STOCHASTIC ANALYSIS OF POPULATION DYNAMICS SUBJECT TO CHANGES AT THE RANDOM TIME MOMENTS

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Abstract. The paper presents a mathematical model of a predator-prey population dynamics given in a form of Markov dynamic impulse-type system, allowing discontinuities of trajectories at random time moments. The stochastic approximation procedure allows to analyse the qualitative behaviour of trajectories of the ecosystem.

Key words: stochastic modelling, logistic equations, stochastic approximation

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1 Introduction

The method of qualitative analysis of predator-prey population behaviour by means of differential equations was first proposed at the beginning of the last century in [1,2]. These models assume continuous contact of predator population, with phase coordinate $\{y(t), t \geq 0\}$, with the prey population, with a phase coordinate $\{x(t), t \geq 0\}$. Subsequently, numerous papers on the analysis of a more general system of equations find a stable coexistence of populations (see the review in [3]). The most popular and quite common system of differential equations describing the dynamics of populations of predator-prey ecosystem is Kolmogorov model [4]:

$$\frac{dx}{dt} = \alpha(x)x - V(x)y, \qquad \frac{dy}{dt} = M(x)y, \qquad (1.1)$$

with different types of right part of the equation. The simplest prey-predator model, the Lotka-Volterra model, has a form (1.1) with $a(x) \equiv \alpha, V(x) = \beta x$ and $M(x) = -\delta + \gamma\beta x$, and was analysed in detail by authors [1,2]. All the parameters in the equation (1.1) are positive, therefore the unique nontrivial equilibrium state of the system is the centre type fixed point $\{y = \alpha / \beta; x = \delta / \gamma\beta\}$ and all phase trajectories have the form of closed orbits. The equation (1.1) allows to explain the often observable fluctuations in predator-prey populations. However, this model is not robust i.e., small perturbations in the right-hand side of the equation (1.1) can significantly change the phase portrait. Later, a more realistic model with

$a(x) = r(1 - K^{-1}x), V(x) = \beta x$ and $M(x) = -\delta + \gamma\beta x$ was analysed in many papers (see the review in [3]). This model allows us to detect the asymptotically stable equilibrium and possibility of damped oscillations of predator and prey population size in case of the sufficiently high birth rate of the prey population. There are also the more complicated structurally stable prey-predator mathematical models of type (1.1) which can explain persistent oscillations in a form of a sable limit cycle. Most popular of this type model is proposed in paper [5] as a system of differential equations (1.1) with

$$a(x) = r(1 - K^{-1}x), V(x) = mx(A + x)^{-1} \quad \text{and} \quad M(x) = -\delta + \gamma mx(A + x)^{-1}$$

Despite the plausible qualitative description of the dynamics of populations using different variants of equations (1.1), it can be argued that this equation describes the behaviour of predator-prey ecosystem only as an average. In contrast, real populations are subject to random perturbations, which do not allow population size to remain constant. This makes it necessary to consider possible random perturbations in analysis. For such cases, our paper offers a population dynamic modelling method that employs Markov dynamic impulse-type systems approach, allowing for discontinuity of trajectories at random time moments.

2 Stochastic approximation procedure

Let us formally describe the proposed predator-prey model. We assume that the dynamics of populations are not only determined by the system of equations (1.1), but also depend on the stationary Markov Poisson piecewise constant random process $\{\xi(t), t \geq 0\}$ defined by its infinitesimal operator [6]:

$$(Q_\varepsilon v)(z) = \frac{1}{\varepsilon}\int_0^1 (v(u) - v(z))du \qquad (2.1)$$

where ε is the small positive parameter. It means that if at the time $t_0 \geq 0$ process $\xi(t)$ is equal to $\xi(t_0) = z$, then in the time interval $t \in [t_0, t_0 + \tau)$, where τ has an exponential distribution with the parameter ε^{-1}, it maintains its value until the moment $t_0 + \tau$ when the process jumps to the value $\xi(t_0 + \tau) = \eta$, where η is independent on τ uniformly on the segment [0, 1] distributed random variable. The random variables τ and η do not depend on history of the process $\{\xi(s), s \leq t\}$. Consequently, for small $\varepsilon > 0$ dynamical characteristics of the predator-prey system change very frequently. These changes happen only at the discrete random time moments $t \in \{\tau_k, k \in N\}$. The length of intervals $\tau_k - \tau_{k-1}$ have the exponential distribution with the parameter $\lambda = \varepsilon^{-1}$. Our model for dynamics of predator-prey populations is given as

