Stochastic analysis of a pulse-type prey-predator model

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A stochastic Lotka-Volterra model, a so-called pulse-type model, for the interaction between two species and their random natural environment is investigated. The effect of a random environment is modeled as random pulse trains in the birth rate of the prey and the death rate of the predator. The generalized cell mapping method is applied to calculate the probability distributions of the species populations at a state of statistical quasistationarity. The time evolution of the population densities is studied, and the probability of the near extinction time, from an initial state to a critical state, is obtained. The effects on the ecosystem behaviors of the prey self-competition term and of the pulse mean arrival rate are also discussed. Our results indicate that the proposed pulse-type model shows obviously distinguishable characteristics from a Gaussian-type model, and may confer a significant advantage for modeling the prey-predator system under discrete environmental fluctuations.

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I. INTRODUCTION

The interest in prey-predator systems has recently experienced a rapid growth due to their intrinsic relevance in modern population biology and ecology [1-11]. In this context, for some decades much effort has been devoted to mathematical modeling of the dynamics of interacting species through nonlinear, yet deterministic, set of coupled differential equations [3]; one of the best-known models is the Lotka-Volterra (LV) model, which describes the time evolution of two interacting species: a prey population that grows with a constant birth rate in the absence of a predator species, while the predator population decays with a constant death rate without the presence of a prey species [12,13]. Indeed, since living organisms experience competition with individuals of other species or of their own species, the LV competitive model is quite realistic as the prototype of competitive systems [1,14–17].

It is widely believed that interaction between species and their natural environment greatly influences the global features of ecosystems [14,18–28]. Therefore, a species can survive if it is able to adapt itself to the fluctuations arising in the environment. Such fluctuations are ubiquitous in all aspects of nature (e.g., temperature, rainfall, pollution, disaster, etc.) and may drastically modify the deterministic predictions of the coexistence of the species, and therefore they inspire intense discussion among ecologists [20,21]. Gaussian white noise variations are usually added to the predator death rate and prey birth rate to model the continuous environmental fluctuations [1,14,18]. However, to gain some more realistic and general understanding of the effect of environmental fluctuations leading to extinction of the species, it is highly desirable to adopt so-called stochastic pulse trains rather than Gaussian white noise as the description of fluctuations. One of the main reasons is to account for discrete and drastic actions. In fact, the Gaussian white noise always assumes the presence of continuous perturbations, while in real systems there are some unavoidable sparse, yet drastic, impulses which may qualitatively change the system behavior and even completely invalidate the deterministic predictions. As a consequence, the stochastic perturbations are intrinsically non-Gaussian and a discrete fluctuation model is preferred.

In this paper, we develop a different LV model, of socalled pulse type, which describes the behaviors of two interacting species under discrete environmental fluctuations. While the picture is relatively clear for a stochastic LV model under Gaussian white noise excitation [14], the role of a stochastic pulse train apparently has never been studied. The stochastic pulse train under consideration here is modeled as Poisson white noise. The generalized cell mapping (GCM) method [29–32] is applied to obtain the probability distributions of the predator and prey populations in a state of statistical quasistationarity. Furthermore, we present a global analysis of evolutionary processes that involves population distribution. As a main finding the near extinction probability after starting from a fixed point is obtained.

II. PULSE-TYPE LOTKA-VOLTERRA MODEL

A. The model

For a well-mixed population, the proposed pulse-type stochastic LV model describes the time evolution of the population densities for the species; it reads

$$X_{1} = X_{1}(g_{1} - c_{1}X_{1} - c_{2}X_{2}) + X_{1}\xi_{1}(t),$$
$$\dot{X}_{2} = X_{2}(-g_{2} + c_{3}X_{1}) + X_{2}\xi_{2}(t),$$
(1)

where $X_1(t) \ge 0$ and $X_2(t) \ge 0$ are two stochastic processes, representing the population densities of prey and predator species, respectively, and the overdot stands for the time derivative. (In the present paper, capital letters stand for stochastic processes or stochastic variables, while lowercase letters stand for deterministic quantities.) Each species is

