PHYSICAL REVIEW E **70**, 041910 (2004)

Stochastic analysis of the Lotka-Volterra model for ecosystems

G. Q. Cai and Y. K. Lin
Center for Applied Stochastics Research, Florida Atlantic University, Boca Raton, Florida 33431, USA

(Received 4 May 2004; revised manuscript received 8 July 2004; published 29 October 2004)

A stochastic Lotka-Volterra-type model for the interaction between the preys and the predators in a random environment is investigated. A self-competition mechanism within the prey population itself is also included. The effect of a random environment is modeled as random variations in the birth rate of the preys and the death rate of the predators. The stochastic averaging procedure of Stratonovich and Khasminskii is applied to obtain the probability distributions of the system state variables at the state of statistical stationarity. Asymptotic behaviors of the system variables are discussed, and the mean transition time from an initial state to a critical state is obtained. Effects on the ecosystem behaviors of the self-competition term, of the random variation in the prey birth rate, and of the random variation in the predator death rate are investigated.

DOI: 10.1103/PhysRevE.70.041910 PACS number(s): 87.23.Cc, 05.10.Gg, 02.50.Fz

I. INTRODUCTION

A well-known mathematical model describing the behaviors of two interacting species, referred to hereafter as preys (or host) and predators (or parasite), is the Lotka-Volterra model [1–5], governed by the following differential equations:

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

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

where x_1 and x_2 are the population densities of preys and predators, respectively, and a, b, c, and f are positive constants. Equations (1) indicate that the prey population would grow exponentially without the presence of the predators, and the population of the predators would decrease exponentially without the preys. The interactive terms x_1x_2 provide a balance between the two populations.

System (1) has an unstable equilibrium state (0, 0), and a stable nonasymptotic equilibrium state $(c/f, a/b)$. It possesses a first integral

$$r(x_1,x_2) = fx_1 - c - c\ln\frac{fx_1}{c} + bx_2 - a - a\ln\frac{bx_2}{a} = k, \tag{2}$$

where k is a non-negative constant. It can be shown that $r(x_1,x_2)=0$ at the point $(c/f, a/b)$, that $r(x_1,x_2)\geqslant 0$ for any positive x_1 and x_2, and that $r(x_1,x_2)=k$ describes a periodic trajectory, namely a limit cycle of system (1). Depicted in Fig. 1 are the equilibrium point O, corresponding to $k=0$, and three limit cycles, corresponding to three positive k values, determined with system parameters $a=0.9, b=1, c=0.5$, and $f=0.5$ (all parameter values are nondimensionalized in the paper). It shows that the prey and predator populations are changing periodically with time, along a path in the phase plane (the x_1-x_2 plane), which depends only on the initial states of x_1 and x_2. It also shows that a high level of prey density and/or predator density can lead to very low levels for both, even in an invariant environment.

System (1) fails to describe some basic phenomena of a realistic prey-predator ecosystem in at least two ways. First, in the absence of the predators, the prey population will grow without limit, contrary to what is expected of nature. Secondly, changes in the environment are always present which are not accounted for in the governing equations. To improve the classical Lokta-Volterra model, May [3] added a self-competition term to the prey equation and a Gaussian white-noise variation in the prey birth rate. He then used a perturbation scheme and a path-integration approach to obtain approximate solutions for the associated Fokker-Planck equation (e.g., [6]), governing the probability densities of the prey and predator populations at both the transient and stationary states. Arnold *et al.* [7] introduced a random variation in the prey birth rate, and modeled the variation as a Gaussian white noise in the Itô sense [8], but without a self-competition term in the prey equation. Khasminskii and Klebaner [9] modified the model of Arnold *et al.* by adding another Gaussian white noise to the predator death rate, and interpreted both Gaussian white noises in the Stratonovich sense [10], namely, in the sense of a limit of a physical noise. In both [7,9], asymptotic analyses were conducted to show that no stationary state exists for the system. Dimentberg [11,12] used the same model as May [3], and found an exact