- the differential equations for time intervals $\tau_{k-1} \leq t < \tau_k$;

$$\frac{dx(t)}{dt} = a(x(t))x(t), \quad \frac{dy(t)}{dt} = [-\delta + M(x(t))]y(t); \qquad (2.2)$$

- the conditions of jumps for $t \in \{\tau_k, k \in N\}, k \in \mathbf{N}$:

$$x(t) = x(t-) - \varepsilon y(t)G(\xi(t-), x(t-))$$ (2.3)

where, $G(\xi, x)$ and $M(x)$ are nonnegative and

$$\mathbf{E}\{G(\xi(t), x)\} \equiv \int_0^1 G(z, x)dz = V(x), \mathbf{E}\{| G(\xi(t), x)|^2\} \equiv D(x).$$

Probabilistic properties of phase coordinates $\{x(t+s), y(t+s), s \geq 0\}$ are independent of the history of these processes before the time t. Therefore, a vector stochastic process $\{x(t), y(t), t > 0\}$ possesses the Markov property and its probability characteristics are completely determined by the infinitesimal operator [6]:

$$(L(\varepsilon)v)(x, y) := \lim_{s \downarrow 0} \frac{1}{s}[\mathbf{E}\{v(x(t+s), y(t+s)) / v(x(t) = x, y(t) = y\} - v(x, y)]$$ (2.4)

where $v(x, y)$ is a bounded and continuously differentiable function. The previous formula shows the dependence of the infinitesimal operator on the small parameter ε that defines the intensity of contacts between predator and prey. If $\tau \geq s$, there is no contact between predator and prey species in the time interval $[t, t+s)$. Therefore, under condition $x(t) = x, y(t) = y$ the increments on this interval are as follows: $x(t+s) - x(t) = sxa(x) + o(s)$, $y(t+s) - y(t) = s[-\delta + M(x)]y + o(s)$. If $\tau < s$, then in the time interval $(t, t+s)$ one contact between predator and prey individuals will take place and $x(t+s) - x(t) = sxa(x) - \varepsilon yG(\xi(t-), x) + o(s)$After substitution of these increments into formula (2.4) we can define the weak infinitesimal operator for the Markov process defined by equations (2.2) - (2.3) as:

$$(L(\varepsilon)v)(x, y) = xa(x)\frac{\partial}{\partial x}v(x, y) + \varepsilon^{-1}E\{v(x - \varepsilon yG(\xi(t), x), y) - v(x, y)\} +$$

$$+[-\delta + M(x)\}]y\frac{\partial}{\partial y}v(x, y)$$

It can be shown that there exists a limit $\lim_{\varepsilon \to 0}(L(\varepsilon)v)(x, y) = \bar{L}v(x, y)$, where

$$\bar{L}v(x, y) = [xa(x) - yV(x)]\frac{\partial}{\partial x}v(x, y) + [-\delta + M(x)]y\frac{\partial}{\partial y}v(x, y)$$ (2.5)