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characterized by the natural growth (mortality) rate $g_i > 0$ and the competition parameter $c_i > 0$. The interactive terms $c_2X_1X_2$ and $c_3X_2X_1$ are, respectively, the relative decrease (increase) of the prey (predator) populations due to predation and provide a balance between the two species, and $-c_1X_1^2$ is the so-called prey self-competition term due to the natural fact that the energy resources consumed by the prey are exhaustible. $\xi_1(t)$ and $\xi_2(t)$ are two independent Poisson white noises defined as [33]

$$\xi(t) = \sum_{k=1}^{N(t)} Y_k \delta(t - t_k), \qquad (2)$$

where $\delta(\cdot)$ is the Dirac delta function and N(t) denotes a Poisson counting process with mean arrival rate $\lambda > 0$ (i.e., the mean number of δ impulses per unit time) and gives the number of pulses that arrive in the time interval [0,t]; $\{Y_k, k \ge 1\}$ is a collection of real-valued identically distributed independent random variables; Y_k represents the random magnitude of the impulse, which is independent of the pulse arrival time t_k .

Poisson white noise $\xi(t)$ is characterized by its correlation functions

$$R^{(n)}[\xi(t_1),\xi(t_2),\ldots,\xi(t_n)] = \lambda E[Y^n]\delta(t_2-t_1)\ldots\,\delta(t_n-t_1)$$
(3)

$$(n=1,2,\ldots,\infty),$$

where $E[\cdot]$ denotes the mathematical expectation value. For the limiting case when λ approaches infinity and, at the same time, the intensity of the Poisson white noise $I = \lambda E[Y^2]$ keeps a constant value, the cumulants of orders higher than 2 tend to zero, and the Poisson white noise $\xi(t)$ tends to Gaussian noise.

B. The deterministic counterpart

To understand the importance of external fluctuations and their effects on the population distribution and extinction probability, we examine first the deterministic counterpart of Eq. (1), namely,

$$\dot{x}_1 = x_1(g_1 - c_1 x_1 - c_2 x_2),$$

$$\dot{x}_2 = x_2(-g_2 + c_3 x_1),$$
 (4)

where the term $-c_1x_1^2$ models the effect of intraspecific competition. The system (4) admits at most three equilibria in the first quadrant: two unstable saddle points at E_1 , (0,0) (total extinction), and E_2 , $(g_1/c_1,0)$ (extinction of the predator), and one nontrivial stable equilibrium state at E_3 , $[g_2/c_3, (g_1 - g_2c_1/c_3)/c_2]$ (coexistence of prey and predator). The x_2 and x_1 axes are, respectively, the stable and unstable manifolds of E_1 . The x_1 axis is the stable manifold of E_2 . There is a heteroclinic orbit which connects the two distant saddle points, starting from E_1 , walking along the x_1 axis, and ending in E_2 . Local stability analysis yields the eigenvalues $-c_1g_2/(2c_3) \pm \sqrt{-4c_3^2g_1g_2 + c_1^2g_2^2 + 4c_1c_3g_2^2}/(2c_3)$ for the stability matrix of E_3 . So E_3 is an asymptotic stable fixed point for $c_1 \neq 0$, while for $c_1=0$ it becomes a neutrally stable fixed point and the system (4) possesses a first integral

$$H(x_1, x_2) = c_3 x_1 + c_2 x_2 - g_2 \ln \frac{c_3 x_1}{g_2} - g_1 \ln \frac{c_2 x_2}{g_1} - g_1 - g_2,$$
(5)

where $H(x_1, x_2) \ge 0$ is the conserved quantity and $H(x_1, x_2)$ =0 at the equilibrium E_3 . The phase plane is thus segregated into a collection of nested closed orbits, where each one is characterized by a different value of H, as illustrated in Fig. 1(a). Also depicted in Figs. 1(b) and 1(c) are two trajectories of system (4), corresponding to two different values of c_1 =0.05 and 0.2, respectively, and with the same $g_1=1$, g_2 =0.5, c_2 =1, and c_3 =0.5 (all parameter values are nondimensionalized in the present paper). The motion of the system begins from the point (3.5, 1.5). It was found that the populations of species show the following asymptotic behaviors depending on the value of c_1 . (i) In the absence of the prey self-competition term, there is a neutrally stable fixed point $(g_2/c_{32}g_1/c_2)$ surrounded by periodic closed orbits which depends only on the initial states. (ii) When the prey selfcompetition term is present, both populations exhibit an oscillation with decreasing amplitude. It spirals inward from the initial point (3.5, 1.5), eventually reaching the asymptotic stable equilibrium $[g_2/c_3, (g_1-g_2c_1/c_3)/c_2]$, and the speed of approach is proportional to c_1 . The angular velocity of the cyclic motion is plotted against time in Fig. 2, and is shown to become regular after several cycles. Also the motion shows a periodic tendency. Without any external perturbation, the deterministic LV model predicts in general the coexistence of both species.

