

Stochastic analysis of time-delayed ecosystems

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The predator-prey-type ecosystem is investigated, taking into account the time-delay effect of the prey population on the predator population, as well as random variations in the birth rate of the preys and the death rate of the predators. The stochastic averaging procedure is applied to obtain the probability distributions of the predator and prey populations at the state of statistical stationarity. It is found that two system parameters, quantifying the effects of prey self-competition and the time delay, respectively, play the most important roles. Results are also obtained from Monte Carlo simulations to compare with the analytical results.

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I. INTRODUCTION

The classical Lotka-Volterra-type model [1,2], describing the interaction between preys and predators in an ecosystem, has been investigated extensively [3–6]. Some improvements to the original model have been suggested, such as adding a prey self-competition term [3], a predator saturation term, and a predator competition term [7,8]. In these models, the interaction between predators and preys is instantaneous; namely, an increase or decrease in prey population will affect the growth rate of the predator population immediately. In the real world, however, it is expected that the change of prey population can affect the growth rate of the predator population only after a time lag. Different types of models have been introduced [4,5,9–15] to account for the time-delay effect, and it has been found that the effect may indeed change the system behaviors substantially. However, all the above models were deterministic; namely, the coefficients in the governing equations were assumed to be known constants and the inputs to the system were assumed to be precisely known. Such assumptions are idealistic since changes in the environment are always present, and in most cases, they cannot be predicted in advance. It is of interest to note that random variabilities of system properties have been considered in some earlier works [e.g., [4,16–21]], but only for the non-delayed-type predator-prey models.

In the present paper, the stochastic modeling and analysis are extended to delayed-type predator-prey ecosystems. The stochastic averaging method of Stratonovich and Khasminskii [22–24] is applied to obtain the stationary probability distributions for the prey and predator populations. Monte Carlo-type simulations are also carried out to substantiate the accuracy of the analytical results.

II. DETERMINISTIC DELAYED-TYPE PREDATOR-PREY SYSTEM

Without considering random uncertainty, or the effect of time delay, the logistic model describing the dynamics of a predator-prey ecosystem is governed by the following differential equations [3]:

$$\dot{x}_1 = x_1(a_1 - sx_1 - bx_2),$$

$$\dot{x}_2 = x_2(-c + fx_1), \quad (1)$$

where x_1 and x_2 are the population densities of preys and predators, respectively, and a_1 , s , b , c , and f are positive constants. It is noted that the term $-sx_1^2$ in the first equation of Eqs. (1) reflects the effect of self-competition among the preys. Without this term, the prey population will grow without limit in the absence of predators, contrary to what is expected of a real system. The term fx_1x_2 in the second equation of Eqs. (1) implies that the change in the prey density x_1 will affect the change rate of the predator population instantaneously, which is unrealistic since it takes time for the predator population to adjust to the change. On the other hand, a growth in predator population will consume more preys and lead to an immediate decrease of the prey population. Thus, the delay effect occurs essentially in the predator population. To account for such a time-delay effect, it has been suggested that the term fx_1x_2 be changed to [4,5,10,11]

$$fx_2 \int_{-\infty}^t F(t-\tau)x_1(\tau)d\tau, \quad (2)$$

where $F(t)$ is called the delay function and is suitably modeled for a specific predator-prey system. Equation (2) implies that this delayed effect depends not on the population at a particular instant in the past; rather, it depends on the average of the past populations. Thus, equation set (1) is modified to

$$\begin{aligned} \dot{x}_1 &= a_1x_1 - sx_1^2 - bx_1x_2, \\ \dot{x}_2 &= -cx_2 + fx_2 \int_{-\infty}^t F(t-\tau)x_1(\tau)d\tau. \end{aligned} \quad (3)$$

It is convenient to write Eqs. (3) in an alternative form

$$\begin{aligned} \dot{x}_1 &= a_1x_1 - sx_1^2 - bx_1x_2, \\ \dot{x}_2 &= -cx_2 + fx_2 \int_0^{\infty} F(\tau)x_1(t-\tau)d\tau \end{aligned} \quad (4)$$

and normalize function $F(t)$ as follows:

$$\int_0^\infty F(\tau)d\tau = 1. \tag{5}$$

Define

$$\gamma = \int_0^\infty \tau F(\tau)d\tau, \tag{6}$$

which is a measure of the average delay time. Two reasonable choices for $F(t)$ are

$$F(t) = \frac{1}{\gamma} e^{-t/\gamma}, \tag{7}$$

$$F(t) = \frac{4}{\gamma^2} t e^{-2t/\gamma}. \tag{8}$$

Model (7) indicates that the effect of the prey population on the predator population diminishes gradually with an increasing time lag. In contrast, this effect reaches a maximum at a certain time lag in the delay model (8).