The system of differential equations

$$\frac{d\bar{x}}{dt} = \bar{x}a(\bar{x}) - yV(\bar{x}), \frac{d\bar{y}}{dt} = [-\delta + M(\bar{x})]\bar{y}$$ (2.6)

has been proven [7] to be an averaged system for the initial Markov dynamical system and the deviations of the solutions of the Markov dynamical system (2.2) - (2.3) from the corresponding solutions of the equation (2.6) have an order of $\sqrt{\varepsilon}$. Therefore, we can present the solution of the equations (2.2) - (2.3) in the form of a sum

$$x(t) = \bar{x}(t) + \sqrt{\varepsilon}X_\varepsilon(t), \quad y(t) = \bar{y}(t) + \sqrt{\varepsilon}Y_\varepsilon(t)$$ (2.7)

and can proceed to the construction of a system of equations for two-dimensional Markov nonhomogeneous process $\{X_\varepsilon(t), Y_\varepsilon(t)\}$. In order to calculate infinitesimal operator for this process we have: $(\Lambda(\varepsilon)v)(X, Y) = (\Lambda(t)v)(X, Y) + O(\sqrt{\varepsilon})$, where

$$(\Lambda(t)v)(X,Y):=$$
$$= v'_X(X,Y)\left\{\left[a'(\overline{x}(t))\overline{x}(t)X + [a(\overline{x}(t))X - V(\overline{x}(t))]Y\right] - \overline{y}(t)V'(\overline{x}(t))\}X\right\} + \tag{2.8}$$
$$+ v'_Y(X,Y)\left\{XM'(\overline{x}(t))\}\overline{y}(t) + [-\delta + M(\overline{x}(t))\}Y]\right\} + \frac{1}{2}v''_{XX}(X,Y)\left(\overline{y}(t)\right)^2 D(\overline{x}(t))\},$$

and $v(X,Y)$ is an arbitrary twice continuous differentiable function with bounded derivative. As proven in [7], for a sufficiently small   the probabilistic characteristics of the process $\{X_\varepsilon(t),Y_\varepsilon(t)\}$ do not differ much from the corresponding characteristics of the Markov process $\{X(t),Y(t)\}$ defined by generator (2.8) on any finite time interval with the length of the order of $1/\sqrt{\varepsilon}$. By definition [6] the formula (2.8) corresponds to a two-dimensional diffusion Markov vector-process $\vec{X}(t):=\begin{pmatrix} X(t) \\ Y(t) \end{pmatrix}$, defined by the equation:

$$d\vec{X}(t) = A(\overline{x}(t),\overline{y}(t))\vec{X}(t)dt + \vec{b}(\overline{x}(t),\overline{y}(t))dw(t) \tag{2.9}$$

where

$$A(\overline{x}(t),\overline{y}(t)) = \begin{pmatrix} a'(\overline{x}(t))\overline{x}(t) + a(\overline{x}(t)) - \overline{y}(t)V'(\overline{x}(t)) & -V(\overline{x}(t)) \\ M'(\overline{x}(t))\overline{y}(t) & -\delta + M(\overline{x}(t)) \end{pmatrix}, \tag{2.10}$$

$$\vec{b}(\overline{x}(t),\overline{y}(t)) = \begin{pmatrix} \overline{y}(t)\sqrt{D(\overline{x}(t))} \\ 0 \end{pmatrix} \tag{2.11}$$

and $w(t)$ is a standard Wiener process. Using the definition [9] of the stochastic Ito differential equations we can derive the ordinary differential equation

$$\frac{d}{dt}Q(t) = A(\overline{x}(t),\overline{y}(t))\vec{X}(t) + \vec{X}(t)A^T(\overline{x}(t),\overline{y}(t)) + \vec{b}(\overline{x}(t),\overline{y}(t))\vec{b}^T(\overline{x}(t),\overline{y}(t)) \tag{2.12}$$

for covariance matrix of the solution of the equation (2.6).