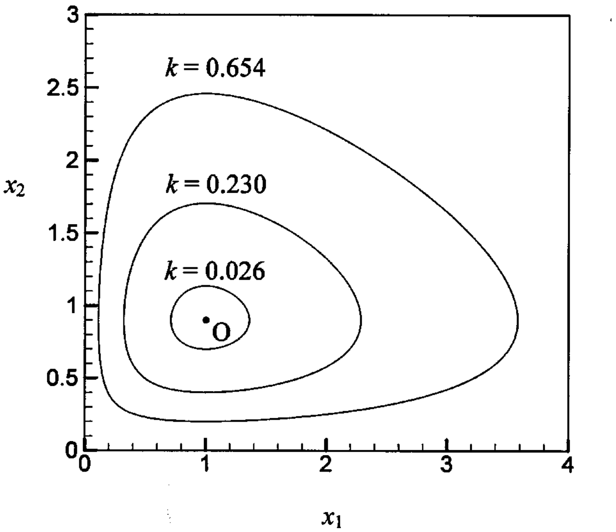

FIG. 1. Equilibrium point and limit cycles of system (1).

solution for the stationary probability density. Rozenfeld *et al.* [13] considered the case of both periodic and random variations in the prey birth rate, and carried out a Monte Carlo type simulation to investigate the possibility of stochastic resonance of the system.

In the present paper, an improved stochastic model is considered which includes a self-competition term in the prey equation and random variations in both the prey birth rate and the predator death rate. The stochastic averaging method of Stratonovich [10] and Khasminskii [14] is applied to obtain the joint stationary probability distributions for the prey and predator populations, their asymptotic behaviors, and the mean transition time from a normal population state to a more dangerous state close to extinction. The Monte Carlo type simulations are carried out to substantiate the accuracy of the analysis.

II. STOCHASTIC LOTKA-VOLTERRA MODEL

The stochastic Lotka-Volterra model to be investigated in the following is governed by

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

$$\dot{X}_2 = X_2(-c + fX_1) + X_2 W_2(t), \tag{3}$$

where $X_1(t)$ and $X_2(t)$ are two stochastic processes, representing the prey and the predator population densities, respectively, and where $W_1(t)$ and $W_2(t)$ are two independent Gaussian white noises in the Stratonovich sense. The tradition of using a capital letter to represent a random variable or a stochastic process will also be followed henceforth. The autocorrelations of the white noises are given by

$$E[W_i(t)W_i(t+\tau)] = D_i \delta(\tau), \quad i = 1,2, \tag{4}$$

where $E[\ ]$ denotes an ensemble average, D_i is the intensity of $W_i(t)$, and $\delta(\ )$ is the Dirac delta function. Comparison between Eq. (3) and Eq. (1) shows that a term $-sX_1^2$ is added to the prey equation to model the self-competition nature of the preys, and $W_1(t)$ and $W_2(t)$ are introduced to model the random variations in the prey birth rate and the predator death rate, respectively.

A. The deterministic counterpart

To provide a background for the stochastic analysis, we examine first the deterministic counterpart of Eq. (3), namely,

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

$$\dot{x}_2 = x_2(-c + fx_1). \tag{5}$$

System (5) has an asymptotic stable equilibrium at $x_1 = c/f$ and $x_2 = (a_1 - sc/f)/b$. Figure 2 depicts two trajectories of system (5), corresponding to two different values of $s=0.1$ and 0.02, respectively, and with the same $a_1=1, b=1, c=0.5$, and $f=0.5$. The motion of the system begins from point (3.5, 0.5). The term $-sx_1^2$ models the effect of interspecies competition. With the larger $s=0.1$, the system reaches its equilibrium faster, while with the smaller $s=0.02$, the system moves around the stable equilibrium with a decreasing amplitude. In the absence of the predators, the prey density reaches its equilibrium state of a_1/s, which is inversely proportional to s, as expected. When the predators are present, however, the interaction between the prey and the predator populations is the more important factor, whereas the value of s affects only the density of the predators at the equilibrium state. Note that systems (1) and (5) have the same equilibrium state if