Expanding $x_1(t-\tau)$ in a Taylor series about $\tau=0$, taking the first-order approximation, applying Eq. (6), substituting into the second equation of Eqs. (4), and applying Eq. (6), we obtain

$$\dot{x}_2 = -cx_2 + fx_1x_2 - f\gamma x_2\dot{x}_1. \tag{9}$$

Combination of the first equation of Eqs. (4) and (9) results in

$$\begin{aligned} \dot{x}_1 &= a_1x_1 - sx_1^2 - bx_1x_2, \\ \dot{x}_2 &= -cx_2 + f(1 - \gamma a_1)x_1x_2 + sf\gamma x_1^2x_2 + bf\gamma x_1x_2^2. \end{aligned} \tag{10}$$

It is noted that systems (3) and (10) have the same equilibrium point

$$x_{10} = \frac{c}{f}, \quad x_{20} = \frac{a}{b} \tag{11}$$

if

$$a = a_1 - \frac{sc}{f}. \tag{12}$$

System (10) will be used henceforth to investigate the effects of the time delay. It is of interest to note that only the mean value γ of the delay function $F(t)$ is required for the ensuing analysis, not the specific form of $F(t)$.

It can be shown that the equilibrium point (x_{10}, x_{20}) given in Eqs. (11) is asymptotically stable if $\gamma=0$ and the other parameters are not zero and that it is unstable if $s=0$ and the other parameters are not zero. Therefore, while the prey self-competition term stabilizes the system, the time-delay term plays a role of destabilizing the system. Combining the two effects, the entire region of positive s and γ is divided into stable and unstable subregions if other parameter values are fixed. Figure 1 shows the two subregions for system (10) with $a_1=0.9, b=1, c=0.5$, and $f=0.5$. For a physically meaningful and stable ecological system, the pair of s and γ values must fall in the stable region.

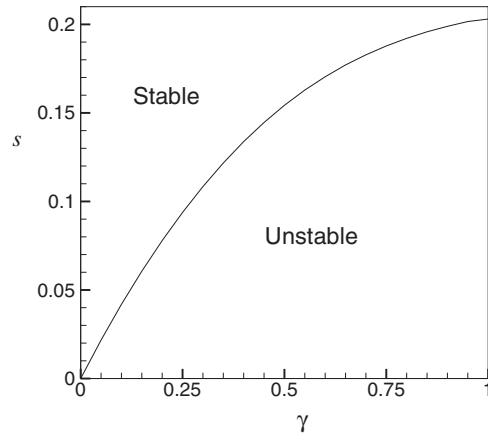


FIG. 1. Stable and unstable regions for the deterministic system (10) with $a_1=0.9, b=1, c=0.5$, and $f=0.5$.

Two trajectories of system (10) are depicted in Fig. 2, beginning from the same initial point (3.0, 1.0) and corresponding to two pairs of s and γ values in the stable region, not far from the stability boundary. The other parameter values are the same as those in Fig. 1—i.e., $a_1=0.9, b=1, c=0.5$, and $f=0.5$. It shows that the system reaches its equilibrium slowly with many cycles of decreasing amplitude.

