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Lotka-Volterra system in a random environment

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Classical Lotka-Volterra (LV) model for oscillatory behavior of population sizes of two interacting species (predator-prey or parasite-host pairs) is conservative. This may imply unrealistically high sensitivity of the system's behavior to environmental variations. Thus, a generalized LV model is considered with the equation for preys' reproduction containing the following additional terms: quadratic "damping" term that accounts for interspecies competition, and term with white-noise random variations of the preys' reproduction factor that simulates the environmental variations. An exact solution is obtained for the corresponding Fokker-Planck-Kolmogorov equation for stationary probability densities (PDF's) of the population sizes. It shows that both population sizes are independent γ-distributed stationary random processes. Increasing level of the environmental variations does not lead to extinction of the populations. However it may lead to an intermittent behavior, whereby one or both population sizes experience very rare and violent short pulses or outbreaks while remaining on a very low level most of the time. This intermittency is described analytically by direct use of the solutions for the PDF's as well as by applying theory of excursions of random functions and by predicting PDF of peaks in the predators' population size.

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I. INTRODUCTION

Classical Lotka-Volterra (LV) model for oscillatory behavior of population sizes of two nonlinearly interacting species (predator-prey or parasite-host pairs) [1–4] is conservative. This means that sustained oscillations are regarded as being completely controlled by initial conditions, which are "never forgotten" by the system. Such nonrobust models have certain well-known drawbacks, in particular, they imply unrealistically high sensitivity of the system's behavior to environmental variations. The asymptotically stable models with internal dissipation and sustained external excitation may be more adequate in this respect. Thus, the corresponding "generalized LV model" [3,4] may be written as

$$\dot{u} = -mu + k\beta uv, \quad \dot{v} = \alpha v[1+\xi(t)] - \beta uv - \gamma v^2,$$

$$\langle \xi(t)\rangle = 0, \quad \langle \xi(t)\xi(t+\tau)\rangle = D\delta(\tau), \tag{1}$$

where $u(t)$ and $v(t)$ are population sizes of predators (or parasites) and preys (or hosts), respectively, whereas $\xi(t)$ is a zero-mean Gaussian random white noise with intensity D and δ is Dirac delta function, this white noise is interpreted in the Stratonovich sense, as a "physical" white noise [5–8]. The random variations in the preys' reproduction rate α simulate temporal variations of the environmental conditions (actually temporal random variations in the death rate of predators m were also accounted for in Refs. [3,4]). The term with squared v governs self-limitation in the growth of the prey population size in the absence of the predators. And as far as random oscillations in the system (1) are considered, it provides "damping," or feedback, which allows the system to "withstand" random environmental variations. The latter are confined in this paper to those of the preys' reproduction factor.

The extended stochastic versions of the LV model—system (1) and its generalizations to the cases of multiple interacting species and/or more sophisticated interaction laws (rather than that of just product-type)—have been studied in Refs. [3–5], [9–14]. Equilibrium states and their stability have been studied by direct application of the stochastic differential equations (SDE) calculus [9,10]. Probability densities of the population sizes had been analyzed in Ref. [10] for the case, where environmental variations may be represented as deterministic functions of time, depending on a finite number of random parameters (variables). The approach based on the Fokker-Planck-Kolmogorov (FPK) partial differential equation had been adopted in Refs. [4] and [11] for approximate analysis of the stationary and transitional probability densities, respectively, for the cases where (random) variations in population sizes are small compared with the corresponding mean values; direct perturbational approach and path integral approaches were used in Refs. [4] and [11], respectively. It should be noted that in the important case of intermittent behavior in population size(s) the level of random variations may be higher—and even much higher—compared with the corresponding mean values, and the above analyses may become inadequate for these cases. More sophisticated stochastic models of population dynamics, including, for example, those with multiple stable equilibrium states, have been studied in Refs. [12–14] by direct numerical simulation.

The system (1) had been studied in Ref. [3] by linearization in the vicinity of its stable equilibrium state. Stochastic stability analysis for the linearized equations indicated instability in the mean square of the population sizes at sufficiently high intensity of the white-noise fluctuations. This result had been interpreted in Ref. [3] as a potential for extinction of the populations due to environmental variations. However, exact solution for the complete (nonlinearized) system (1), obtained in Refs. [7,8], indicates that this is not the case: the populations cannot be killed solely by the above environmental variations [of course as long as the continuous model (1) remains applicable].

