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TRANSIENT DYNAMICS OF VERHULST MODEL WITH FLUCTUATING SATURATION PARAMETER*

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The stochastic Verhulst equation for the population density with fluctuating volume of resources is considered. Using the exact solution of this equation, the conditional probability density function is calculated for the excitation in the form of Lévy white noise with one-sided stable distribution. The phenomenon of transient bimodality and non-monotonic relaxation of mean population density for the white noise with Lévy–Smirnov stable distribution are found. An exact expression for the transitional time from bimodality to unimodality is obtained. It is interesting that for such a case the correlation function of population density in a steady state has a simple exponential form, and the correlation time does not depend on noise parameters.

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1. Introduction

The behavior of nonlinear dynamical systems in the presence of random perturbations attracted much attention in connection with the concept of noise-induced transitions and a wide range of applications in physics, chemistry and biology [1]. Transitions caused by noise are usually associated with a change in the number of extrema in the probability distribution of variable and may depend both quantitatively and qualitatively from statistics of noise.

The logistic model, proposed in the XIX century by the Belgian mathematician Verhulst, is one of the classic examples of self-organization in natural and artificial systems [2, 3, 4]. This model occurs in population

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dynamics of photons in a single-mode laser [5], self-replication of macromolecules [6], freezing of supercooled liquids [7], nonequilibrium chemical kinetics [8, 9, 10, 11] and autocatalytic chemical reactions [12], dynamics of biological populations [13, 14, 15], spread of viral epidemics [16], tumor growth [17, 18], *etc.*

The probabilistic and momentum characteristics of solution of the stochastic Verhulst equation have been investigated for Gaussian [1, 19] and Poisson [20] fluctuations of the growth rate and also for the case of complete correlation with fluctuations of the saturation parameter [12, 13, 18, 21, 22]. Some exact results for Malthus–Verhulst–Bernoulli equation with nonlinear coupled fluctuations in the form of Markovian dichotomous noise and periodical excitation with random phase have been obtained in Refs. [23, 24]. In particular, a non-monotonic relaxation of mean population density to stationary value was found.

In this paper, we analyze Verhulst model for evolution of biological population with fluctuating volume of resources. An excitation in the form of white noise with one-sided stable probability distribution gives a possibility to obtain some exact analytical results for statistical characteristics of population density such as the probability distribution of transitions and the correlation function in a steady state.

2. Statement of a problem

For definiteness, we will adhere to the population biology terminology and consider Verhulst model for the population density $x(t)$ with fluctuating volume of resources (saturation parameter)

$$\frac{dx}{dt} = rx - \xi(t)x^2\,, \tag{1}$$

where r is the rate of population growth and $\xi(t)$ is white non-Gaussian noise with one-sided probability distribution ($\xi(t) \geq 0$). As shown in [25], such noise is the first derivative of the generalized Wiener process (Lévy noise) $L(t)$, having infinitely divisible probability distribution [26]. This allows us to write the characteristic functional of white non-Gaussian noise $\xi(t)$, taking a positive values, in the following form (see Ref. [27])

$$\Theta_t\,[k] = \left\langle \exp\left\{ i\int\limits_0^t k\,(\tau)\,\xi\,(\tau)\,d\tau \right\} \right\rangle = \exp\left\{ \int\limits_0^t d\tau \int\limits_0^\infty \frac{e^{ik(\tau)z}-1}{z^2}\,\rho\,(z)\,dz \right\}, \tag{2}$$

where $k(t)$ is some deterministic function and $\rho(z)$ is a non-negative kernel function which is proportional to the probability density of jumps of Lévy process $L(t)$. In particular, putting in Eq. (2) $k(t) = k =$ const. we obtain the characteristic function of corresponding Lévy noise

$$\phi_L(k,t) = \left\langle e^{ikL(t)} \right\rangle = \exp\left\{ t \int_0^\infty \frac{e^{ikz} - 1}{z^2}\, \rho(z)\, dz \right\}. \tag{3}$$