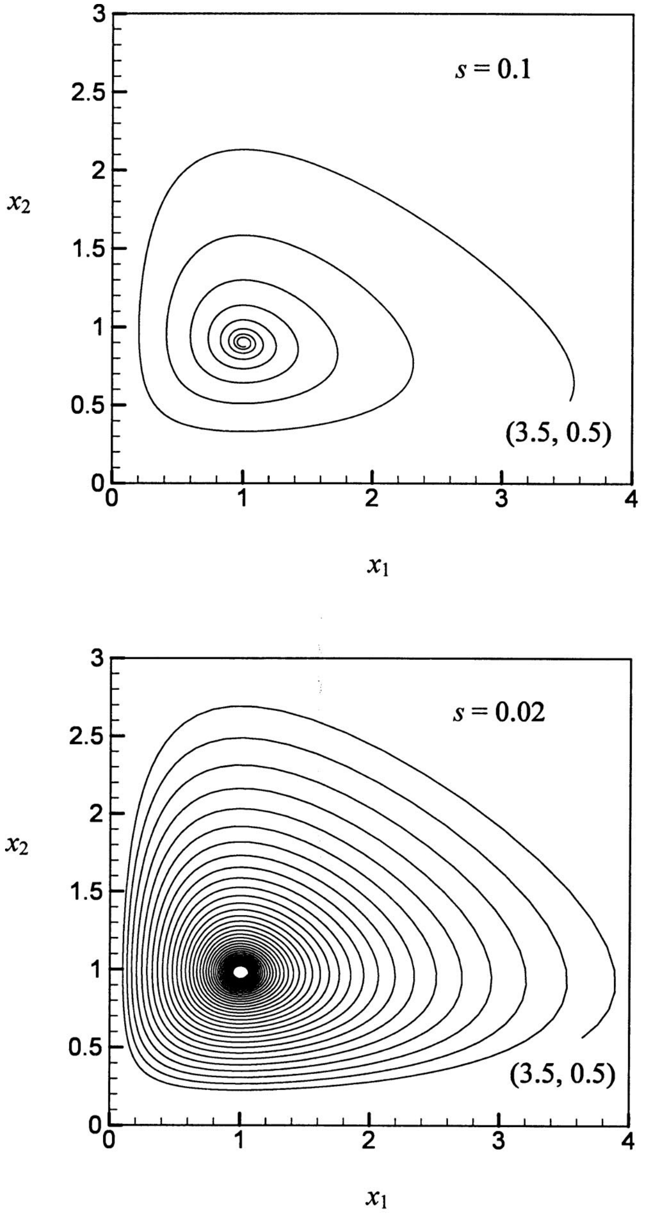

FIG. 2. Trajectories of system (5) for two different values of s.

$$a = a_1 - \frac{sc}{f}. \tag{6}$$

By comparing Figs. 1 and 2, it can be seen that, with a small s, namely a slowly varying $r(x_1, x_2)$, system (5) is close to system (1) as expected.

The ecosystem described by equation set (1) is periodic, and for a trajectory $r(x_1,x_2)$, the period is determined from

$$T(r) = \oint dt = \oint \frac{dx_2}{x_2(fx_1 - c)} = \oint \frac{dx_1}{x_1(a - bx_2)}, \qquad (7)$$

where x_1 and x_2 are related by $r(x_1,x_2)=k$. By including a self-competition term $-sx_1^2$ for the preys as in equation set (5), the period changes slowly. It may be regarded as the quasiperiod at a given instant of time.

B. Stochastic averaging

Return now to the stochastic model (3), and rewrite Eq. (3) in the form of the Itô stochastic differential equations [8],

$$\mathrm{d}X_1 = X_1\left(a - bX_2 - \frac{s}{f}(-c + fX_1) + \frac{1}{2}D_1\right)\mathrm{d}t + \sqrt{D_1}X_1\mathrm{d}B_1(t),$$

$$\mathrm{d}X_2 = X_2\left(-c + fX_1 + \frac{1}{2}D_2\right)\mathrm{d}t + \sqrt{D_2}X_2\mathrm{d}B_2(t), \qquad (8)$$

where $B_1(t)$ and $B_2(t)$ are two independent unit Wiener processes (e.g., [6]). Comparing Eq. (8) with Eq. (3), the additional terms $\frac{1}{2}D_1X_1\mathrm{d}t$ and $\frac{1}{2}D_2X_2\mathrm{d}t$ in the equation set (8) are known as the Wong-Zakai correction terms (e.g., [6]), which must be incorporated when $W_1(t)$ and $W_2(t)$ in Eq. (3) are interpreted as white noises in the physical Stratonovich sense [10].