On the other hand, such a major event as stochastic instability of the linearized set of equations, as discovered in Ref. [3], cannot remain completely unnoticed by the system. The complete "nonlocal" nonlinear solution for the joint probability density function (PDF) of the population sizes, which indicates both of these state variables to be γ-distributed stationary random processes, may experience major transformations with increasing D [7,8]. Namely, the PDF(s) of $u(t)$ and/or $v(t)$ may become singular at their origin(s). This singularity is integrable, so that the populations still do exist. However, their behavior may become very different indeed from that in case of small environmental variations, exhibiting so-called on-off intermittency, particularly of predators, or parasites. Namely, very rare short and intensive pulses, or outbreaks in $u(t)$ may be observed, with very small level of u between these pulses; similar behavior of $v(t)$ is also possible. The analytical description of such a behavior is presented in this paper, as based on the use of the theory of excursion of random functions and on probabilistic predicting peaks of $u(t)$.

II. BASIC EXACT SOLUTION FOR PROBABILITY DENSITY OF POPULATION SIZES

The logarithmic transformation

$$x = \ln u, \quad v = \ln v, \tag{2}$$

reduces the SDEs (1) to the form

$$\dot{x} = \partial H/\partial y, \quad \dot{y} = -\partial H/\partial x - g(\partial H/\partial y) + \alpha\xi(t), \tag{3}$$

where

$$H(x,y) = k\beta\exp(y) - my + \beta\exp(x) - (\alpha - \gamma m/k\beta)x \quad \text{and} \quad g = \gamma/k\beta, \tag{4}$$

(the common chain rule for differentiation has been used here for the "physical" white noise rather than Ito differentiation formula [5–8]). Note, that the function H is different from Hamiltonian of the classical conservative LV system, which corresponds to the case of zero density-dependent coefficient, i.e., $\gamma = 0$. The difference will be seen to become especially important for small values of the parameter $\alpha - \gamma m/k\beta$ in the Eq. (4). This parameter is assumed in the following to be positive and arbitrary otherwise.

The transformed random state variables have a joint PDF, which will be denoted by $p(x,y,t)$. This PDF satisfies the well-known FPK equation [4–8], which for the present case of the SDEs (3) and (4) is written as [7,8]

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial x}\left(\frac{\partial H}{\partial y}p\right) + \frac{\partial}{\partial y}\left[\frac{\partial H}{\partial x}p + g\frac{\partial H}{\partial y}p\right] + \frac{\alpha^2 D}{2}\frac{\partial^2 p}{\partial y^2}. \tag{5}$$

Direct substitution shows, that the PDE (5) has the following exact stationary (independent of time) solution:

$$p(x,y) = C\exp[-(2\gamma/k\beta D\alpha^2)H(x,y)], \tag{6}$$

where C is a constant to be found from the normalization condition for the PDF [expression (4) for g had been used here].

Returning in the Eq. (6) to the original state variables u, v and imposing the normalization condition within the first quadrant of the (u,v) plane (that is, within positive values of each of these state variables) yields the joint stationary PDF $w(u,v)$ of the population sizes as a product of the individual one-dimensional (1D) PDF's of u and v [7,8],

$$\begin{gathered} w(u,v) = w_u(u)w_v(v), \\ w_u(u) = [(\delta/k)(\delta u/k)^{(\delta u_0/k)-1} \times\exp(-\delta u/k)]/\Gamma(\delta u_0/k), \\ w_v(v) = [\delta(\delta v)^{\delta v_0 - 1}\exp(-\delta v)]/\Gamma(\delta v_0); \\ u_0 = (\alpha - \gamma m/k\beta)/\beta; \quad v_0 = m/k\beta, \quad \delta = 2\gamma/D\alpha^2. \end{gathered} \tag{7}$$

Here Γ is the Euler gamma function, whereas u_0, v_0 are clearly seen to be steady-state values of $u(t)$, $v(t)$, respectively, in the absence of the environmental variations; that is, they correspond to zero right-hand sides of the Eqs. (1) with $\xi(t) \equiv 0$. The equilibrium point (u_0, v_0) is a stable focus or stable node as long as $\gamma > 0$. The solution (7) implies that both population sizes are independent γ-distributed stationary random processes. Their mean values and variances can be easily calculated as u_0, v_0 and $u_0 k/\delta$, v_0/δ, respectively.

