ON PREDATOR-PREY POPULATION DYNAMICS UNDER STOCHASTIC SWITCHED LIVING CONDITIONS

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Abstract. The dynamical system theory has been extensively used in the contemporary ecology. Such theory is used to describe biological systems and their main features, to predict their behaviour under certain conditions, to find suitable explanations to biological phenomena, etc. [1; 2]. One of the advantages of the mathematical design is that models can depend only on a small number of parameters, still possessing capacity to describe biological systems adequately [3]. There are several types of mathematical models that are used. The most commonly applied type of models is differential and difference equations that describe dynamics of populations of given species [4]. Such models can serve as powerful tools to describe theoretical features of dynamics of populations. However, detailed data that allow estimation of parameters for such models are not always available [3; 5]. Another type of models is developed via implementation of Markov chains that describe stochastic dynamics of populations of given species [6; 7]. Parameters of such models can be estimated based on census data on the number of species that are usually more available [3]. Obviously, such models incorporate stochastic nature of life environments and stochastic nature of regulation processes [8]. Here we show how differential models can be extended to describe both underlying deterministic population dynamics and stochastic transitions between the observed states. To perform our proposal approach we deal with the classic Lotka-Volterra equation for the dynamics of predator-prey system analysis. Assuming stochastic switching for some parameters we analyze this dynamical system as the ergodic Markov chain. Applying statistical approach jointly with MATHEMATICA, R, and MATLAB as the statistical software tools, we estimate the Markov transition probabilities and parameters of the steady-state stationary distribution. Our mathematical design can be used to explore both theoretical features of mathematical models and their compliance with the real data.

Keywords: dynamical systems, stochastic switching, Lotka-Volterra equations.

Introduction

Dynamical system theory has been successfully applied to describe various biological systems, to predict and explain their behavior [1; 3]. Commonly used mathematical models are deterministic difference and differential equations. However, during the past years both theoretical biologists and practitioners have claimed that deterministic models do not necessarily describe biological systems properly and further investigation was needed [9-11]. One of the obvious improvements is consideration of the stochastic nature of biological systems and their habitats [9; 12]. Stochastic dynamics of biological systems has been observed in practice [8; 13] and various approaches for modeling have been offered [12]. Usually such models are assumed to be memoryless or markovian [12]. Markovian models are used to describe stochastic transitions between the finite number of system's states. The advantage of such models is that their parameters can be estimated based on census data which are usually more available [3]. Moreover, stochastic switching between several states of biological system is observed in practice [13]. Here we describe how deterministic differential models can be extended to incorporate the stochastic nature of the biological systems and capture both underlying deterministic dynamics and stochastic transitions between several observed states. We use classic predator-prey Lotka-Volterra equations and incorporate stochastic switching of the model parameters. Lotka-Volterra equations are a well-known model that was extensively studied and improved [14], and used to describe real-world data [15]. However, some criticism of deterministic Lotka-Voltera system was also proposed and further improvements were offered [10; 16]. We analyze the system as the ergodic Markov chain and apply statistical modeling jointly in MATHEMATICA, R and MATLAB to estimate Markov transition probabilities and steady-state distributions. Our mathematical design can be used to explore both theoretical features of mathematical models and their compliance with the real data.

Model description

Lotka-Volterra deterministic differential equations are commonly used to describe predator-prey, competition and other interactions between two populations. Throughout the paper we use the following form of the equations

$$\begin{cases} \dfrac{dx_1}{dt} = x_1(a_1 - b_{11}x_1 - b_{12}x_2) \\ \dfrac{dx_2}{dt} = x_2(a_2 - b_{21}x_1 - b_{22}x_2) \end{cases}, \quad (1)$$

where x_1 is the total number of predator species, x_2 is the total number of prey species. Terms a_1 and a_2 describe propagation of species, terms b_{11} and b_{21} describe completion within same populations, terms b_{12} and b_{22} describe interaction between two populations.