C. Generalized cell mapping method

Since the nonlinear system with Poisson white noise reveals an inherently non-Gaussian nature, the exact solution to this system is not available even for a simple two-species pulse-type LV model. Hence, quite advanced techniques may be required to find approximate solutions to the problem. In the past few decades, considerable effort has been made and a GCM method has been developed for the global analysis of nonlinear dynamical systems [29–32].

The GCM method is an effective and efficient method for stochastic analysis of the proposed pulse-type LV model. It is performed by considering the population evolution process at discrete time instants and by discretization of the state space; hence the time- and state-space continuous Markov vector process is reduced to a Markov chain. The time axis is divided into small time intervals Δt and $p_x(\mathbf{x}_0, t_i)$ denotes the probability density function (PDF) at the time $t_i=t_0+i\Delta t$, i=0,1,2,.... The PDF at the subsequent instant t_{i+1} , is given by the convolution integral

$$p_{\mathbf{x}}(\mathbf{x}, t_{i+1}) = \int_{\mathbf{R}^2} q_{\mathbf{x}}(\mathbf{x}, t_{i+1} | \mathbf{x}_0, t_i) p_{\mathbf{x}}(\mathbf{x}_0, t_i) d\mathbf{x}_0, \qquad (6)$$

where $q_{\mathbf{x}}(\mathbf{x}, t_{i+1} | \mathbf{x}_0, t_i)$ is the transition PDF of the state vector from the state $\mathbf{x}(t_0) = \mathbf{x}_0$ at the time t_i to the state $\mathbf{x}(t) = \mathbf{x}$ at the time t_{i+1} , and \mathbf{R}^2 is the phase space.



FIG. 1. (Color online) Trajectories of system (4) starting at (3.5,1.5) for three different prey self-competition parameters $c_1 = (a) 0$, (b) 0.05, and (c) 0.2.

If the time interval Δt is short enough and if the mean arrival rate λ is low, it follows from the Poisson law that the probability of occurrence of more than one impulse in this time interval may be neglected and the following asymptotic form of the transition probability density may be assumed:



FIG. 2. (Color online) Angular velocity of the cyclic motion of system (4) starting at (3.5,1.5) for three different prey self-competition parameters c_1 = (a) 0, (b) 0.05, and (c) 0.2.

$$q_{\mathbf{x}}(\mathbf{x}, t_{i+1} | \mathbf{x}_{0}, t_{i}) = P_{0}(t_{i+1} | t_{i}) q_{\mathbf{x}}^{(0)}(\mathbf{x}, t_{i+1} | \mathbf{x}_{0}, t_{i}) + [1 - P_{0}(t_{i+1} | t_{i})] \\ \times q_{\mathbf{x}}^{(1)}(\mathbf{x}, t_{i+1} | \mathbf{x}_{0}, t_{i}) + O((\lambda \Delta t)^{2}),$$
(7)

where

$$P_0(t_{i+1}|t_i) = \Pr\{N(t_{i+1}) = 0 | N(t_i) = 0\} = \exp[-\lambda(t_{i+1} - t_i)],$$
(8)

$$q_{\mathbf{x}}^{(0)}(\mathbf{x}, t_{i+1} | \mathbf{x}_{0}, t_{i}) = \delta(x_{1} - x_{1}(t_{i+1} | \mathbf{x}_{0}, t_{i})) \,\delta(x_{2} - x_{2}(t_{i+1} | \mathbf{x}_{0}, t_{i}))$$
(9)

is the transition probability density conditional on no impulse arrival, and $\mathbf{x}(t_{i+1}|\mathbf{x}_0, t_i)$ denotes the deterministic drift from the initial state \mathbf{x}_0 at $t=t_0$ obtained from the initial value problem originating from Eq. (4). Surely Eq. (7) is satisfied at best for sparse pulse trains where λ is small. Algorithms have been devised for evaluation of $q_{\mathbf{x}}^{(1)}(\mathbf{x}, t_{i+1}|\mathbf{x}_0, t_i)$ [31].