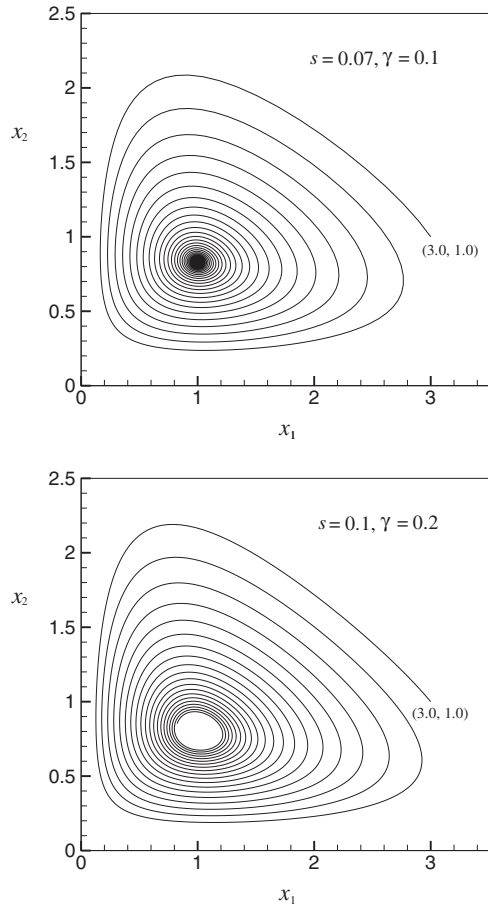


FIG. 2. Trajectories of the deterministic system (10) for two cases not far from the stability boundary.

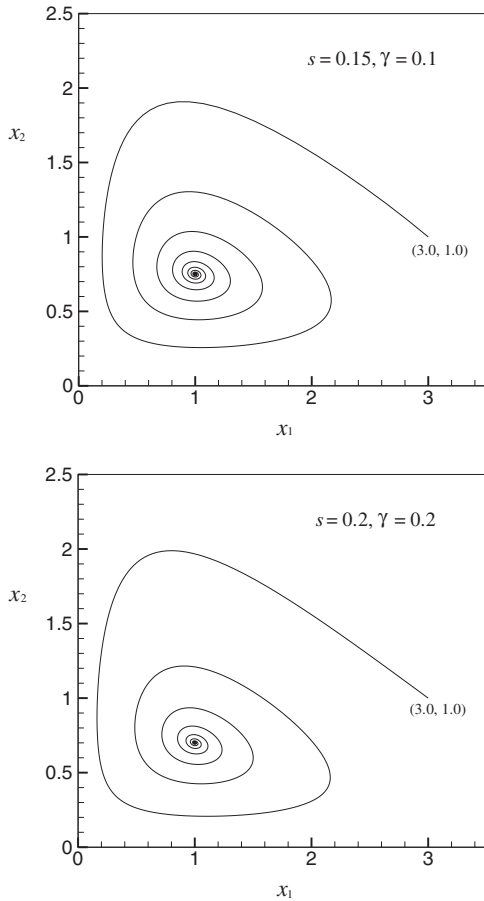


FIG. 3. Trajectories of the deterministic system (10) for two cases far from the stability boundary.

On the other hand, the system approaches its equilibrium faster and with fewer cycles for cases also in the stable region, but far from the stability boundary, as shown in Fig. 3. This is expected since systems farther from the stability boundary are more stable.

III. STOCHASTIC MODEL FOR THE DELAYED PREDATOR-PREY SYSTEM

The ecosystem model of equation set (10) shows that the ecosystem will eventually reach the equilibrium point of fixed populations of predator and prey. It fails to describe some natural phenomena of an ecosystem; in particular, the environment may change randomly, and it causes random variations in the prey growth rate and the predator death rate. Instead of the deterministic model (10), a stochastic model is proposed as follows:

$$\dot{X}_1 = X_1[a_1 - sX_1 - bX_2 + W_1(t)],$$

$$\dot{X}_2 = X_2[-c + f(1 - \gamma a_1)X_1 + sf\gamma X_1^2 + bf\gamma X_1 X_2 + W_2(t)], \quad (13)$$

where $X_1(t)$ and $X_2(t)$ are two stochastic processes, representing the prey and predator population densities, respec-

tively, and where $W_1(t)$ and $W_2(t)$ are two independent Gaussian white noises in the Stratonovich sense [22]. The tradition of using a capital letter to represent a random variable or a stochastic process will also be followed henceforth. The two independent white noises $W_1(t)$ and $W_2(t)$ are introduced to model the random variations in the prey birth rate and the predator death rate, respectively, and their autocorrelation functions are given by

$$E[W_i(t)W_j(t+\tau)] = D_i\delta(\tau), \quad i = 1, 2, \quad (14)$$

where D_i ($i=1, 2$) are known as the intensities of the white noises and $\delta(\tau)$ is the Dirac delta function.