Consider first of all conditions for existence of the above stationary PDF's of $u(t)$ and $v(t)$. Whilst the latter is seen to exist always, as long as all parameters of the extended LV model (1) are strictly positive, the former does exist only provided that the (asymptotically stable) steady-state size of the predators population is positive, that is, if

$$u_0 = (\alpha/\beta)(1 - v_0/v_*) > 0, \quad \text{or} \quad v_0 < v_*,$$

where

$$v_* = \alpha/\gamma. \tag{8}$$

If the opposite inequality is satisfied, the PDF of $u(t)$ has a nonintegrable singularity at $u = 0$, and thus degenerates into the Dirac delta function at zero. The physical meaning is clear from the Eq. (8), where v_* is clearly seen to be the steady-state number of preys in the absence of predators. Namely, whenever growth of the prey population is restricted by the interspecific competition within the population, the predators "are not needed" for the equilibrium, and the solution $u = 0$, $v = v_*$ is established in the absence of the environmental variations. The first Eq. (1) becomes completely irrelevant in this one-dimensional case. The γ-distribution for the preys' population size has been obtained for this extreme case in Ref. [4] as a solution to the stationary FPK equation, which is found to be the ODE rather than PDE in the 1D case.

This interpretation clearly correlates with the fact that the point $u = 0$, $v = v_* = \alpha/\gamma$ is actually the unstable equilibrium point of the system (1) with $\xi(t) \equiv 0$, with the other equilibrium point (u_0, v_0) being stable as long as $\alpha - \gamma m/k\beta > 0$ (yet another unstable equilibrium point (0, 0) does exist also, which remains unaffected by variations of the parameter $\alpha-\gamma m/k\beta$). At the bifurcation point $\alpha=\gamma m/k\beta$ these two equilibrium states merge, leaving only one equilibrium point $u=0$, $v=v_*=\alpha/\gamma$ for $\alpha-\gamma m/k\beta<0$, which becomes stable in this case. As will be seen, the on-off intermittency becomes especially pronounced in the proximity of the bifurcation point, that is for small values of $1-v_0/v_*$.

Assume now that the inequality (8) is satisfied. The solution (7) indicates, that both PDF's (of $u(t)$ and of $v(t)$) do exist then, no matter how intensive are the white-noise environmental variations. However, an important change in the population(s) may appear indeed for sufficiently large D's (whereas for sufficiently small D both PDF's are asymptotically Gaussian with sharp peaks at their respective mean values u_0,v_0). It can be seen, that if $\delta v_0<1$ $(\delta u_0/k<1)$, then $w_v(v)[w_u(u)]$ has a singularity at $v=0$ $(u=0)$. The singularity is integrable, so that the stationary PDF does exist always, as had been noted in [7,8]. The question is: what does such a singularity mean as far as the real populations are considered?

It will be shown in the following that the singularity(ies) in the PDF(s) may basically imply the intermittency effect, or rare spontaneous on-off epidemic-type outbreaks in the population size(s). The first indicator for such a behavior may be obtained by calculating ratio of stay times above and below the mean level, say, for the parasites. Interpreting this ratio as that of the corresponding cumulative probabilities and using the Eq. (7) yields

$$\lambda_u=\frac{\text{Prob}(u>u_0)}{\text{Prob}(u<u_0)}=\frac{\int_{u_0}^{\infty}w_u(u)du}{\int_0^{u_0}w_u(u)du}=\frac{\Gamma(z_0,z_0)}{\Gamma(z_0)-\Gamma(z_0,z_0)},$$