The random process $x(t)$ is Markovian, and, using previously obtained in Ref. [27] results (see Eq. (15)) with Eqs. (1) and (2), we can write closed Kolmogorov's equation for its probability density function $P(x,t)$

$$\frac{\partial P}{\partial t} = -r \frac{\partial}{\partial x}(xP) + \int_0^\infty \frac{\rho(z)}{z^2} \left[\exp\left(z \frac{\partial}{\partial x} x^2 \right) - 1 \right] P(x,t)\, dz\,. \tag{4}$$

However, we will not solve complex integro-differential equation (4) and choose another way.

The exact solution of stochastic Eq. (1) reads

$$x(t) = \frac{x_0\, e^{rt}}{1 + x_0 \int_0^t \xi(\tau)\, e^{r\tau} d\tau}\,, \tag{5}$$

where $x_0 = x(0)$ is the initial value of population density. For a convenience, we introduce a new random process

$$\eta(t) = \int_0^t e^{-r(t-\tau)} \xi(\tau)\, d\tau\,, \tag{6}$$

having, in accordance with Eq. (2), the following characteristic function

$$\vartheta_t(k) = \left\langle e^{ik\eta(t)} \right\rangle = \exp\left\{ \int_0^t d\tau \int_0^\infty \frac{e^{ikze^{-r\tau}} - 1}{z^2} \rho(z)\, dz \right\}. \tag{7}$$

After this, the solution of Eq. (5) can be written as

$$x(t) = \frac{1}{\eta(t) + e^{-rt}/x_0}\,. \tag{8}$$

Our main goal is to find the evolution of the conditional probability density function of random process $x(t)$. To do this, one has to wrap Eq. (7), *i.e.* find the probability distribution of random process (6) using the reverse Fourier transform, and then apply the standard procedure for conversion of the probability densities of random variables after a nonlinear transformation (8).

3. Calculation of conditional probability density function

Further we analyze the probability distribution of population density for some special cases of one-sided function $\rho(z)$, specifying the statistics of white noise $\xi(t)$. For example, the kernel function in the form

$$\rho\left(z\right)=\nu ze^{-\mu z}\,,\qquad z\geq 0\,, \tag{9}$$

where ν and μ are some positive parameters, corresponds to the Lévy process $L(t)$ with gamma-distribution. In fact, substituting Eq. (9) in Eq. (3) and making the reverse Fourier transform, we arrive at

$$P_L\left(z,t\right)=\frac{\mu^{\nu t}z^{\nu t-1}e^{-\mu z}}{\Gamma\left(\nu t\right)}\,,\qquad z\geq 0\,,$$

where $\Gamma(x)$ is the gamma-function. After substitution of Eq. (9) in Eq. (7) we obtain

$$\vartheta_t\left(k\right)=\exp\left\{-\frac{\nu}{r}\left[\mathrm{Li}_2\left(\frac{ik}{\mu}\right)-\mathrm{Li}_2\left(\frac{ik}{\mu}\,e^{-rt}\right)\right]\right\}\,. \tag{10}$$

Here $\mathrm{Li}_n(z)$ is the polylogarithms expressed by the following power series

$$\mathrm{Li}_n\left(z\right)=\sum_{k=1}^{\infty}\frac{z^k}{k^n}\,.$$

Since Eq. (10) already contains a special function, it is impossible to find the probability distribution of random process $\eta(t)$ in closed analytical form as well as the probability distribution of population density $x(t)$.