The phase plane \mathbf{R}^2 is discretized into a finite number N of small cells, called the cell state space \mathbf{Z}^2 . In this paper, we assume that cells in \mathbf{Z}^2 are rectangular in shape and of equal size, and each cell is indexed by an integer. The probability of being in the *k*th cell at the time t_i is

$$P_k^{(i)} = \int_{C_k} p_{\mathbf{x}}(\mathbf{x}, t_i) d\mathbf{x}, \qquad (10)$$

where C_k is the domain occupied by the *k*th cell in \mathbb{Z}^2 .

Equation (6) can be approximated by the evolution equation of a discrete Markov chain in the cell state space \mathbb{Z}^2 as follows:

$$P_{j}^{(i+1)} = \sum_{k=1}^{N} Q_{jk} P_{k}^{(i)}, \qquad (11)$$

$$Q_{jk} = \int_{C_j} q_{\mathbf{x}}(\mathbf{x}, t_{i+1} | \mathbf{x}_k, t_i) d\mathbf{x}, \qquad (12)$$

where Q_{jk} , the element in the *j*th row and *k*th column of the one-step transition probability matrix **Q**, represents the probability of the system being in the *j*th cell at time t_{i+1} when the system is initially in the *k*th cell with probability 1, and \mathbf{x}_k is the center of the *k*th cell. The transition probability Q_{jk} will not depend on time t_i conditional on a stationary Markov process. The most interesting feature of the GCM method is that the one-step transition probability matrix **Q** contains global properties of the system in the cell state space and also governs temporal evolution of the probability vector **P**, provided that an initial vector $\mathbf{P}^{(0)}$ is specified. Once **Q** is at hand, the complete evolution history of the system can be computed simply by iterating Eq. (11),

$$\mathbf{P}^{(i)} = \mathbf{Q}\mathbf{P}^{(i-1)} = \mathbf{Q}^{i}\mathbf{P}^{(0)}.$$
(13)

The stationary distribution $\mathbf{P}^{(\infty)}$ may be obtained as $i \rightarrow \infty$. Obviously, $\mathbf{P}^{(\infty)} = \mathbf{Q} \mathbf{P}^{(\infty)}$, determining $\mathbf{P}^{(\infty)}$ as the normalized eigenvector associated with the largest eigenvalue $\lambda = 1$ of the matrix \mathbf{Q} .

Since extinction occurs when the population of the species decreases to a critical value and crosses the barrier, the barrier is regarded as absorbing. In the cell state space, all the cells lying inside the extinction domain E are called sink cells, for which the one-step transition probability should be represented as $Q_{jk} = \delta_{jk}$, $j \in E$. Then, the extinction time probability at t_i for a system originally in some nonextinction cell k can be evaluated in the following way:

$$P_{ext}^{(i)} = \sum_{j \in E} P_j^{(i)}, \quad P_j^{(0)} = \delta_{jk}.$$
 (14)

D. Monte Carlo simulations

We carried out extensive stochastic simulations to support and corroborate our results. The simulation results are obtained by generating independent time series of the compound Poisson process and integrating Eq. (1) numerically using the Runge-Kutta scheme to obtain the corresponding time series of the population density. The near extinction time probability is estimated with sample averages over 40 000 realizations.

E. Quasistationary population probability distributions

In this section, we focus on the quasistationary population density probability distributions of the proposed pulse-type LV system (1). Here the term "quasistationary" indicates the state of statistical stationarity, which means that the statistics, such as the probability density function, do not change with respect to time until the extinction of one species. For illustrative purpose, the parameters $g_1=1$, $g_2=0.5$, $c_2=1$, c_3 =0.5 were assigned, and the quasistationary distributions of the species populations were obtained by the GCM method. The computation domain is taken to be $[0,3] \times [0,2]$. It is divided into 600×400 cells of dimensions 0.005 units. The mapping step time Δt is chosen to be 1.5. Shown in Figs. 3 and 4 are the quasistationary probability densities $p(x_1)$ and $p(x_2)$ of the prev population $X_1(t)$ and the predator population $X_2(t)$, respectively, with mean arrival rate $\lambda_1 = \lambda_2 = 0.1$ and intensity $I_1 = I_2 = 0.005$ of the Poisson white noises. Also depicted in Figs. 3 and 4 are results obtained from the Monte Carlo (MC) simulation. The agreement between both results is good.