$$z_0=\delta u_0/k, \tag{9}$$

where the function Γ that depends on two arguments is the incomplete gamma function. (Similar ratio may be calculated for preys, using the last expression (9) with $z_0=\delta v_0$ instead of $z_0=\delta u_0/k_*$) Asymptotic expressions for the complete and incomplete gamma functions indicate that this ratio approaches zero with $z_0\to0$, and approaches unity with $z_0\to\infty$. Full curve of λ vs z_0 in Fig. 1 shows this drop to be very drastic when z_0 is small. Thus the on-off intermittent behavior may be expected indeed for $u(t)$ in this case. Of a certain special interest may be the case where $v(t)$ remains close to its mean or expected level. As can be seen from the Eqs. (7)–(9), this will happen if

$$\delta v_0\gg1,\quad \delta u_0/k\ll1,\quad \text{or}$$

$$\alpha(1-v_0/v_*)\ll k\beta D\alpha^2/2\gamma\ll m. \tag{10}$$

Thus, the on-off intermittency in, say, population of parasites with almost constant corresponding size of the hosts' population may be observed under one of the following conditions:

(1) High death rate of predators m.

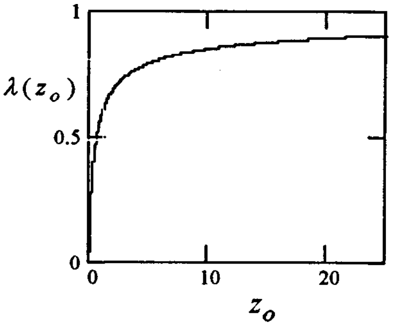

FIG. 1. Ratio of stay times above and below mean level for a γ-distributed stationary random process. Here $z_o=\delta u_o/k$ for $u(t)$ and $z_o=\delta v_o$ for $v(t)$, with the corresponding mean values being u_o and v_o, respectively.

(2) Small excess of the "isolated" equilibrium value of the preys' population size v_*, as governed by the interspecific competition, over its expected value v_0; this is case of proximity to the bifurcation point of the system (1) without parameter variations.

Figure 2 illustrates behavior of both populations as obtained by direct Monte Carlo simulation of the system (1). The intermittency in $u(t)$ is seen clearly, which, however, is different from other known cases of intermittency, as studied for example in Ref. [15]. A nonlinearly damped pendulum under white-noise vertical vibrations of its suspension point had been shown in Ref. [15] to exhibit intermittency whenever the intensity of the excitation only slightly exceeds its critical value for instability of the linearized model. The response PDF was shown, by approximate stochastic averaging method, to have the integrable singularity at zero in this case—similarly to the present case with the PDF's (7). The observed response samples, however, exhibited oscillatory behavior in Ref. [15], so that even the name "turbulence" had been used. On the contrary, just a single peak or outbreak, say in $u(t)$ is observed in the present case, so that this intermittency in the LV system may be called "quasistatic." Its analytical study will be continued in the Sec. III whereas in the remaining part of this section the dependence of population sizes on the "new" parameters γ and D will be summarized.

First of all, as can be seen from the Eq. (7), the PDF's of both $u(t)$ and $v(t)$ degenerate into Dirac delta-functions at zero if $\gamma=0$, $D\neq0$. This means extinction of both populations in the absence of the interspecific competition of preys—the same conclusion as had been made in [3,5]. Furthermore, proportional increase of γ and D (with fixed value of δ) in the range of small nonzero values of both these parameters does not change properties of both populations as long as the ratio v_0/v_* remains much smaller than unity [see Eqs. (7) and (8)]. This limiting case may be called "quasiconservative," since each response cycle is close to that of free oscillations of the classical LV system. It may be analyzed by the asymptotic method of averaging over the period of the corresponding conservative system, as had been shown in Ref. [3] for certain predator-prey pairs with more