As well-known [28], the entire class of stable probability distributions $P_{\alpha,\beta}(x)$ with the following characteristic functions

$$\theta_{\alpha,\beta}\left(k\right)=\exp\left\{-\left|k\right|^{\alpha}\exp\left(\frac{i\pi\beta}{2}\,\mathrm{sgn}\left(k\right)\right)\right\} \tag{11}$$

can be presented in the form of a set of diamond points at the parameter plane (α,β) (see the shaded area in Fig. 1)

$$\left|\alpha-1\right|+\left|\beta\right|\leq 1\,.$$

In Fig. 1 a part of horizontal axis $\beta=0$ inside the diamond corresponds to the α-stable symmetric probability density functions, while the points of the thick line $\beta=-\alpha$ correspond to the one-sided stable distributions.

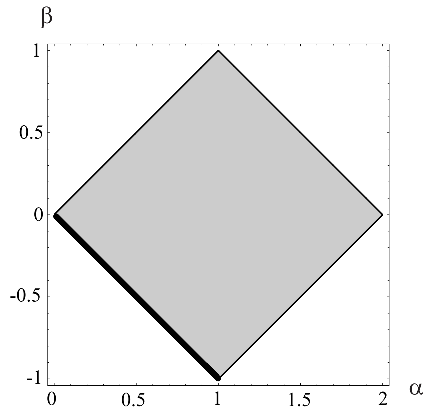

Fig. 1. The range of parameters (shaded area) corresponding to the stable probability laws. The thick side of the diamond corresponds to the one-sided stable distributions [28].

The stable probability distributions derived by the reverse Fourier transform of characteristic functions (11)

$$P_{\alpha,\beta}(x) = \frac{1}{\pi} \operatorname{Re} \left\{ \int_0^\infty \exp\left(-ikx - k^\alpha e^{i\pi\beta/2}\right) dk \right\} \tag{12}$$

can be expressed in analytical form only in rare cases and has a heavy tails: $P_{\alpha,\beta}(x) \sim 1/|x|^{\alpha+1}$ at $|x| \to \infty$. As a result, all stable probability density functions have infinite variance except the Gaussian distribution, which corresponds to the point $(2,0)$ in Fig. 1. Moreover, all one-sided stable probability distributions have also an infinite mean value. In particular, calculating the integral (12) for $\alpha = 1/2$, $\beta = -1/2$ we arrive at one-sided Lévy–Smirnov distribution

$$P_{1/2,-1/2}(x) = \frac{1}{2\sqrt{\pi}\, x^{3/2}}\, e^{-1/(4x)}, \qquad x \geq 0\,. \tag{13}$$

Let us consider now the random excitation $\xi(t)$ with one-sided stable probability distribution in Verhulst equation (1). In view of stability, the random process $\eta(t)$, obtained by linear integral transformation (6) of $\xi(t)$, should have the same distribution as $\xi(t)$. This allows us to simplify the calculations.

Choosing the following power kernel function

$$\rho(z) = qz^{1-\alpha}, \qquad z \geq 0 \quad (0 < \alpha < 1) \tag{14}$$

in Eq. (3) and calculating the integral, we obtain the characteristic function in the form (11) with $\beta = -\alpha$, *i.e.* arrive to Lévy noise $L(t)$ with one-sided stable probability distribution. Substituting Eq. (14) in Eq. (7), performing the double integration and taking into account Eq. (11), we arrive at

$$\vartheta_t(k) = \theta_{\alpha,-\alpha}(k\,\sigma(t)) \,, \tag{15}$$

where

$$\sigma(t) = \sigma\left(1 - e^{-r\alpha t}\right)^{1/\alpha}, \qquad \sigma = \left[\frac{q\,\Gamma(1-\alpha)}{r\alpha^2}\right]^{1/\alpha}. \tag{16}$$

In accordance with Eq. (15), the probability distribution of random process $\eta(t)$ reads

$$P_\eta(y,t) = \frac{1}{\sigma(t)}\,P_{\alpha,-\alpha}\left(\frac{y}{\sigma(t)}\right). \tag{17}$$