In order to show the non-Gaussian characteristics of the pulse-type LV model, the quasistationary population probability distributions of the traditional stochastic LV model, for which the environmental fluctuations are modeled as Gaussian white noises, are also computed by using MC simulation and included in Figs. 3 and 4. There is no doubt that the non-Gaussian behavior of the system depends on the mean arrival rate λ of Poisson white noise [33]. However, the inherent characteristics of the prey-predator system should also be taken into account. Here we focus on the effects of changing the prey self-competition parameter c_1 . Three different self-competition intensities corresponding to $c_1 = 0.1, 0.2, \text{ and } 0.3, \text{ respectively, are considered. It is shown$ that the quasistationary PDF of the pulse-type model is much peakier than that of the Gaussian one. With increasing c_1 , the distinction between the two cases becomes more remarkable.

F. Time evolution of the population probability

One of the major advantages of the GCM method as a global analysis approach is that it can depict not only the quasistationary solution, but also the complete evolution history of our pulse-type LV system simply by iteration of the evolution equation of the Markov chain (13). Figure 5 shows the time evolution of the population probability at 5, 10, 20, and 50 iterations, when it is initially distributed at its coexistence fixed point (1,0.9) with probability 1. The evolution history corresponding to another deterministic initial condi-



FIG. 3. (Color online) Probability densities of the prey population obtained for three different prey self-competition parameters c_1 = (a) 0.1, (b) 0.2, and (c) 0.3.

tion (2,1.5) is reported in Fig. 6. In both cases, the system is assigned the same parameters as those in the previous section, i.e., $g_1=1$, $g_2=0.5$, $c_1=0.1$, $c_2=1$, $c_3=0.5$, $\lambda_1=\lambda_2=0.1$, $I_1=I_2=0.005$, and mapping step time $\Delta t=1.5$. It is seen from these figures that the population distribution shows a station-



FIG. 4. (Color online) Probability densities of the predator population obtained for three different prey self-competition parameters c_1 = (a) 0.1, (b) 0.2, and (c) 0.3.

ary tendency after 50 iterations despite the different initial states.

G. Near extinction probability

The probability that one or both species die out in the course of time is of special interest within population dynam-



FIG. 5. (Color online) Snapshots of contour pictures of the time evolution of the population probability at different instants when initially distributed at its coexistence fixed point (1,0.9) with probability 1. (a) 5, (b) 10, (c) 15, and (d) 50 iterations.

ics from the biological viewpoint [14,21,34]. While the deterministic LV model with self-competition term $-c_1X_1^2$ predicts the existence of one asymptotic fixed point, associated with the coexistence of all the species, resulting in regular oscillations of the population densities, the fluctuations arising in the system dramatically invalidate this picture and play an essential role in the discussion of extinction: Starting at the fixed point, after long enough time one of the two species dies out. From a realistic perspective, we expect the coexistence of the species to be in a harmonious state, that is, the state for each species population is within moderate limits. The situation of a very low species population should be avoided as much as possible. For this purpose, it is useful to investigate the time it takes for the species population to move from a normal level to a critically low one, so that effective measures can be designed and applied to avoid its happening, or to lengthen the transition time. We address this issue by introducing an artificial absorbing barrier at low species population densities rather than the natural absorbing boundary where the species densities vanish, and studying the transition time probability for near extinction. Intuitively, each trajectory performs a drift-jump process in the phase portrait and interpolates between the deterministic cycles. Assume that the impulse arrives at the time t_1 with the strength Y_1 . Up to the time t_1 the system is performing a deterministic drift from the initial state \mathbf{x}_0 at time t_0 . At time t_1 a discontinuous change of the state of magnitude Y_1 takes place. Then the system continues performing deterministic drift with a modified initial value. The process continues until the trajectory eventually hits the artificial absorbing boundary of the cell state space. A first indication of the actual emergence of this scenario can be inferred from the stochastic trajectory shown in Fig. 7.