3 Impulse type logistic equation

Suppose that the dynamics of the prey population $x(t)$ in absence of contacts with predators may be described by the logistic growth equation

$$\frac{dx(t)}{dt} = rx(t)(1 - K^{-1}x(t)). \tag{3.1}$$

This model assumes that in the absence of a predator the prey population has a potential carrying capacity $K > 0$ and develops according to the logistic law with an intrinsic growth rate $r > 0$. Predator and prey individuals interact at random, and these time moments of interaction $\mathrm{T}:=\{\tau_k, k \in N\}$ are discontinuities for the piece wise constant Poisson process with the infinitesimal operator (1.4). If the predator-prey contact occurs at time t and predator population size at that moment is $y(t)$, then the prey's population size drops by

$$x(t) - x(t-) = -\varepsilon y(t)g(\xi(t-))x(t-)) \tag{3.2}$$

where $g(\xi(t)) > 0$, $\mathrm{E}\{g(\xi(t))\} = \beta > 0$, $\mathrm{E}\{g^2(\xi(t))\} = b^2$. The dynamics of the predator population at any time continuously changes according to

$$\frac{dy(t)}{dt} = \left[-\delta + \gamma\beta x(t) \right] y(t) \tag{3.4}$$

where $\gamma > 0$. Later we will use the results of the previous section with $a(x) = rx(1 - K^{-1}x), M(x) = \gamma\beta x, G(\xi, x) = g(\xi)x$. The averaged dynamics of the predator-prey system may be given in the form of ordinary differential equations

$$\frac{d\overline{x}}{dt} = [r(1 - K^{-1}\overline{x}) - \beta\overline{y}]\overline{x}, \quad \frac{d\overline{y}}{dt} = \left(-\delta + \gamma\beta\overline{x} \right)\overline{y} \tag{3.5}$$

This dynamical system has 3 fixed points [8]:
- the saddle point $A_1 = (0,0)$;
- the point $A_2 = (K,0)$ that is asymptotically stable for $\delta > K\gamma\beta$ and a saddle for $\delta < K\gamma\beta$
- the point $A_3 = \left(\dfrac{\delta}{\gamma\beta}, \dfrac{r(\gamma\beta - K^{-1}\delta)}{\gamma\beta^2} \right)$ that has positive coordinates and for $\delta < K\gamma\beta$ is asymptotically stable.

Following these conclusions about the averaged system, we can analyse normalized deviations from the averaged trajectory

$$\left\{ X_\varepsilon(t+s), Y_\varepsilon(t+s) \right\} = \left\{ \varepsilon^{-1/2}(x(t+s) - \overline{x}(t+s)), \ \varepsilon^{-1/2}(y(t+s) - \overline{y}(t+s)) \right\} \tag{3.6}$$

using an approximation by the equation (2.9) with

$$A(x, y)) = \begin{pmatrix} r(1 - K^{-1}x)x - \beta y & -\beta x \\ \gamma\beta y & -\delta + \gamma\beta x \end{pmatrix}, \qquad \vec{b}(x, y) = \begin{pmatrix} bxy \\ 0 \end{pmatrix} \tag{3.7}$$

If $\delta > K\gamma\beta$, then [8] $\lim\limits_{t\to\infty} \overline{y}(t) = 0$, $\lim\limits_{t\to\infty} \overline{x}(t) = K$,

$$\lim\limits_{\to\infty t} A(\overline{x}(t), \overline{y}(t)) = \begin{pmatrix} -rK & -\beta K \\ 0 & \delta + \gamma\beta \end{pmatrix} := H, \quad \lim\limits_{\to\infty t} \vec{b}(\overline{x}(t), \overline{y}(t)) = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

and the eigenvalues of matrix H are negative. This means that the covariance matrix Q(t) defined by the equation (2.19) tends to zero and random oscillations at the neighbourhood of the equilibrium A_2 decay.

If $\delta < K\gamma\beta$ then [8] any solution of equation (3.5) tends to the equilibrium point A_3 and

$$\lim\limits_{t\to\infty} A(\overline{x}(t), \overline{y}(t)) = \hat{A} = \begin{pmatrix} -\dfrac{r\delta^2}{K\gamma^2\beta^2} & -\dfrac{\delta}{\gamma} \\ \dfrac{r(K\gamma\beta - \delta)}{K\beta} & 0 \end{pmatrix}, \quad \lim\limits_{t\to\infty} \vec{b}(\overline{x}(t), \overline{y}(t)) = \hat{b} = \begin{pmatrix} \dfrac{r(\gamma\beta - K^{-1}\delta)b}{\gamma^2\beta^3} \\ 0 \end{pmatrix}$$