Using well-known relation of the probability theory regarding a nonlinear transformation of random variables, from Eqs. (8) and (17) we find finally the non-stationary probability distribution of population density

$$P(x,t) = \frac{1}{x^2\sigma(t)}\,P_{\alpha,-\alpha}\left(\frac{1}{\sigma(t)}\left(\frac{1}{x} - \frac{e^{-rt}}{x_0}\right)\right). \tag{18}$$

Equation (18) determines the evolution of the probability density function from initial state to the following steady state in asymptotics ($t \to \infty$) (see Eqs. (16) and (18))

$$P_{\mathrm{st}}(x) = \frac{1}{x^2\sigma}\,P_{\alpha,-\alpha}\left(\frac{1}{x\sigma}\right). \tag{19}$$

4. Analysis of transient bimodality

Further we demonstrate our general results (18) and (19) for white non-Gaussian noise $\xi(t)$ with Lévy–Smirnov stable distribution ($\alpha = 1/2$). From Eqs. (13), (16) and (18) we find

$$P(x,t) = \frac{2q\left(1 - e^{-rt/2}\right)}{r\sqrt{x}\left(1 - xe^{-rt}/x_0\right)^{3/2}}\exp\left\{-\frac{4\pi q^2 x\left(1 - e^{-rt/2}\right)^2}{r^2\left(1 - xe^{-rt}/x_0\right)}\right\}. \tag{20}$$

The plots of non-stationary probability distribution of population density (20) are shown in Fig. 2 for different times. The thick dashed line corresponds to the following asymptotic distribution ($t \to \infty$)

$$P_{\mathrm{st}}(x) = \frac{2q}{r\sqrt{x}}\,e^{-4\pi q^2 x/r^2}\,, \qquad x > 0\,. \tag{21}$$

As seen from Fig. 2, the initial distribution in the form of delta-function immediately transforms into bimodal at $t > 0$ (see the curves for $t = 0.1$ and $t = 0.4$) with two peaks corresponding to the scenarios of annihilation and survival of biological population. Then, after some transitional time $t_c = 0.737645$ (thick solid curve in Fig. 2), the probability density function becomes again unimodal with one maximum at the origin (see the curve for $t = 1.5$), approaching in the limit of large times to the steady state distribution (thick dashed curve in Fig. 2). Thus, the fluctuations in resources with infinite mean value lead to annihilation of the population in most likely scenario, in contrast to the fluctuations in the growth rate, when the maximum is shifted to non-zero values [19, 20].

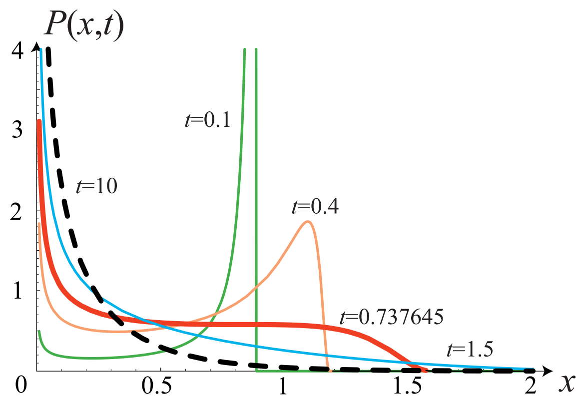

Fig. 2. The evolution of the probability distribution of population density. The thick solid curve corresponds to the transition from bimodality to unimodality ($t = 0.737645$) and thick dashed curve corresponds to the steady-state distribution ($t = 10$). The parameters are $x_0 = 0.8$, $r = 1$, $q = 0.5$.