Now, consider a stochastic process

$$R(X_1,X_2) = fX_1 - c - c\ln\frac{fX_1}{c} + bX_2 - a - a\ln\frac{bX_2}{a} \qquad (9)$$

which is the random counterpart of $r(x_1,x_2)$ in Eq. (2). Using the Itô differential rule [15], we have from Eqs. (8) and (9)

$$\mathrm{d}R = \left[-\frac{s}{f}(fX_1 - c)^2 + \frac{1}{2}fD_1X_1 + \frac{1}{2}bD_2X_2\right]\mathrm{d}t + \sqrt{D_1}(fX_1 - c)\mathrm{d}B_1(t) + \sqrt{D_2}(bX_2 - a)\mathrm{d}B_2(t). \qquad (10)$$

Assume that the coefficient s of the self-competition term is small, indicating that the term has a small influence when the prey density is small. Assume also that D_1 and D_2 are small, namely, the random disturbances are small. Then $R(t)$ is a slowly varying process. In this case, the stochastic averaging method [10,14] can be applied to obtain an averaged Itô stochastic differential equation for R,

$$\mathrm{d}R = m(R)\mathrm{d}t + \sigma(R)\mathrm{d}B(t), \qquad (11)$$

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

$$m(R) = \frac{1}{2}fD_1\langle X_1\rangle_t + \frac{1}{2}bD_2\langle X_2\rangle_t - \frac{s}{f}\langle (fX_1 - c)^2\rangle_t, \qquad (12)$$

$$\sigma^2(R) = D_1\langle (fX_1 - c)^2\rangle_t + D_2\langle (bX_2 - a_1)^2\rangle_t, \qquad (13)$$

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

$$\langle [\ ]\rangle_t = \frac{1}{T}\oint [\ ]\mathrm{d}t = \frac{1}{T}\oint \frac{[\ ]\mathrm{d}x_2}{x_2(fx_1 - c)} = \frac{1}{T}\oint \frac{[\ ]\mathrm{d}x_1}{x_1(a - bx_2)}. \qquad (14)$$

When performing stochastic averaging, the deterministic variables x_1, x_2, and r are, of course, replaced by their stochastic counterparts X_1, X_2, and R, respectively. The quasiperiod T is given in Eq. (7), again with x_1, x_2, and r replaced by their random counterparts. The result obtained from each time average is a function of R. The following time averages can be obtained directly from Eqs. (1) and (2):

$$\langle X_1\rangle_t = \frac{c}{f}, \quad \langle X_2\rangle_t = \frac{a}{b}, \quad \langle X_1X_2\rangle_t = \frac{ac}{bf}, \qquad (15)$$

$$a\langle (fX_1 - c)^2\rangle_t = c\langle (bX_2 - a)^2\rangle_t. \qquad (16)$$

Defining

$$g(R) = a\oint \frac{(fX_1 - c)\mathrm{d}X_2}{X_2}, \qquad (17)$$

we have

$$\langle (fX_1 - c)^2\rangle_t = \frac{g(R)}{aT(R)}, \quad \langle (bX_2 - a)^2\rangle_t = \frac{g(R)}{cT(R)}. \qquad (18)$$

It follows from Eqs. (12) and (13) that

$$m(R) = \frac{1}{2}cD_1 + \frac{1}{2}aD_2 - \frac{s}{af}\frac{g(R)}{T(R)}, \qquad (19)$$

$$\sigma^2(R) = \frac{1}{ac}(cD_1 + aD_2)\frac{g(R)}{T(R)} \qquad (20)$$

using Eqs. (15) and (18). Equations (11), (19), and (20) constitute the governing law for the one-dimensional Markov process $R(t)$ (e.g., [6]).

The stochastic process $R(t)$, as defined in Eq. (9), is a function of two stochastic processes, namely the prey density X_1 and the predator density X_2, and it can be considered as a representation of the system state. Under the conditions of small random variations in the prey birth rate and the predator death rate, and weak self-competition within the prey population, $R(t)$ is a slowly varying stochastic process.