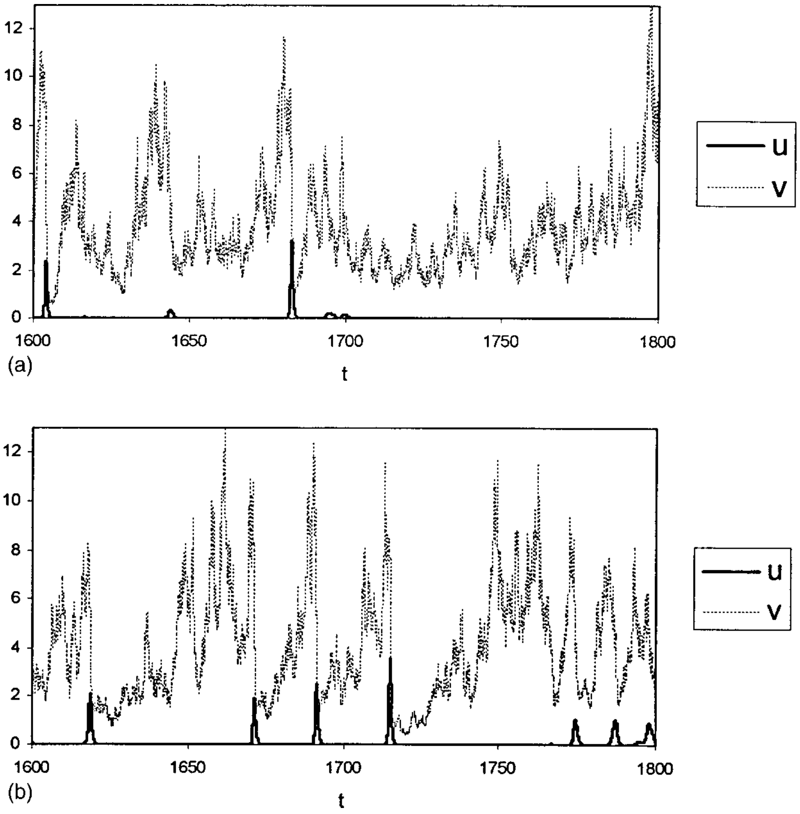

FIG. 2. Samples of $u(t)$ and $v(t)$ as obtained by Monte Carlo simulation for the system with $\alpha=1/4$, $m=4$, $k=1$, $\beta=1$ and also $\gamma=0.06$, $D=1.92$ (a) and $\gamma=0.05$, $D=1.6$ (b). (all quantities nondimensional).

complicated interactions than in the classical LV system for nonstochastic case, and in Ref. [7], [8] for the stochastic case.

With further increase of γ and D, however, the influence of the former of these parameters on the predators' population becomes more complicated, as long as it leads to reduction of the expected number of predators (but not preys). The reduction is seen to be especially drastic when the corresponding limiting value of the preys' population size due to interspecific competition v_* becomes only slightly higher than its expected size v_0. This is the case, where predators become close to extinction due to food shortage, and the on-off intermittent behavior in their population size may be expected indeed. Two pairs of short samples of population sizes in Fig. 2 were obtained for the same time interval and same values of parameters of the classical LV system, namely $\alpha=1/4$, $m=4$, $k=1$, $\beta=1$, whereas $\gamma=0.06$, $D=1.92$ in Fig. 2(a) and $\gamma=0.05$, $D=1.6$ in Fig. 2(b). Thus, in both cases $\delta=1$, $\delta v_0=4$, and the samples of $v(t)$ are seen to be very similar accordingly; this should be expected since they have the same PDF. And as long as the parameter δv_0 of this PDF is larger than unity, the process $v(t)$ does not exhibit any intermittency. On the other hand, values of $\delta u_0/k$ are different in these two cases but less than unity in both. Thus, intermittency in $u(t)$ is seen in both cases accordingly, with outbreaks in $u(t)$ being more violent and more frequent in Fig. 2(b) where u_0 is higher. The expected frequency of such outbreaks will be considered in the Sec. III.