Using Eq. (12), equation set (13) can be rewritten as

$$\dot{X}_1 = X_1 \left[a - bX_2 - \frac{s}{f}(fX_1 - c) + W_1(t) \right],$$

$$\dot{X}_2 = X_2 [(-c + fX_1)(1 + s\gamma X_1) + f\gamma X_1(bX_2 - a) + W_2(t)]. \quad (15)$$

A. Stochastic system behavior

Due to the random variabilities in the prey growth rate and predator death rate, the behavior of the stochastic system (13) is substantially different from that of its deterministic counterpart. One significant change is that an equilibrium state of the deterministic system no longer exists; it is replaced by a distribution of states described by probability or statistical properties. Figure 4 illustrates such distributions for the stochastic system (13) with $a_1=0.9$, $b=1$, $c=0.5$, $f=0.5$, $D_1=D_2=0.01$, and with two different sets of s and γ values. The case of $s=0.07$ and $\gamma=0.1$ corresponds to a state closer to the stability boundary shown in Fig. 1, while the case of $s=0.2$ and $\gamma=0.2$ corresponds to a state farther from the boundary. As expected, the first case has a larger area of distribution of the stationary states, indicating a less stable system.

The above observation shows that probabilistic measures are needed to describe the system random behaviors, which will be investigated in the following sections.

B. Stochastic averaging

Consider first the deterministic conservative system

$$\dot{x}_1 = x_1(a - bx_2),$$

$$\dot{x}_2 = x_2(-c + fx_1)(1 + s\gamma x_1). \quad (16)$$

System (16) has the same equilibrium point as that of systems (15) without random variations—namely, system (10). However, it is stable and nonasymptotic. System (16) possesses a first integral

$$r(x_1, x_2) = fx_1 - c - c \ln \frac{fx_1}{c} + bx_2 - a - a \ln \frac{bx_2}{a} - cs\gamma x_1 + \frac{1}{2}fs\gamma x_1^2 + \frac{c^2s\gamma}{2f}. \quad (17)$$

It can be shown that $r(x_1, x_2)=0$ at the equilibrium point

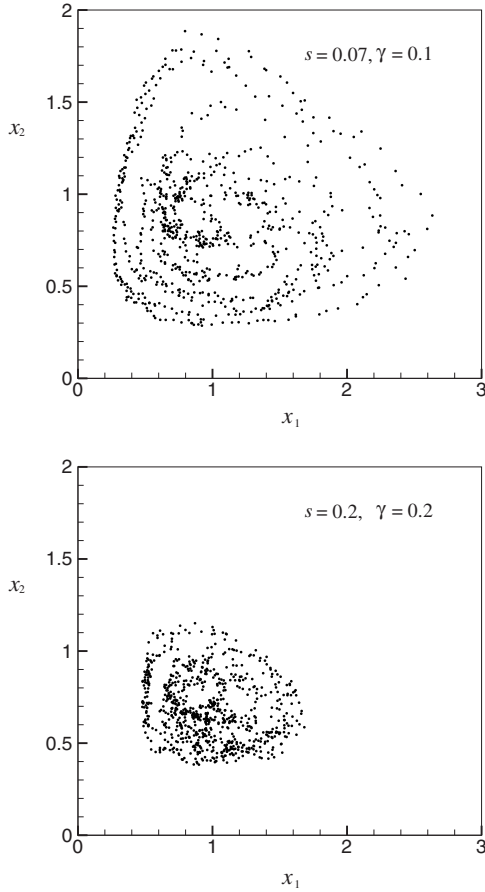


FIG. 4. Sample points of stochastic system (13) in the state of statistical stationarity for two different sets of the parameter pair (s, γ) . The set of $s=0.2$ and $\gamma=0.2$ is farther from the stability boundary; the set of $s=0.07$ and $\gamma=0.1$ is closer to the stability boundary.

$(c/f, a/b)$ and that $r(x_1, x_2) > 0$ for any other positive x_1 and x_2 . For a positive constant K , $r(x_1, x_2) = K$ represents a periodic trajectory. Its period can be determined from

$$T(K) = \oint dt = \oint \frac{dx_2}{x_2(-c + fX_1)(1 + s\gamma X_1)} = \oint \frac{dx_1}{x_1(a - bX_2)}, \quad (18)$$

where x_1 and x_2 are related by $r(x_1, x_2) = K$. System (16) will serve as a base for applying the stochastic averaging technique [22–24].

Figure 5 depicts the equilibrium point O and three periodic trajectories for system (16) with parameters $a=0.9$, $b=1$, $c=0.5$, $f=0.5$, $s=0.1$, and $\gamma=0.2$. The equilibrium point O corresponds to $K=0$, and the three different periodic trajectories correspond to three different K values, respectively.