C. Stationary probability distributions

The probability density of R at the stationary state, denoted by $p(r)$, is governed by the following Fokker-Planck equation (e.g., [6]):

$$\frac{\mathrm{d}}{\mathrm{d}r}[m(r)p(r)] - \frac{1}{2}\frac{\mathrm{d}^2}{\mathrm{d}r^2}[\sigma^2(r)p(r)] = 0, \qquad (21)$$

where r is the state variable of the stochastic process $R(t)$. With appropriate boundary conditions at $r=0$ and ∞, to be explained in Sec. II D, Eq. (21) can be solved to obtain

$$p(r) = \frac{C_1}{\sigma^2(r)}\exp\int\frac{2m(r)}{\sigma^2(r)}dr$$
$$= C\frac{T(r)}{g(r)}\exp\int\frac{ac(cD_1 + aD_2)T(r) - \dfrac{2sc}{f}g(r)}{(cD_1 + aD_2)g(r)}dr, \tag{22}$$

where C and C_1 are two normalization constants. By noticing that

$$\frac{\mathrm{d}g(r)}{\mathrm{d}r} = a\oint\frac{f}{x_2}\frac{\partial x_1}{\partial r}dx_2 = a\oint\frac{fx_1\mathrm{d}x_2}{x_2(fx_1 - c)} = afT(r)\langle x_1\rangle_t$$
$$= acT(r), \tag{23}$$

Eq. (22) is simplified to

$$p(r) = CT(r)\exp(-\beta r), \tag{24}$$

where β is a constant given by

$$\beta = \frac{2sc}{f(cD_1 + aD_2)}. \tag{25}$$

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

$$p(r,x_1) = p(r)p(x_1|r), \tag{26}$$

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

$$p(x_1|r)\mathrm{d}x_1 = \frac{\mathrm{d}t}{T(r)} = \frac{\mathrm{d}x_1}{|\dot{x}_1|T(r)} = \frac{\mathrm{d}x_1}{|x_1(a - bx_2)|T(r)}. \tag{27}$$

Substituting Eq. (27) into Eq. (26),

$$p(r,x_1) = \frac{p(r)}{|x_1(a - bx_2)|T(r)}, \tag{28}$$

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

$$p(x_1,x_2) = p(r,x_1)\left|\frac{\partial(r,x_1)}{\partial(x_1,x_2)}\right|$$
$$= \frac{p(r)}{x_1x_2T(r)}$$
$$= \frac{C}{x_1x_2}\exp[-\beta r(x_1,x_2)], \tag{29}$$

where $\partial(r,x_1)/\partial(x_1,x_2)$ is the Jacobian of transformation. Upon substituting Eq. (2) into Eq. (29), we obtain

$$p(x_1,x_2) = p(x_1)p(x_2), \tag{30}$$

where

$$p(x_1) = \frac{(\beta f)^{\beta c}}{\Gamma(\beta c)}x_1^{\beta c-1}\exp(-\beta fx_1), \tag{31}$$

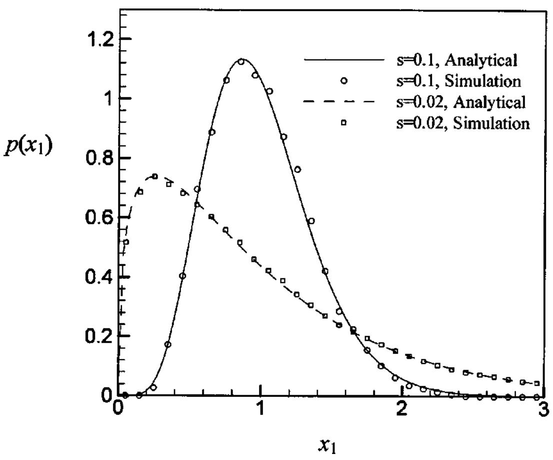

FIG. 3. Probability densities of the prey population obtained for $D_1=D_2=0.01$ and two different s values.

$$p(x_2) = \frac{(\beta b)^{\beta a}}{\Gamma(\beta a)}x_2^{\beta a-1}\exp(-\beta bx_2), \tag{32}$$

and $\Gamma(\ )$ is the gamma function. Equation (30) implies that $X_1(t)$ and $X_2(t)$ are independent when they reach the state of statistical stationarity, which is an unexpected result for system (3) with nonlinear coupling between X_1 and X_2. Equations (31) and (32) show that nontrivial $p(x_1)$ and $p(x_2)$ exist only if $\beta>0$ and $a>0$. These conditions lead to

$$0 < s < \frac{fa_1}{c}. \tag{33}$$

The system will diverge without the self-competition term, namely if $s=0$, since no restriction will be imposed on the growth of the prey population. On the other hand, if $s>fa_1/c$, the growth of the prey population will be over-restricted, leading to extinction of the predators.