In our formulation, the near extinction probability corresponds to the probability that after time *t* the population has reached a critical state x_{ic} . The same system parameters were selected for numerical calculation, i.e., $g_1=1$, $g_2=0.5$, c_1 =0.1, $c_2=1$, $c_3=0.5$, and the noise intensities $I_1=I_2=0.01$ were assigned. The initial populations were assumed to be at their equilibrium state, i.e., $x_1=g_2/c_3=1$, $x_2=(g_1$ $-g_2c_1/c_3)/c_2=0.9$. Without loss of generality, the critical values were chosen to be $x_{1c}=x_{2c}=0.1$, at which the popula-



FIG. 6. (Color online) Snapshots of contour pictures of the time evolution of the population probability at different instants when initially distributed at (2,1.5) with probability 1. (a) 5, (b) 10, (c) 15, and (d) 50 iterations.

tion were near extinction. The near extinction time probability P_{ext} calculated by the GCM method is shown in Fig. 8, accompanied with MC simulation results. The agreement between the two results is very good. As is well known [31], the accuracy and the stability of the GCM results are highly dependent on the transition time step Δt , the cell sizes Δx_i , and the mean arrival rate λ_i . The crucial assumption, affecting the accuracy of the obtained results that only one pulse arrives in the transition time sets limits for λ_i and Δt as $\Sigma \lambda_i \Delta t \ll 1$. Therefore, an increase in the mean arrival rate must be accompanied by a shorter time step to guarantee higher accuracy. Shown in Fig. 8(a) are the results obtained for $\lambda_1 = 0.1$ and varying λ_2 . Those obtained for $\lambda_2 = 0.2$ and varying λ_1 are shown in Fig. 8(b). Also depicted in Figs. 8(a) and 8(b) are results for the Gaussian white noise case with the same intensities $I_1 = I_2 = 0.01$. It is seen from these two figures that the pulse-type LV model has significant distinguishable characteristics from the Gaussian one, and the mean arrival rate plays an important role in detrmining the near extinction time. With a decreasing mean arrival rate, the near extinction time becomes shorter. This reveals the natural



FIG. 7. (Color online) A single stochastic trajectory obtained from MC simulation. It walks out from the fixed point, eventually reaching the absorbing boundary.



FIG. 8. (Color online) Near extinction time probability when starting at the equilibrium state. The pulse-type LV model with different pulse mean arrival rates are compared with the Gaussian-type one: (a) computed for λ_1 =0.1 and three different λ_2 values, and (b) computed for λ_2 =0.2 and three different λ_1 values.

fact that a sparse pulse excitation, which corresponds to higher probability of a dominant single fluctuation, has a more remarkable effect in reducing the survival probability of the prey-predator ecosystem than a dense one, even if the two excitations share the same noise intensity. Comparing Figs. 8(a) and 8(b), the effect of λ_2 is seen to be greater than that of λ_1 . Since the proposed pulse-type LV model satisfies some basic phenomena of natural reality by taking discrete and drastic fluctuations into consideration, it has an advantage over the traditional Gaussian one.

III. CONCLUSION

Environmental fluctuations acting on ecosystems can be a source of new phenomena which may qualitatively change the system behavior, eliciting the extinction of species. The Gaussian assumption is usually made in the modeling of noise. While Gaussian white noise provides an efficient model of various environmental actions, for a broader class of realistic fluctuations such as pollution, disasters, rainfall, etc., the assumption of Gaussianity is not justified by the natural evidence. So there has been sustained interest in research into a stochastic ecosystem model under pulse-type disturbances that originate from discrete events. Motivated by this realistic requirement, we propose a pulse-type LV model to describe the behaviors of the prey-predator ecosystem under discrete fluctuations. The pulse-type fluctuations are modeled as Poisson white noises. The species interaction is also taken into account by including the prey selfcompetition term. Since an exact solution is unavailable due to the inherently non-Gaussian nature of the problem, the GCM method is adopted to investigate the transient and quasistationary probability distributions of the species populations, and also the near extinction time probability is obtained. The validity of the GCM method is proved by MC simulations. We pay special attention to the effects of the prey self-competition parameter c_1 and pulse mean arrival rate λ_i . Our analysis and numerical simulations reveal that, with a larger c_1 and a smaller λ_i , the proposed pulse-type LV model shows significantly different behavior from the Gaussian one. It is also found that the near extinction time probability is sensitive to λ_i . For a given time, the survival probability decays with a sparser pulse excitation. We suggest that more attention should be paid to the dynamic behavior of prey-predator ecosystems under continuous perturbations and discrete fluctuations.

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