Returning to the stochastic system (15), its corresponding Ito stochastic differential equations (e.g., [25]) are given by

$$dX_1 = X_1 \left[a - bX_2 + \frac{s}{f}(fX_1 - c) + \frac{1}{2}D_1 \right] dt + \sqrt{D_1}X_1 dB_1(t)$$

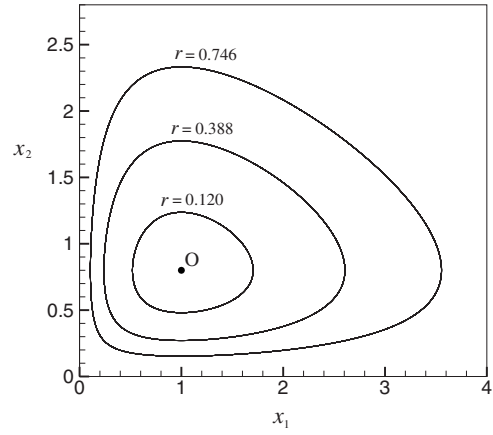


FIG. 5. Equilibrium and periodic trajectories of the deterministic system (16).

$$dX_2 = X_2 \left[(-c + fX_1)(1 + s\gamma X_1) + f\gamma X_1(bX_2 - a) + \frac{1}{2}D_2 \right] dt + \sqrt{D_2}X_2 dB_2(t). \quad (19)$$

The stochastic counterpart of Eq. (17) is

$$R(X_1, X_2) = fX_1 - c - c \ln \frac{fX_1}{c} + bX_2 - a - a \ln \frac{bX_2}{a} - cs\gamma X_1 + \frac{1}{2}fs\gamma X_1^2 + \frac{c^2s\gamma}{2f}, \quad (20)$$

which is a function of the stochastic processes X_1 and X_2 ; hence, it is also a stochastic process. The Ito equation for $R(X_1, X_2)$ can be obtained by applying the Ito differential rule [26], resulting in

$$dR = \left[-\frac{s}{f}(fX_1 - c)^2(1 + s\gamma X_1) + f\gamma X_1(bX_2 - a)^2 + \frac{1}{2}D_1X_1(f - sc\gamma + 2fs\gamma X_1) + \frac{1}{2}bD_2X_2 \right] \times dt + \sqrt{D_1}(fX_1 - c)(1 + s\gamma X_1)dB_1(t) + \sqrt{D_2}(bX_2 - a)dB_2(t). \quad (21)$$

Assume that the coefficients s of the self-competition term and parameter γ of the delay time are small and that the intensities D_1 and D_2 of the white noises $W_1(t)$ and $W_2(t)$ are also small. These assumptions are generally valid for real ecosystems. Then the right-hand-side of Eq. (21) is small, indicating that $R(t)$ is a slowly varying random process. In this case, the stochastic averaging method [22–24] is applicable. The averaged version of Eq. (21) can be cast in the standard form of an Ito equation,

$$dR = m(R)dt + \sigma(R)dB(t), \quad (22)$$

in which $m(R)$ and $\sigma(R)$ are called the drift coefficient and the diffusion coefficient, respectively, and they are obtained as follows:

$$m(R) = -\frac{s}{f}\langle(fX_1 - c)^2(1 + s\gamma X_1)\rangle_t + f\gamma\langle X_1(bX_2 - a)^2\rangle_t + \frac{1}{2}D_1\langle X_1(f - sc\gamma + 2fs\gamma X_1)\rangle_t + \frac{1}{2}aD_2, \quad (23)$$

$$\sigma^2(R) = D_1\langle(fX_1 - c)^2(1 + s\gamma X_1)^2\rangle_t + D_2\langle(bX_2 - a)^2\rangle_t, \quad (24)$$

where $\langle[\cdot]\rangle_t$ denotes the time average in one quasiperiod, defined as

$$\begin{aligned} \langle[\cdot]\rangle_t &= \frac{1}{T} \oint [\cdot] dt = \frac{1}{T} \oint \frac{[\cdot] dX_2}{X_2(fX_1 - c)(1 + s\gamma X_1)} \\ &= \frac{1}{T} \oint \frac{[\cdot] dX_1}{X_1(a - bX_2)}. \end{aligned} \quad (25)$$

For a given R , X_1 and X_2 are related according to Eq. (20), and the quasiperiod T is given in Eq. (18) with x_1 and x_2 replaced by their random counterparts X_1 and X_2 , respectively. In deriving Eq. (23), use has been made of $\langle X_2 \rangle_t = a/b$ according to the first equation of Eqs. (16). The time-average terms in Eqs. (23) and (24) can be calculated numerically for given parameters a , b , c , f , s , and γ .