Under assumption $\delta < K\gamma\beta$ the eigenvalues of matrix $\hat{A}$ are negative. This means that at a sufficiently small neighbourhood of the stable equilibrium point A_3 the process $\vec{X}(t)$, as defined by the equation (2.9), under zero initial condition is a diffusion process [8] with a covariance matrix $Q(t)$, as defined by equation (2.12). After further computations we may conclude that in the case of $\delta < K\gamma\beta$ the populations of the prey and the predator are stabilizing near the fixed

point A3 and probabilistic characteristics of deviations from this equilibrium may be approximately considered as independent normally distributed random variables with variances correspondingly

$$(\mathbf{D}_\varepsilon(t)) \quad \approx \varepsilon \frac{b\delta r^2(\gamma\beta - K^{-1}\delta)(2\gamma\beta + K^{-1}\delta)}{\gamma^3\beta^4} \quad , \quad \mathbf{D}_\varepsilon(y(t)) \approx \varepsilon \frac{b\delta r^2(\gamma\beta - K^{-1}\delta)^2(2\gamma\beta + K^{-1}\delta)}{\gamma^3\beta^5}$$

4 The random impulsive Holling type model

One of the most popular models of the dynamics of interacting predator and prey populations, such as those found within invertebrate and similar domains of life, in mathematical biology is the system of ordinary differential equations proposed in [5] and in detail analysed in [10]:

$$\frac{dx}{dt} = rx\left(1 - K^{-1}x\right) - \frac{mx}{A+x}y, \qquad \frac{dy}{dt} = \left(-\delta + \gamma\frac{mx}{A+x}\right)y \tag{4.1}$$

where phase variables x and y denote the density of prey and predator populations respectively. In this model it is assumed that in the absence of a predator the prey population has a potential carrying capacity K and develops according to the logistic law with an intrinsic growth rate r. In the absence of a prey the predator population exponentially decreases to zero with the intrinsic growth rate δ. The mutual influence of changes in the densities of the prey and predator in model (4.1) is considered by the trophic function $mxy(A+x)^{-1}$, where the positive parameter m is the consumption rate or prey per unit of time by the predator. The positive parameter A reflects the saturation of the amount of prey consumed and, in addition, depends on the rate of reaction of the predator, i.e., the time between attacks on the prey. The parameter γ in formula (4.1) is a conversion factor that determines the effect of the prey consumed on the growth rate of the population of the predator. The model (4.1) is popular because under certain assumptions about positiveness of parameters r, K, m, A, δ and γ it is structurally stable [2] with a unique asymptotically stable periodic trajectory. In this section we propose an impulsive Markov type model (2.2) - (2.3) with

$$a(x) = r\left(1 - K^{-1}x\right), M(x) = \gamma\frac{mx}{A+x}, G(\xi, x) = \frac{q(\xi)x}{A+x} \tag{4.2}$$

where $q(\xi(t)) \geq 0, \mathrm{E}\{q(\xi(t))\} \equiv m > 0, \quad \mathrm{E}\{q^2(\xi(t))\} \equiv \sigma^2$, that makes it possible to take into account the stochastic character of the trophic function considered in the Holling type II model (4.1). Substituting

$$a(x) = r\left(1 - K^{-1}x\right), \int_0^1 G(z, x)dz = V(x) = \frac{mx}{A+x}, M(x) = \frac{\gamma mx}{A+x} \tag{4.3}$$

into the equation (2.8), the average population dynamics $\{\overline{x}(t), \overline{y}(t)\}$ may be analysed by that equation (4.1), and [7] for any positive number T and M there exists such positive numbers ε_0 that

$$\sup_{t < T\varepsilon^{-1}} \mathbf{E}\{|x_\varepsilon(t) - \overline{x}(t)| + |y_\varepsilon(t) - \overline{y}(t)|\} \leq M\varepsilon \tag{4.4}$$