Consequently, parameters a_1, a_2, b_{11}, b_{21} and b_{22} are chosen to be positive and parameter b_{12} is chosen to be negative. Deterministic Lotka-Volterra system has four equilibrium states, of which we are interested in stable focus that corresponds to stable coexistence of two populations:

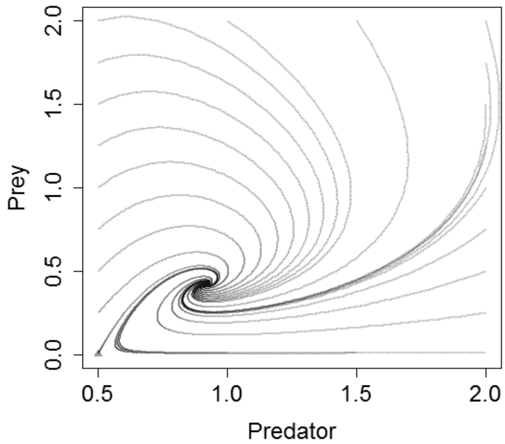

Fig. 1. **Phase plot for deterministic Lotka-Volterra system with stable focus**

Location of the focus depends on the chosen parameters of the system and is given by the formula

$$u_1 = \frac{a_1 b_{22} - a_2 b_{12}}{b_{11} b_{22} - b_{12} b_{21}}, \quad u_2 = \frac{a_2 b_{11} - a_1 b_{21}}{b_{11} b_{22} - b_{12} b_{21}} \quad (2)$$

where we assume that $b_{11}b_{22} - b_{12}b_{21} \neq 0$.

The parameters of the model that are used in the formula have a definite meaning, i.e. a_1 and a_2 are the rates at which predator and prey species propagate, etc. These parameters are determined by internal and external factors for two populations. Here we assume that external factors, such as weather conditions or human interference possess stochastic nature. For the sake of simplicity, we assume that external factors can be only in one of the two states, switching between these two states at random moments in time. That is, we assume that the parameters of the model switch between two following sets of values:

Table 1

Two sets of possible values of system parameters

Set 1	**Set 2**
a_1= A$_1$, a_2= A$_2$, b_{11}= B$_{11}$, b_{21}= B$_{21}$, b_{22}= B$_{22}$, b_{12}= B$_{12}$	a_1= C$_1$, a_2= C$_2$, b_{11}= D$_{11}$, b_{21}= D$_{21}$, b_{22}= D$_{22}$, b_{12}= D$_{12}$

If at the first moment the system was described by Set 1, after some time it switches to Set 2, then again to Set 1 and so on. Obviously, between the switching moments the system is non-random, it is described by deterministic Lotke-Voltera model and has stable focus as one of the equilibrium states. Thus, modeling used is described by the following scheme:

Table 2

Modeling scheme

Step1	Step 2	Step 3	Step 4	…
Solve deterministic Lotka-Volterra equation with parameters from Set 1	Change parameters from Set 1 to Set 2	Solve deterministic Lotka-Volterra equation with parameters from Set 2	Change parameters from Set 2 to Set 1	…

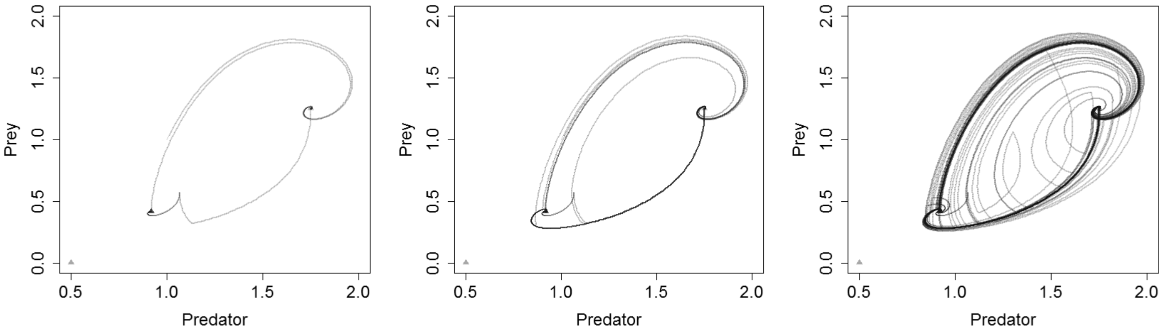

Fig. 2. **Phase plot for different number of switching times (from left to right: 5 switchings, 16 switchings, 100 switchings)**

"Fig. 2" shows phase plots for increasing number of switching times (with same set values). It can be clearly seen that equilibrium state jumps between two points and system moves toward current equilibrium state between the switching times. Time between switching is assumed to have exponential distribution with parameter c:

$$P\{t > z\} = e^{-\frac{z}{c}}. \tag{3}$$

The average time between the moments of switching is equal to c (inverse of the coefficient in the exponent). We assume that mean time c is large enough so that the system has time to reach small epsilon region of the equilibrium states. That is, $c >> T$ where T is relaxation time of the system and the system spends most of the time near equilibrium states.

