta_2 - \alpha_2\beta_1) < \{(\alpha_1\beta_2 - \alpha_2\beta_1)\tau - \alpha_1 - \beta_2\}$,

where $(\alpha_1\beta_2 - \alpha_2\beta_1) = \frac{bmfx^{*2}y^*}{(my^*+x^*)^2} > 0$.

Then after some calculation using [40], we obtain the fluctuation intensities of u and v as

$$\sigma_u^2 = \frac{\beta_1^2+\beta_2^2-(\alpha_1\beta_2-\alpha_2\beta_1)(1+\beta_2\tau)}{2H(\alpha_1\beta_2-\alpha_2\beta_1)},$$

and

$$\sigma_v^2 = \frac{(1+\beta_2\tau)(\alpha_1^2+\alpha_2^2)-(\alpha_1\beta_2-\alpha_2\beta_1)}{2(1+\beta_2\tau)H(\alpha_1\beta_2-\alpha_2\beta_1)},$$

where $H = \big[\{(\alpha_1\beta_2-\alpha_2\beta_1)\tau-\alpha_1-\beta_2\}^2 - 4(1+\beta_2\tau)(\alpha_1\beta_2-\alpha_2\beta_1)\big]^{1/2}$.

Let

$$\Omega_1 = \frac{\beta_1^2+\beta_2^2-(\alpha_1\beta_2-\alpha_2\beta_1)(1+\beta_2\tau)}{2(\alpha_1\beta_2-\alpha_2\beta_1)},$$

$$\Omega_2 = \frac{(1+\beta_2\tau)(\alpha_1^2+\alpha_2^2)-(\alpha_1\beta_2-\alpha_2\beta_1)}{2(1+\beta_2\tau)(\alpha_1\beta_2-\alpha_2\beta_1)}.$$

Following the criteria of stability in the stochastic environment [22], it is seen that the deterministic stability criteria is not enough to determine the stability of the system in a rapidly fluctuating environment. If $H \ll \Omega_i$ $(i = 1, 2)$, in rapidly fluctuating environment then populations exhibit abnormally large fluctuations which rapidly lead to extinction. In the intermediate region where H and Ω_i $(i = 1, 2)$ are commensurate, the populations are likely to undergo significant fluctuations, even though they persist for long times. Finally, if $H \gg \Omega_i$ $(i = 1, 2)$ population fluctuations are relatively small and the environment is effectively deterministic. These results are in good agreement with those of Maiti and Samanta [30], May [22], Prajneshu [31], Samanta [32] and Samanta and Maiti [33].

4 Concluding remarks

Although numerous population models have been proposed and studied in the literature, most of them are built on the classical Lotka-Volterra platform which is incapable of describing the vast biodiversity that we are part of and has a limited scope of application. In this paper, we have considered a time-delayed predator-prey model with a Michaelis-Menten type ratio-dependent functional response for prey and predator. Dynamical behaviours of the resulting model (2) are studied critically. Dissipativity of the system (2) is discussed, which, in turn, implies that the system is biologically well behaved. Some useful results on deterministic extinction are mentioned. The stability of the interior equilibrium E^* is discussed. When $\tau = 0$, a criterion for Hopf bifurcation is derived by taking the capturing rate c as bifurcation parameter. These results are illustrated through computer simulation. For $\tau \neq 0$ it has been shown both analytically and numerically that using the time-delay as control, it is possible to break the stable (spiral) behaviour of the system (2) and drive it to an unstable (cyclic) state. Also it is possible to keep the population levels at a required state using the above control.

To study the effect of environmental fluctuation on the time-delayed predator-prey system (2), we have superimposed Gaussian white noises on (2) and then study non-equilibrium fluctuation and stability of the resulting stochastic model (10) by using Fourier transform technique. Following the criteria of stability in the stochastic environment [22], it is seen that the environmental noises have a destabilizing effect on the system when $H \ll \Omega_i$ $(i = 1, 2)$. Also the deterministic system and the noise-induced stochastic system may behave alike with respect to stability when $H \gg \Omega_i$ $(i = 1, 2)$. Further, in the intermediate region where H and Ω_i $(i = 1, 2)$ are commensurate, the populations are likely to undergo significant fluctuations, even though they persist for long times.