for all $\varepsilon < \varepsilon_0$. As shown in [10,11], the system of equations (4.1) with the parameter values $m=5$, $A=18$, $\gamma=2$, $\delta=4$ has a unique asymptotically stable periodic trajectory, which corresponds to initial values $\bar{x}(0)=20, \bar{y}(0)=3$.
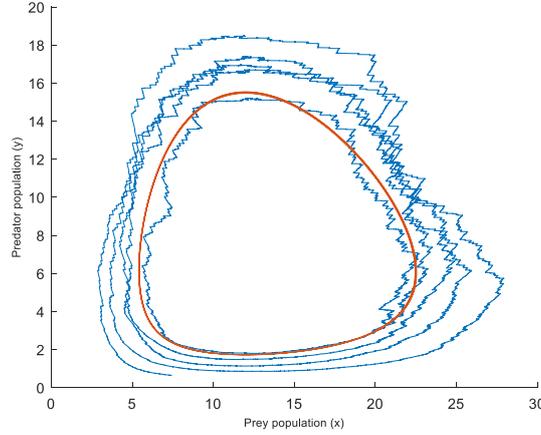
Fig. 4.1. Phase trajectory of Markov process (2.2) - (2.3) - (4.1) and the limit cycle.

In Figure 4.1 the trajectory shows the solution of the system of equations (2.2) - (2.3) - (4.1) for $\varepsilon = 0.01$ corresponding to the initial conditions above, and defined by equation (4.1) limit cycle. We may approximate the normalized deviations from the averaged trajectories

$$X_\varepsilon(t) = \frac{x_\varepsilon(t) - \bar{x}(t)}{\sqrt{\varepsilon}}, Y_\varepsilon(t) = \frac{y_\varepsilon(t) - \bar{y}(t)}{\sqrt{\varepsilon}} \qquad (4.5)$$

by the vector solution $\vec{X}(t) := \begin{pmatrix} X(t) \\ Y(t) \end{pmatrix}$ of the equation (2.9)

$$d\vec{X}(t) = A(\bar{x}(t), \bar{y}(t))\vec{X}(t)dt + \vec{b}(\bar{x}(t), \bar{y}(t))dw(t) \qquad (4.6)$$

Where

$$A(\bar{x}, \bar{y}) = \begin{pmatrix} \left(1 - \dfrac{2}{K}\bar{x}\right)r - \dfrac{A\bar{y}m}{\left(A + \bar{x}(t)\right)^2} & -\dfrac{\bar{x}m}{A + \bar{x}} \\ \gamma\bar{y}\dfrac{mA}{\left(A + \bar{x}\right)^2} & -\delta + \gamma\dfrac{\bar{x}m}{A + \bar{x}} \end{pmatrix}, \qquad (4.7)$$

$$\vec{b}(\bar{x}, \bar{y}) = \sigma \begin{pmatrix} \sqrt{\dfrac{\bar{y}\bar{x}}{2\left(A + \bar{x}\right)}} \\ 0 \end{pmatrix} \qquad (4.8)$$

and there are zero initial conditions. The covariance matrix $Q(t)$ for the process $\vec{X}(t)$ is the matrix solution of a system of ordinary differential equations

$$\frac{d}{dt}Q(t) = A(\bar{x}(t), \bar{y}(t))Q(t) + Q(t)A^T(\bar{x}(t), \bar{y}(t)) + \vec{b}(\bar{x}, \bar{y})\vec{b}^T(\bar{x}, \bar{y})$$

Now we can approximate the finite dimensional distributions of the process $\{x_\varepsilon(t), y_\varepsilon(t)\}$ by the corresponding distributions of the process $\{\tilde{x}_\varepsilon(t) = \bar{x}(t) + \sqrt{\varepsilon}X(t), \tilde{y}_\varepsilon(t) = \bar{y}(t) + \sqrt{\varepsilon}\ Y(t)$

However, the variances of the normalized deviations increase very rapidly. For example, $\mathrm{E}\{|X(20)|^2\}=10000$ but the aforementioned cycle ordinate does not exceed the value 25.

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