C. Stationary probability densities

Equation (22) implies that $R(t)$ is a one-dimensional Markov process. The stationary probability density of $R(t)$, denoted by $p(r)$, is governed by the following Fokker-Plank equation (e.g., [24])

$$\frac{d}{dr}[m(r)p(r)] - \frac{1}{2} \frac{d^2}{dr^2}[\sigma^2(r)p(r)] = 0, \quad (26)$$

where r is the state variable of the stochastic process $R(t)$. Equation (26) can be solved to obtain

$$p(r) = \frac{C}{\sigma^2(r)} \exp \int \frac{2m(r)}{\sigma^2(r)} dr, \quad (27)$$

where C is the normalization constant.

The joint probability density of $R(t)$ and $X_1(t)$ can be written as

$$p(r, x_1) = p(r)p(x_1|r), \quad (28)$$

where $p(x_1|r)$ is the conditional probability density of $X_1(t)$ given $R(t)=r$. It can be obtained as follows:

$$p(x_1|r)dx_1 = \frac{dt}{T(r)} = \frac{dx_1}{|\dot{x}_1|T(r)} = \frac{dx_1}{|x_1(a - bx_2)|T(r)}, \quad (29)$$

where $T(r)$ is given by Eq. (18). Substituting Eq. (29) into Eq. (28),

$$p(r, x_1) = \frac{p(r)}{|x_1(a - bx_2)|T(r)}, \quad (30)$$

in which x_2 is treated as a function of x_1 and r . Thus, the joint probability density $p(x_1, x_2)$ follows as

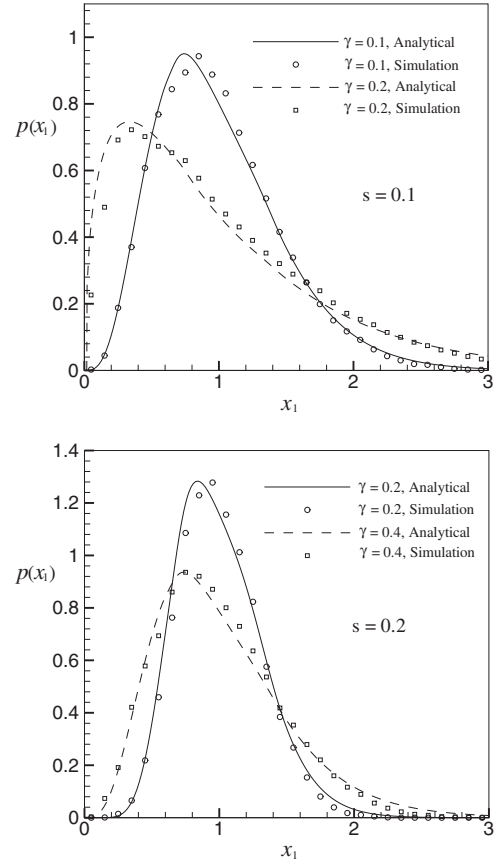


FIG. 6. Probability densities of the prey population for different values of the parameters s and γ .

$$p(x_1, x_2) = p(r, x_1) \left| \frac{\partial(r, x_1)}{\partial(x_1, x_2)} \right| = \frac{p(r)}{x_1 x_2 T(r)}, \quad (31)$$

where $\frac{\partial(r, x_1)}{\partial(x_1, x_2)}$ is the Jacobian of transformation and r is treated as a function of x_1 and x_2 according to Eq. (17). The marginal probability densities of X_1 and X_2 can then be obtained as

$$p(x_1) = \int_0^\infty p(x_1, x_2) dx_2, \quad p(x_2) = \int_0^\infty p(x_1, x_2) dx_1. \quad (32)$$

If no delay is taken into consideration—i.e., $\gamma=0$ —then Eq. (27) results in

$$p(r) = CT(r)\exp(-\beta r), \quad (33)$$

where β is a constant given by

$$\beta = \frac{2sc}{f(cD_1 + aD_2)}. \quad (34)$$

Result (33) was obtained previously in [21] for the system without considering the time delay.