Definition of the Markov chain

We define states of the Markov chain in the following manner. We choose two rectangle regions around the equilibrium states and define Markov chain states as the number of the region:

$$\begin{aligned} &Markov\ chain\ state = 1,\ if\ r \in \Pi_1 \\ &Markov\ chain\ state = 2,\ if\ r \in \Pi_2\ , \\ &Markov\ chain\ state = 3,\ else \end{aligned} \tag{4}$$

where r is a location of the system, Π_1 is the first rectangle and Π_2 is the second rectangle (Fig. 3).

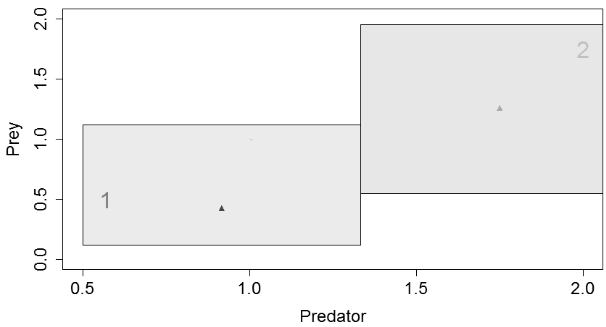

Fig. 3. **Regions that define Markov chain states:** region 1 = area inside left rectangle; region 2 = area inside right rectangle

Markov chain states are defined as the number of the region when the system is located at a stationary regime. That is, states of the Markov chain are defined only when the system reaches stationary mode. The idea behind such definition is as follows. If the system with described switching is observed during a long period of time, stationary regime should be reached. We record locations of the system with time intervals equal to c, assuming that the system is observed in discrete moments in time. As a result of the modeling with switching moments we obtain the sequence of the Markov chain states

$$1, 3, 3, 2, 3, 1, 3, 1, 2, 1, 3, 1, 1, 3, 1 \ldots \quad (5)$$

The obtained sequence form the Markov chain properties of which can be studied via modeling.

Modeling procedure

The system depends on the following.

S1) Parameters of the Lotka-Volterra system a_1, a_2, b_{11}, b_{21}, b_{22} and b_{12}.

S2) Rectangles Π_1, Π_2 that define regions on phase plot and respective Markov chain states ("Fig. 3").

S3) Average time c between switching (check formula 3)

Modeling of the system depends on the following.

S4) Values chosen in S1)-S3)

S5) Time step value dt used for modeling (it should be $dt << c$ so that the system has time to reach epsilon-region of the equilibrium state)

S6) Number of switching moments N.

As a result of modeling the sequence of the Markov chain states (formula 5) are obtained and can be used to estimate transition probabilities:

$$\hat{P} = \begin{bmatrix} \hat{p}_{11} & \hat{p}_{12} & \hat{p}_{13} \\ \hat{p}_{21} & \hat{p}_{22} & \hat{p}_{23} \\ \hat{p}_{31} & \hat{p}_{32} & \hat{p}_{33} \end{bmatrix}. \quad (6)$$

Probabilities are calculated as follows

$$\hat{p}_{ij} = \frac{n_{ij}}{n_{i1} + n_{i2} + n_{i3}}; \; i, j \in \{1,2,3\}, \quad (7)$$

where n_{ij} is the total number of transactions from state i to state j in the sequence (5).

In addition, empirical distributions of x_1 and x_2, and two-dimensional distribution of (x_1,x_2) at the switching moments can be obtained and investigated.

Modeling results

Here we present the modeling results. The modeling procedure is as follows. First we choose two sets of values for system parameters, average time between the switching moments c, rectangles Π_1, Π_2, time step dt, number of the switching moments N. Next we generate N time intervals that have exponential distribution and sum those up to get the total modeling time. Third, we simulate the system, switching parameters between sets as long as the time reaches the next switching interval. We assume that the system reaches stationary mode as long as half modeling time has passed. For the stationary regime we record Markov chain states and locations of the system with time intervals equal to c, assuming that the system is observed in discrete moments in time. We plot phase plot, histograms of x_1 and x_2, Markov chain transition matrices and two-dimensional distribution of (x_1, x_2).