Yet another example of the on-off intermittency is illustrated in Fig. 3, for the case $\alpha=1$, $m=1$, $\beta=k=1$, $\gamma=0.5$, $D=5$. Here both δv_0 and $\delta u_0/k$ are less than unity, and the on-off intermittency is seen in both populations accordingly. It may be added, that all samples in the Figs. 2 and 3 exhibit

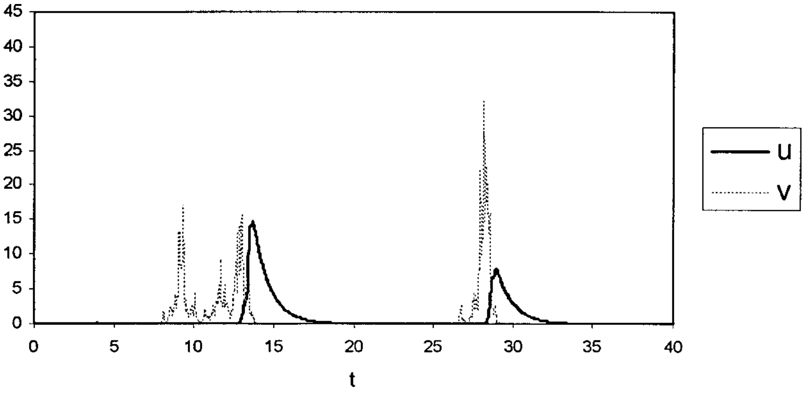

FIG. 3. Samples of $u(t)$ and $v(t)$ as obtained by Monte Carlo simulation for the system with $\alpha=1$, $m=1$, $\beta=k=1$, $\gamma=0.5$, $D=5$ (all quantities nondimensional).

behavior, which does not resemble-oscillations in the classical LV system. This should be expected in view of sufficiently high values of γ and thus of v_0/v_*, which make the system (1) strongly nonconservative.

III. EXCURSIONS AND PEAKS OF PREDATORS' POPULATION SIZE

Using the basic solution (7) certain other response characteristics of interest may be calculated. The first of these as based on the theory of excursions of random functions [16] is an expected number $n_+(u)$ of upcrossings per unit time of a given arbitrary level u by $u(t)$. Substituting Eq. (7), together with the first Eq. (1) into the basic relation [16] for such upcrossings yields [7,8]

$$\begin{aligned} n_+(u) &= \int_0^\infty \dot{u} w(u,\dot{u}) d\dot{u} = \int_{v_0}^\infty k\beta u(v-v_0) w(u,v) dv \\ &= (k\beta/\delta)(\delta v_0)^{\delta v_0}(\delta u/k)^{\delta u_0/k}\exp(-\delta v_0 - \delta u/k) \\ &\quad \times [\Gamma(\delta v_0)\Gamma(\delta u_0/k)]^{-1}. \end{aligned} \tag{11}$$

The latter formula provides just the expected frequency of oscillations if upcrossings of the mean or expected level ($u = u_0$) are considered,

$$\begin{gathered} n_+(u_0) = n_\infty f(\delta v_0) f(\delta u_0/k), \\ n_\infty = \lim_{\delta\to\infty} n_+(u_0) = \Omega/2\pi, \\ \Omega = \beta(k u_0 v_0)^{1/2}, \\ f(z) = [(2\pi)^{1/2} z^{z-1/2}\exp(-z)]/\Gamma(z), \end{gathered} \tag{12}$$

(the quantity Ω can be clearly identified here as the system's natural frequency of small oscillations, that is, oscillations with small deviations of $u(t)$, $v(t)$ from their steady values). This expression clearly indicates, in particular, that the peaks of $u(t)$ may become very rare indeed when u_0 is small—particularly, at small values of the second cofactor in the Eq. (8), that is, if the expected preys population size v_0 approaches its "isolated" equilibrium value v_* as governed by interspecific competition. Furthermore, ratio of the two quantities in the left-hand sides of Eqs. (11) and (12) may be calculated as

$$\overline{n}(u) = n_+(u)/n_+(u_0) = (u/u_0)^{\delta u_0/k}\exp[-(\delta/k)(u-u_0)]. \tag{13}$$

This function has its peak at $u = u_0$ (with the peak value clearly being equal to unity). For small values of u_0 it decreases very rapidly with decreasing u below this mean level, whereas its decay rate with increasing u for $u > u_0$ is much slower. This behavior perfectly correlates with the pulse shape of $u(t)$ as illustrated in Fig. 2, which corresponds to the "quasistatic" on-off intermittency. Expected number of crossings of a certain very small level $u > u_0$, which may be assigned as a threshold for extinction of the population, may be used to predict probability for extinction. Such a prediction may be based on the asymptotic Poisson law for crossings of levels with large deviations from mean [16].