It is of interest to note that if $D_2=0$, i.e., in the absence of $W_2(t)$, Eqs. (23) and (29)–(32) reduce to the exact solutions obtained by Dimentberg [11,12].

Shown in Fig. 3 is the probability density $p(x_1)$ of the prey population X_1 for the stochastic system (3), calculated from Eq. (31), with $a_1=1, b=1, c=0.5, f=0.5, D_1=D_2=0.01$, and for two different s values of 0.1 and 0.02. Also depicted in Fig. 3 are results obtained from the Monte Carlo type simulation. The theoretical and simulation results agree very well in both cases. With a large self-competition coefficient $s=0.1$, the prey density is nearly centered around $x_1=c/f=1$, which is the equilibrium point for the deterministic counterpart without random variations in the prey birth rate and the predator death rate. In this case, the system is more stable in terms of the relative prey and predator populations. With a small $s=0.02$, the peak of the prey probability density is shifted to a value smaller than the equilibrium point $x_1=1$, and the probability for a high prey population becomes higher, for which the system is less stable.

Figures 4 and 5 show the effects of changing the intensities D_1 and D_2, respectively, of random variations $W_1(t)$ and $W_2(t)$ on the probability density of X_1. The system parameters selected for computation are $a_1=1, s=0.1, b=1, c=0.5,$

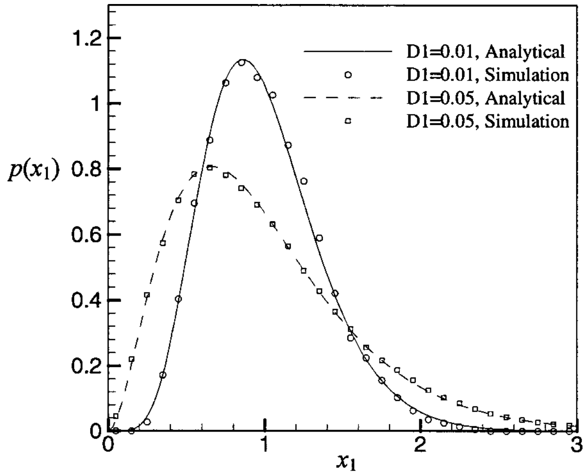

FIG. 4. Probability densities of the prey population obtained for $s=0.1, D_2=0.01$, and two different D_1 values.

and $f=0.5$. With an increasing D_1 or D_2, similar effects are observed to those of a decreasing s, namely the peak of the probability density is shifted to the left; however, the peak height is lower and the overall probability for a large prey population increases, indicating that the system is less stable.

D. Asymptotic behaviors

Governed by the Itô stochastic differential equation (11), $R(t)$ is a one-dimensional Markov diffusion process. Its behavior at the two boundaries at $R=0$ and $R=\infty$ can be investigated as follows, based on a theory shown in [6].

1. At the left boundary R=0

As can be deduced from Eq. (1), R approaches zero, when X_1 and X_2 approach c/f and a/b, respectively. Thus, we may write

$$\ln\frac{fX_1}{c} = \ln\left(1+\frac{fX_1-c}{c}\right) \approx \frac{fX_1-c}{c} - \frac{1}{2}\left(\frac{fX_1-c}{c}\right)^2, \tag{34}$$

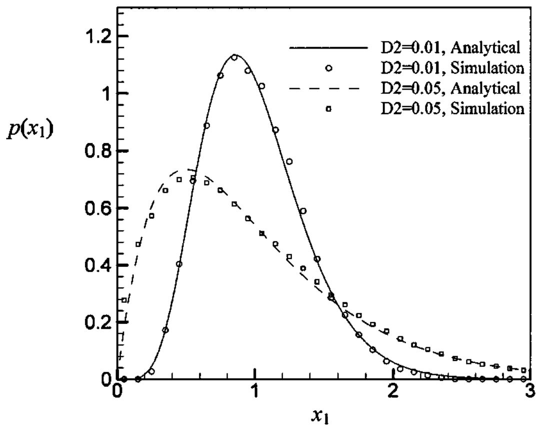

FIG. 5. Probability densities of the prey population obtained for $s=0.1, D_1=0.01$, and two different D_2 values.