It is well known that natural populations of plants and animals neither increase indefinitely to blanket the world nor become extinct (except in some rare cases due to some rare reasons). Hence, in practice, we often want to keep the prey and predator population to an acceptable level in finite time. In order to accomplish this we strongly suggest that in realistic field situations (where effect of time-delay and environmental fluctuation can never be violated), the parameters of the system should be regulated in such a way that E^* is deterministically stable and $H \gg \Omega_i$ $(i = 1, 2)$.

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Appendix

Proof of Theorem 7. The variational matrix at $E^*(x^*, y^*)$ is

$$V(E^*) = \begin{bmatrix} -bx^* + \dfrac{cx^*y^*}{(my^* + x^*)^2} & -\dfrac{cx^{*2}}{(my^* + x^*)^2} \\ \dfrac{fmy^{*2}}{(my^* + x^*)^2} & -\dfrac{fmx^*y^*}{(my^* + x^*)^2} \end{bmatrix}.$$

It is easy to see that the trace of $V(E^*)$ is

$$\operatorname{tr} V(E^*) = -bx^* + (c - fm)\frac{x^*y^*}{(my^* + x^*)^2} = \frac{(c - am - dm)f^2 + (mf - c)d^2}{mf^2}$$

and its determinant

$$\det V(E^*) = \frac{bfmx^{*2}y^*}{(my^* + x^*)^2} > 0.$$

The characteristic equation of $V(E^*)$ is

$$\lambda^2 + P\lambda + Q = 0,$$

where $P = -\operatorname{tr} V(E^*)$ and $Q = \det V(E^*)$.

Since $Q = \det V(E^*) > 0$, it is clear that E^* is locally asymptotically stable or unstable according as $P >$ or < 0.

Hence the theorem. ☐

Proof of Theorem 15. We solve (7) for $\sin \eta_0 \tau$ and substitute in (8). Then we find the value τ^* of τ as given in the statement of Theorem 15. Now, we notice that for $\tau = \tau^*$, the characteristic equation (4) have purely imaginary roots, $\pm i\eta_0$. Again, if $\pm\eta_0$ is a solution of (7) and (8), then η_0^2 is the unique positive root of the equation (9). The theorem will be proved if we can show that $[\frac{d\xi}{d\tau}]_{\tau=\tau^*} > 0$. To show this, we differentiate (7) and (8) with respect to τ and then set $\xi = 0$ to obtain

$$C(\eta)\frac{d\xi}{d\tau} + D(\eta)\frac{d\eta}{d\tau} = G(\eta), \tag{15}$$

$$-D(\eta)\frac{d\xi}{d\tau} + C(\eta)\frac{d\eta}{d\tau} = H(\eta), \tag{16}$$

where

$$\begin{aligned}
C(\eta) &= a_1 - \tau(a_3 \cos \eta\tau + a_2\eta \sin \eta\tau) + a_2 \cos \eta\tau,\\
D(\eta) &= -2\eta + \tau(a_2\eta \cos \eta\tau - a_3 \sin \eta\tau) + a_2 \sin \eta\tau,\\
G(\eta) &= \eta(a_3 \sin \eta\tau - a_2\eta \cos \eta\tau),\\
H(\eta) &= \eta(a_2\eta \sin \eta\tau - a_3 \cos \eta\tau).
\end{aligned}$$

Solving (15) and (16) with $\tau = \tau^*$ and $\eta = \eta_0$, we get

$$\left[\frac{d\xi}{d\eta}\right]_{\tau=\tau^*} = \frac{\eta_0^2 f(\eta_0)}{C^2(\eta_0) + D^2(\eta_0)},$$

which is positive under the condition $f(\eta_0) > 0$ and thus the theorem is established. ☐

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