It may also be of interest to study peaks of $u(t)$, so as to predict (probabilistically) level of the intermittent outbreaks in the parasites' population size together with their frequency. In view of the first Eq. (1) peak of $u(t)$ corresponds to a crossing of the level v_0 by $v(t)$. Denoting peak values of $u(t)$ by $U(t)$, we may then use Eq. (4) for $H(U,v_0)$ as an implicit definition of U in terms of H. Returning in Eq. (4) to the original variables u, v yields then

$$H = k\beta v_0 - m\ln v_0 + \beta U - (\alpha - \gamma m/k\beta)\ln U. \tag{14}$$

Consider now the stationary solution (6) to the FPK Eq. (5), which may be regarded as a probability density $p(H)$ of H (the normalization condition that governs the coefficient C would be different in this case but for simplicity we shall keep the notation). Introducing now nonlinear transformation (14) we may obtain PDF of peaks $p(U)$ in terms of $p(H)$ using basic formula for such a transformation [7,8]. Restricting analysis to the case of "positive" peaks, i.e., those with $U > u_0$, yields then

$$\begin{aligned} p(U) &= p[H(U)]|dH/dU| = C\beta(1-u_0/U)v_0^{\delta v_0} \\ &\quad \times \exp(-\delta v_0) U^{\delta u_0/k}\exp(-\delta U/k). \end{aligned} \tag{15}$$

Normalization condition for this PDF for "positive" peaks may be written as

$$\begin{aligned} \int_{u_0}^\infty p(U)dU &= C\beta(k/\delta)^{(\delta u_0/k)+1} v_0^{\delta v_0}(I_1 - z_0 I_0) \\ &\quad \times \exp(-\delta v_0) = 1, \end{aligned}$$

where

$$z_0 = \delta u_0/k \quad \text{and} \quad I_0 = \int_{z_0}^\infty z^{z_0-1}e^{-z}dz = \Gamma(z_0,z_0),$$

$$I_1 = \int_{z_0}^\infty z^{z_0}e^{-z}dz = \Gamma(z_0+1,z_0).$$

Using relation for the incomplete gamma function [17],

$$\Gamma(z_0+1,z_0) = z_0\Gamma(z_0,z_0) + z_0^{z_0}\exp(-z_0)$$

to calculate the normalization constant, yields finally the PDF of peaks as

$$\begin{aligned} p(U) &= (\delta/k)(1-u_0/U)(U/u_0)^{\delta u_0/k} \\ &\quad \times \exp[-(\delta/k)(U-u_0)] \quad \text{for } U > u_0. \end{aligned} \tag{16}$$

Same approach can be used to calculate the PDF for "negative" troughs of $u(t)$, if desirable, by applying the Eq. (15) with the negative sign of dU/dH.

Solving the equation $(d/dU)[\ln p(U)]=0$ to find maximum of the PDF (16) yields the most probable value U_m of the peak height U as $U_m = u_0 + \sigma_u$. Here $\sigma_u = \sqrt{u_0 k/\delta}$ is a standard deviation of the predators population size, which can be much higher than the mean population size as discussed in the Sec. II.

IV. CONCLUSIONS

Classical LV model is the simplest model for nonlinear dynamic interaction between two populations. Since it had been first developed in 1920's a lot of other models were suggested, with more sophisticated interaction laws [1–4,9–14]. However, the generalized LV model (1) with the simple product-type nonlinear interaction may still provide adequate description for certain specific predator-prey or parasite-host pairs, as long as it accounts for interspecific competition within preys' population and for temporal variations of the environmental conditions. In particular, the important phenomenon of the ''quasistatic'' on-off intermittency can be described, as had been demonstrated in this paper by explicitly calculating certain relevant statistical characteristics of the population sizes oscillations. Since the present type of intermittency implies short violent pulses or outbreaks in the predators' number, the expected time between these pulses (reciprocal to calculated the expected number of pulses per unit time), as well as probabilistic characteristics of their height may be of importance for applications, as long as this kind of behavior is observed for certain forest parasites (see, e.g., Fig. 14 in Ref. [3]; the reported case of seven outbreaks in budworm population in forests of Quebec, Canada since 1710 may also be mentioned here [18]). Such outbreaks may sometimes be observed on the background of almost constant preys' population size—particularly, when the latter is only slightly higher than its threshold value that corresponds to extinction of predators.