To find the time t_c of noise-induced transition from bimodality to unimodality one should equate to zero the first derivative (or the logarithmic derivative) of the distribution (18) with respect to x. As a result, we arrive at

$$[\ln P_{\alpha,-\alpha}(z)]' = -\frac{2}{z + \tau_0(t)}, \tag{22}$$

where

$$z = \frac{1}{x\sigma(t)} - \tau_0(t) > 0, \qquad \tau_0(t) = \frac{e^{-rt}}{x_0\sigma(t)}. \tag{23}$$

For Lévy–Smirnov stable distribution (13) Eq. (22) transforms to the following quadratic equation with respect to $1/z$

$$\frac{\tau_0(t)}{z^2} + \frac{1 - 6\tau_0(t)}{z} + 2 = 0. \tag{24}$$

As seen from Fig. 2, within the time interval $(0, t_c)$ the probability density function has two extrema (minimum and maximum) in the area $x > 0$ and for $t > t_c$ these two extrema disappear. On the other hand, Eq. (24) has not real roots when its discriminant is negative, *i.e.*

$$36\,\tau_0^2\,(t) - 20\,\tau_0\,(t) + 1 < 0\,. \tag{25}$$

According to Eqs. (16) and (23), $\tau_0\,(t) \to \infty$ at $t \to 0$. As a result, we obtain from Eq. (25) the following equation to determine the transitional time t_c

$$\tau_0\,(t_c) = \tfrac{1}{2}\,. \tag{26}$$

Substituting Eqs. (16) and (23) into Eq. (26) and putting $\alpha = 1/2$, we find finally

$$t_c = \frac{2}{r}\,\ln\left(1 + \frac{r}{4q}\sqrt{\frac{2}{\pi x_0}}\right)\,. \tag{27}$$

As can be seen from Eq. (27), the transitional time increases slowly with decreasing all the parameters: the initial value of population density x_0, the noise intensity q and the rate of population growth r.

5. Non-monotonic relaxation of mean population density

Now we analyze a behavior of the mean population density. From Eqs. (18) and (23) we obtain

$$\langle x\,(t)\rangle = \frac{1}{\sigma\,(t)}\int_0^{x_0\,e^{rt}} P_{\alpha,-\alpha}\left(\frac{1}{x\sigma\,(t)} - \tau_0\,(t)\right)\frac{dx}{x} = \int_0^{\infty}\frac{P_{\alpha,-\alpha}\,(z)\,dz}{\sigma\,(t)\,z + e^{-rt}/x_0}\,. \tag{28}$$

Performing the integration in Eq. (28) for Lévy–Smirnov distribution (13) we arrive at

$$\langle x\,(t)\rangle = x_0\,e^{rt}\left[1 - \sqrt{\pi\gamma\,(t)}\;e^{\gamma(t)}\,\mathrm{erfc}\left(\sqrt{\gamma\,(t)}\right)\right]\,, \tag{29}$$

where

$$\gamma\,(t) = \frac{4\pi q^2 x_0}{r^2}\left(e^{rt/2} - 1\right)^2 \tag{30}$$

and $\mathrm{erfc}(x)$ is the complementary error function.

The dependence of mean population density on time, given by Eqs. (29) and (30), for a fixed Malthus factor $r = 1$, fixed noise intensity $q = 0.25$ and different initial values of population density x_0 is depicted in Fig. 3. For all cases we observe a non-monotonic relaxation to the stationary value. This interesting behavior has been first found by Zygadło in his paper [23] for Malthus–Verhulst–Bernoulli model with external excitation in the form of Markovian dichotomous noise and sinusoidal signal with random phase and was confirmed by numerical simulations.

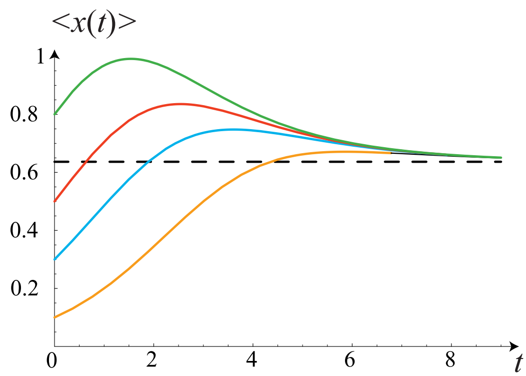

Fig. 3. The non-monotonic relaxation of the mean population density to a stationary value for different initial conditions. The parameters are $r = 1$, $q = 0.25$.