$$\ln\frac{bX_2}{a} = \ln\left(1+\frac{bX_2-a}{a}\right) \approx \frac{bX_2-a}{a} - \frac{1}{2}\left(\frac{bX_2-a}{a}\right)^2. \tag{35}$$

Substituting Eqs. (34) and (35) into the stochastic counterpart of Eq. (2),

$$a(fX_1-c)^2 + c(bX_2-a)^2 \approx 2acR. \tag{36}$$

Using Eqs. (16) and (36), we have

$$\langle (fX_1-c)^2\rangle_t \approx cR, \quad \langle (bx_2-a)^2\rangle_t \approx aR. \tag{37}$$

It follows from Eqs. (12) and (13) that

$$m(R) \to \tfrac{1}{2}(cD_1+aD_2),$$

$$\sigma^2(R) \to (cD_1+aD_2)R \quad \text{as } R\to 0. \tag{38}$$

Since $\sigma(0)=0$, the left boundary at $R=0$ is singular of the first kind [6]. The diffusion exponent, the drift exponent, and the character value for the left boundary are, respectively,

$$\alpha_l=1, \quad \beta_l=0, \quad c_l=1. \tag{39}$$

Therefore, the left boundary is an entrance, as long as $a>0$. This indicates that, with random variations in the birth rate of the preys and/or the death rate of the predators, neither the prey population nor the predator population will be extinct.

2. At the right boundary R→∞

It was shown in [9] that

$$\langle (fX_1-c)^2\rangle_t \approx \tfrac{1}{2}cR, \quad \langle (bX_2-a)^2\rangle_t \approx \tfrac{1}{2}aR \tag{40}$$

as $R\to\infty$. We have, according to Eqs. (12) and (13),

$$m(R) \to -\frac{sc}{2f}R,$$

$$\sigma^2(R) \to \frac{1}{2}(cD_1+aD_2)R \quad \text{as } R\to\infty. \tag{41}$$

Thus, the right boundary at $R=\infty$ is singular of the second kind [6], at which the diffusion exponent, the drift exponent, and the character value are

$$\alpha_r=1, \quad \beta_r=1, \quad c_r=\frac{sc}{f(cD_1+aD_2)}. \tag{42}$$

Therefore, the right boundary is repulsively natural. The self-competition mechanism results in a negative drift term for large R, which guarantees that neither the prey population nor the predator population can grow without restraint. Without the $-sX_1^2$ term in Eq. (3), which is the model considered in the paper by Khasminskii and Klebaner [9], the right boundary $R=\infty$ would have been attractively natural, implying that the prey population could grow without limit, an outcome contrary to what is expected of nature. Therefore, the inclusion of the self-competition term $-sX_1^2$ in the model is necessary.

E. Transition time

It is shown, with the present stochastic model (3), that neither the preys nor the predators will be extinct as long as the condition $a > 0$ is satisfied. However, the situation of a very low prey population should be avoided as much as possible. For this purpose, it is useful to investigate the transition time from a normal level of the prey population to a very low one, so that effective measures can be designed and applied to avoid its happening, or lengthen the transition time. It is seen from Eq. (2) and Fig. 1 that a very small value of either x_1 or x_2 corresponds to a much larger value of r. In the randomized version, these variables are denoted by X_1, X_2, and R, respectively. The time it takes to reach near extinction for either X_1 or X_2 can be investigated, using the classical framework of the first-passage problem in stochastic dynamics (e.g., [6]), namely the time it takes for the random process $R(t)$ to move from a low level r_0 to a high critical level r_c.