While the above conclusions concerning intermittency had been made by analysis of the specific stochastic system (1), it may be speculated that any general dynamic system with randomly varying parameters should exhibit the ''quasistatic'' type of the on-off intermittency in the vicinity of the bifurcation point of its ''mean'' part.

Finally, certain comments on other laws for temporal environmental variations seem to be relevant. In particular, accounting for periodicity (e.g., seasonal) in these variations may be important for certain applications. The case of sinusoidal parameter variations in the LV system has been studied in Ref. [19], where the model (1) was considered with $\xi(t)$ replaced by $\varepsilon \sin \omega t$ and $\gamma=0$. The potential for subharmonic response was discovered, that is, for response with frequency being integer divisor of the excitation frequency; an interesting case of application of the general theory to certain observed phenomena in population dynamics is described in [19]. The subharmonic response, however, may be quite sensitive to imperfect periodicity of the excitation. This had been demonstrated in [20] for a (strongly nonlinear) system with impacts using model of sinusoidal excitation with white-noise phase modulation; this model can be easily incorporated into the stochastic differential equations calculus, as demonstrated in Ref. [21]. The results highlighted excitation/system bandwidth ratio as the key parameter, influencing response both at principal resonance and at subharmonics, in particular, the latter may be greatly reduced by random temporal variations in the excitation frequency. Similar study seems to be appropriate for the system (1) with $\xi(t)$ replaced by the (narrow-band) sinusoid with white-noise phase modulation and $\gamma\neq 0$ (the latter requirement is necessary, as long as such random excitation would always contain a resonant harmonic).

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[1] N. S. Goel *et al.*, Rev. Mod. Phys. **43**, 231 (1971).

[2] J. D. Murray, *Mathematical Biology* (Springer, New York, 1993).

[3] Ju. M. Svirejev and D. O. Logofet, *Stability of Biological Communities* (Nauka, Moscow, 1978), in Russian.

[4] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1973).

[5] C. W. Gardiner, *Handbook of Stochastic Methods* (Springer-Verlag, Berlin, 1985).

[6] Y. K. Lin and G. Q. Cai, *Probabilistic Structural Dynamics* (McGraw-Hill, New York, 1995).

[7] M. F. Dimentberg, *Statistical Dynamics of Nonlinear and Time-Varying Systems* (Research Studies, Taunton, 1988).

[8] M. F. Dimentberg, *Random Processes in Dynamic Systems with Variable Parameters* (Nauka, Moscow, 1989), in Russian.

[9] H. Kesten and Y. Ogura, J. Math. Soc. Jpn **33**, 335 (1981).

[10] S. S. De, Bull. Math. Biol. **46**, 175 (1984).

[11] G. A. Becus, Bull. Math. Biol. **41**, 91 (1979); **41**, 543 (1979).

[12] A. B. Goryachev *et al.*, Chaos **6**, 78 (1996).

[13] B. E. Kendall, Chaos, Solitons Fractals **12**, 321 (2001).

[14] A. F. Rozenfeld *et al.*, Phys. Lett. A **280**, 45 (2001).

[15] P. S. Landa *et al.*, Chaos, Solitons Fractals **9**, 157 (1998).

[16] H. Cramer and M. R. Leadbetter, *Stationary and Related Stochastic Processes* (Wiley, New York, 1967).

[17] I. S. Gradsteyn and I. M. Ryzhik, *Tables of Integrals, Series and Products* (Academic, New York, 1980).

[18] T. Royama, *Analytical Population Dynamics* (Chapman & Hall, London, UK, 1992).

[19] W. M. Schaffer *et al.*, Chaos, Solitons Fractals **12**, 251 (2001).

[20] M. F. Dimentberg *et al.*, Nonlinear Dyn. **17**, 173 (1998).

[21] M. F. Dimentberg, Probab. Eng. Mech. **7**, 131 (1992).