6. Steady state characteristics

As it follows from Eq. (21), the probability distribution of population density in a steady state decreases exponentially at $x \to \infty$. It means that all the moments of $x(t)$ are finite. Calculating from Eq. (21) the characteristic function in a steady state

$$\theta_{\mathrm{st}}(k) = \left(1 - \frac{ikr^2}{4\pi q^2}\right)^{-1/2}$$

and expanding its logarithm in power series in parameter k, we find the cumulants of any order of stationary random process $x(t)$

$$\kappa_n = \frac{(n-1)!}{2}\left(\frac{r^2}{4\pi q^2}\right)^n . \tag{31}$$

In particular, Eq. (31) yields the following expressions for the mean value ($n = 1$) and the variance ($n = 2$) of population density in a steady state

$$\langle x \rangle = \frac{r^2}{8\pi q^2}\,, \qquad \kappa_2 = \frac{r^4}{32\pi^2 q^4}\,. \tag{32}$$

As seen from Eq. (32), the mean value of population density as well as the variance increases with increasing the growth rate, but decreases with increasing the intensity of saturation parameter fluctuations. From Eq. (21) one can also calculate the probability that the population density in a steady state does not exceed its mean value

$$\text{Prob}\left\{x\left(t\right)<\left\langle x\right\rangle\right\}=\text{erf}\left(\frac{1}{\sqrt{2}}\right)\approx 0.68\,,$$

where $\text{erf}(x)$ is the error function.

To calculate the correlation function $K\left(\tau\right)=\left\langle x(t)x(t+\tau)\right\rangle$ of population density in a steady state one can use previously obtained result (28) for the mean value. It is sufficient to multiply Eq. (28) on x_0 and average over the stationary distribution $P_{\text{st}}(x_0)$ (19), *i.e.*

$$K\left(\tau\right)=\int\limits_0^\infty\frac{1}{\sigma x_0}\,P_{\alpha,-\alpha}\left(\frac{1}{\sigma x_0}\right)dx_0\int\limits_0^\infty\frac{P_{\alpha,-\alpha}\left(z\right)dz}{\sigma\left(\tau\right)z+e^{-r\tau}/x_0}$$

or, in accordance with Eq. (16),

$$K\left(\tau\right)=\frac{1}{\sigma^2}\int\limits_0^\infty\frac{P_{\alpha,-\alpha}\left(y\right)dy}{y}\int\limits_0^\infty\frac{P_{\alpha,-\alpha}\left(z\right)dz}{\left(1-e^{-r\alpha\tau}\right)^{1/\alpha}z+e^{-r\tau}y}\,. \tag{33}$$

It is surprising that for the case of white non-Gaussian noise excitation with Lévy–Smirnov stable distribution (13) we can perform the double integration in Eq. (33) in closed analytical form. As a result, we arrive at very simple expression

$$K\left(\tau\right)=\kappa_2\,e^{-r\tau/2}+\left\langle x\right\rangle^2\qquad\left(\tau>0\right)\,. \tag{34}$$

Unexpectedly, but such complex nonlinear system as Verhulst model (1) with multiplicative noise has a simple exponential correlation function (34) in a steady state with the correlation time

$$\tau_{\text{cor}}=\frac{2}{r}\,, \tag{35}$$

which does not depend on the noise intensity q.

7. Conclusions

The strong analytical results for probabilistic characteristics of Verhulst model with fluctuations of the saturation parameter in the form of white non-Gaussian noise with one-sided stable distribution have been obtained using the exact solution of the equation. The noise-induced transitions and non-monotonic behavior of mean population density for the random excitation having Lévy–Smirnov stable distribution have been found and analyzed in detail. Some steady state characteristics such as all-order cumulants and the correlation function have been calculated. In particular, as it was shown, the correlation function has a simple exponential form with the correlation time which is independent on noise intensity.

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