Numerical calculations were carried out to obtain the results for the delayed stochastic system (13) with $D_1=D_2=0.01$ and with other parameters the same as those used when obtaining Fig. 1—i.e., $a_1=0.9$, $b=1$, $c=0.5$, and $f=0.5$. Figure 6 shows the stationary probability densities of

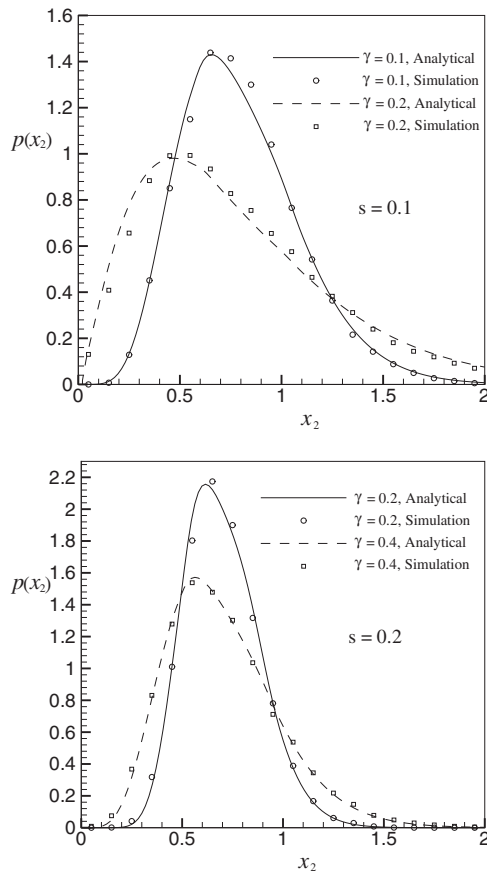


FIG. 7. Probability densities of the predator population for different values of the parameters s and γ .

the prey population for several different combinations of s and γ values within the stable region shown in Fig. 1. For a given s , a larger γ value results in higher probabilities in both lower and higher prey populations, indicating a less stable system. On the other hand, a system with a larger s is more stable. Also depicted in the figure are results obtained using the Monte Carlo simulation technique. The theoretical and simulation results agree quite well. Figure 7 shows the stationary probability densities of the predator population. The same effects of the delay parameter γ and the prey self-competition parameter s can be observed.

Shown in Fig. 8 are the stationary probability densities of the prey and predator populations for two different sets of s and γ values, corresponding to two different points in the stable region. The point corresponding to $s=0.2$ and $\gamma=0.2$ is farther from the stability boundary, while the one corresponding to $s=0.07$ and $\gamma=0.1$ is closer to the stability boundary. In the latter case, the probability densities have lower peaks, which are compensated for with higher values in the lower and higher population ranges. This is expected since the system state is closer to the stability boundary and is less stable.

IV. CONCLUSION

In the present investigation into the interaction between the predators and preys in an ecosystem, the effects of time

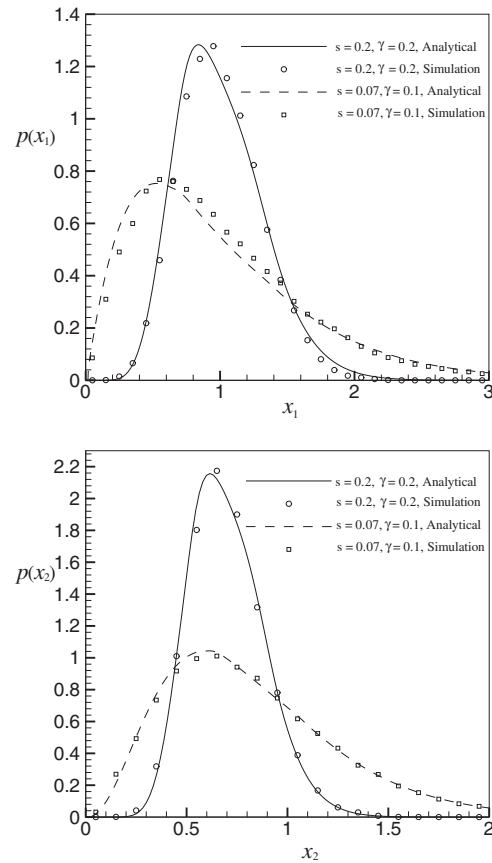


FIG. 8. Probability densities of the predator and prey populations for two different sets of the parameter pair (s, γ) . The set of $s=0.2$ and $\gamma=0.2$ is farther from the stability boundary; the set of $s=0.07$ and $\gamma=0.1$ is closer to the stability boundary.