Since $R(t)$ is a stochastic process, the first time for it to move from an original noncritical state r_0 to reach a critical state r_c, to be referred to as the first-passage time, is a random variable, which is, of course, a function of r_0. The mean first-passage time, denoted by $\mu(r_0)$, is governed by the well-known Pontryagin equation [16],

$$1 + m(r_0)\frac{d\mu}{dr_0} + \frac{1}{2}\sigma^2(r_0)\frac{d^2\mu}{dr_0^2} = 0, \tag{43}$$

where $m(r_0)$ and $\sigma(r_0)$ are given by Eqs. (19) and (20), with R replaced by r_0. The boundary conditions for Eq. (43) are

$$\left.\frac{d\mu}{dr_0}\right|_{r_0=0} = -\frac{1}{m(0)} = -\frac{2}{cD_1 + aD_2} \quad \text{and } \mu(r_c) = 0. \tag{44}$$

The first condition can be obtained directly from Eq. (43), by taking into account that $\sigma^2(0)=0$. The solution for Eq. (43), that satisfies the two boundary conditions, is given by

$$\mu(r_0) = \frac{\beta a f}{s}\int_{r_0}^{r_c} \frac{e^{\beta u}}{g(u)} du \int_0^u T(v)e^{-\beta v} dv, \tag{45}$$

where the constant β is given by Eq. (24) and the function $g(u)$ is the deterministic version of Eq. (17).

The same systems parameters were selected for numerical calculation, i.e., $a_1=1, b=1, c=0.5$, and $f=0.5$. The initial prey population was assumed to be at its equilibrium state, i.e., $x_1=c/f=1$, corresponding to $r_0=0$. The critical value for x_1 was chosen to be $x_{1c}=0.01$ (equivalent to $r_c=1.81$), at which the prey population was near extinction. The mean first-passage time μ, calculated from Eq. (45), is shown in Figs. 6 and 7 for three different s values, 0.01, 0.02, and 0.03. Shown in Fig. 6 are the results obtained for $D_2=0$ and varying D_1. Those obtained for $D_1=0$ and varying D_2 are shown in Fig. 7. It is seen from these two figures that the mean first-passage time is sensitive to the s, D_1, and D_2 values. The effect of the s value is dominant when D_1 and D_2 are small. This effect diminishes at increasing D_1 or D_2, or both D_1 and D_2. Comparing Figs. 6 and 7, the effect of D_1 is seen to be greater than that of D_2, noting that the μ scales are different in these two figures.

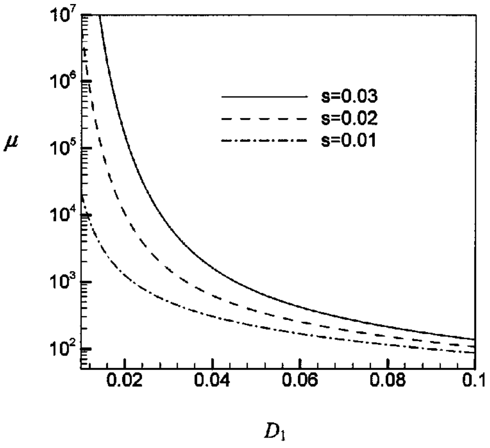

FIG. 6. Mean first-passage time to a critical state, computed for $D_2=0$, varying D_1, and different s values.

III. CONCLUSION

A randomized Lotka-Volterra-type model is used to investigate the interaction between the populations of the preys and the predators in an ecosystem. In particular, the random variations in time of the birth rate of the preys and the death rate of the predators are modeled as Gaussian white noises. A deterministic self-competition term is also included in the prey equation. The stochastic averaging procedure of Stratonovich and Khasminskii is applied in the analysis. The probability distributions at the stationary state of the prey and predator populations are determined, and the average time for the ecosystem to reach a critical state is calculated. It is found that the system behaviors are sensitive not only to the self-competition term, but also the random variations in the prey birth rate and the predator death rate.

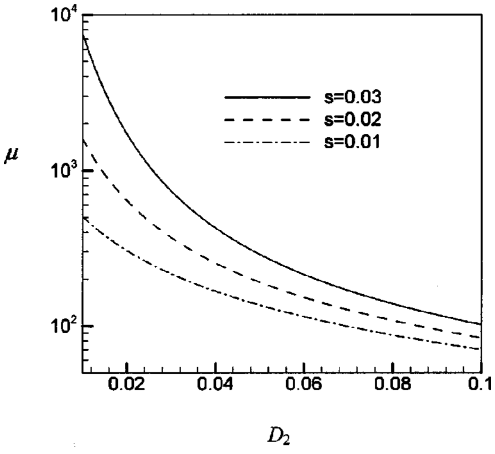

FIG. 7. Mean first-passage time to a critical state, computed for $D_1=0$, varying D_2, and different s values.

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