delay in the interaction and the stochasticity in the environment are taken into consideration. The time delay is described approximately by one parameter, and the stochastic environment is characterized by two Gaussian white noises in the prey birth rate and the predator death rate, respectively. The mathematical procedure of stochastic averaging is applied in the analysis, and the probability distributions of the predator and prey populations in the state of statistical stationarity are obtained theoretically. It is shown that the system behaviors are substantially different when the stochastic variabilities are introduced. A single stable equilibrium in the deterministic system disappears. Instead, a distribution of system states takes place, which agrees better with a real ecosystem.

It is also found that the system stability depends on two parameters: the prey self-competition parameter s and the time-delay parameter γ . The prey self-competition stabilizes the system; i.e., stronger prey self-competition gives rise to a more stable system. In contrast, time delay destabilizes the system. A longer time delay results in a less stable system.

In the present investigation, only certain system parameters are treated as being randomly varying with time.

Similar approaches may apply to other system parameters or for other ecosystems. The random variations are modeled as white noises in the present investigation. They can also be modeled as other type of stochastic processes, Gaussian or

non-Gaussian, broadband or narrow-band, according to the observed statistical properties of the data. Theoretical investigations are important to find out what types of data are most critically needed and what are not.

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- [1] A. J. Lotka, *Elements of Physical Biology* (William and Wilkins, Baltimore, NJ, 1925).
- [2] V. Volterra, *Mem. Acad. Lincei* **2**, 31 (1926).
- [3] V. Volterra, *Lecons sur la theorie mathematique de la lutte pour la vie* (Gauthiers-Vilars, Paris, 1931).
- [4] R. M. May, *Stability and Complexity in Model Ecosystems* (Oxford University Press, New York, 1973).
- [5] R. M. May, *Theoretical Ecology, Principles and Applications*, 2nd ed. (Sinauer Associates, Sunderland, MA, 1981).
- [6] J. D. Murray, *Mathematical Biology* (Springer, New York, 1993).
- [7] M. L. Rosenzweig and R. H. MacArthur, *Am. Nat.* **97**, 205 (1963).
- [8] A. D. Bazykin, *Nonlinear Dynamics of Interacting Populations* (World Scientific, Singapore, 1998).
- [9] G. E. Hutchinson, *Ann. N.Y. Acad. Sci.* **50**, 221 (1948).
- [10] N. MacDonald, *Math. Biosci.* **28**, 321 (1976).
- [11] N. MacDonald, *Math. Biosci.* **33**, 227 (1977).
- [12] R. Nisbet and W. Gurney, *Modeling Fluctuating Populations* (Wiley, New York, 1982).
- [13] E. Korpimaki, *Oikos* **62**, 195 (1993).
- [14] B. Hornfeldt, *Ecology* **75**, 791 (1994).
- [15] P. Turchin, *Complex Population Dynamics* (Princeton University Press, Princeton, 2003).
- [16] L. Arnold, W. Horthemke, and J. W. Stucki, *Biom. J.* **21**, 451 (1979).
- [17] A. F. Rozenfeld *et al.*, *Phys. Lett. A* **280**, 45 (2001).
- [18] R. Z. Khasminskii and F. C. Klebaner, *Ann. Appl. Probab.* **11**, 952–963 (2001).
- [19] M. F. Dimentberg, *Phys. Rev. E* **65**, 036204 (2002).
- [20] M. F. Dimentberg, in *Proceedings of IUTAM Symposium on Nonlinear Stochastic Dynamics*, edited by N. Sri Namachivaya and Y. K. Lin (Kluwer Academic, Dordrecht, 2003), pp. 307–317.
- [21] G. Q. Cai and Y. K. Lin, *Phys. Rev. E* **70**, 041910 (2004).
- [22] R. L. Stratonovich, *Topics in the Theory of Random Noise* (Gordon and Breach, New York, 1963), Vol. 1.
- [23] R. Z. Khasminskii, *Theor. Probab. Appl.* **12**, 144 (1966).
- [24] Y. K. Lin and G. Q. Cai, *Probabilistic Structure Dynamics* (MacGraw-Hill, New York, 2004).
- [25] K. Itô, *Mem. Am. Math. Soc.* **4**, 289 (1951).
- [26] K. Itô, *Nagoya Math. J.* **3**, 55 (1951).