Test 1. Parameters of the model are chosen to switch between two following sets of values (all the parameters except a_2 do not change)

Table 3

Two sets of values of parameters for Test 1

Set 1	Set 2
a_1= 0.1, a_2= 0.4, b_{11}= 0.2, b_{21}= 0.4, b_{22}= 0.08, b_{12}= -0.2	a_1= 0.1, a_2= 0.8, b_{11}= 0.2, b_{21}= 0.4, b_{22}= 0.08, b_{12}= -0.2

Thus, location of the first equilibrium focus (Formula 2, Set1)

$$u_1 = 0.917$$
$$u_2 = 0.417 \quad (8)$$

and

$$u_1 = 1.75$$
$$u_2 = 1.25 \quad (9)$$

for the second equilibrium focus (Set 2).

Other parameters where chosen as follows: c = 40; dt = 0.1; N = 1000; set.seed(20).

Phase plot for Test 1 is given in Fig. 4.

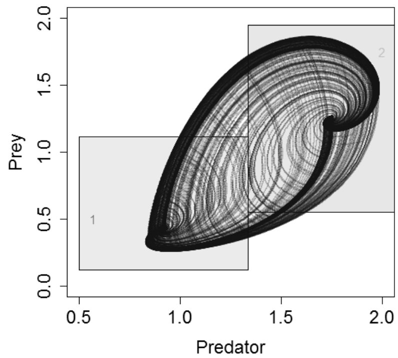

Fig. 4. **Phase plot for Test 1 (c=40, N=1000)**

Empirical distributions of the system locations are given by the following histograms are given in Fig. 5. Two-dimensional distribution is given in Fig. 6.

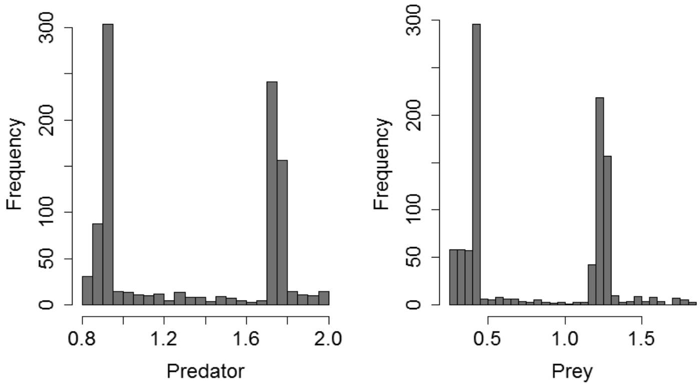

Fig. 5. **Empirical distribution of x_1(left) and x_2(right)**

Estimated matrix with transition probabilities is given by

$$\hat{P} = \begin{bmatrix} 0.58 & 0.40 & 0.02 \\ 0.40 & 0.56 & 0.04 \\ 0.53 & 0.44 & 0.03 \end{bmatrix}. \quad (10)$$

Eigen values are λ_1 = 1.0, λ_2 = 0.165 and λ_3 = 0.0042. As λ_1 is the only vector with property $|\lambda| = 1$ Markov chain is ergodic. Left eigenvector that corresponds to λ_1 is

$$x_\lambda = \begin{bmatrix} 0.490 & 0.478 & 0.032 \end{bmatrix}^T \quad (11)$$

and defines stationary distribution.

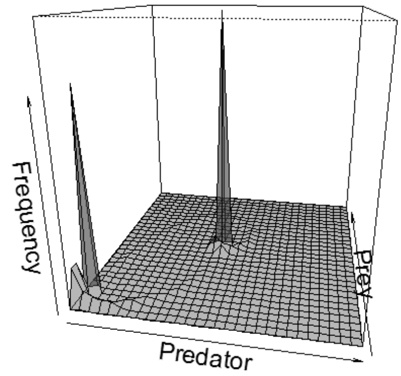

Fig. 6. Two-dimensional distribution for (x_1, x_2) (c=40, N=2000)

Test 2. Parameters are chosen as for Test 1, except parameters c and N. Here we choose c = 80, N = 500. Phase plot for Test 2 is given in Fig. 7.

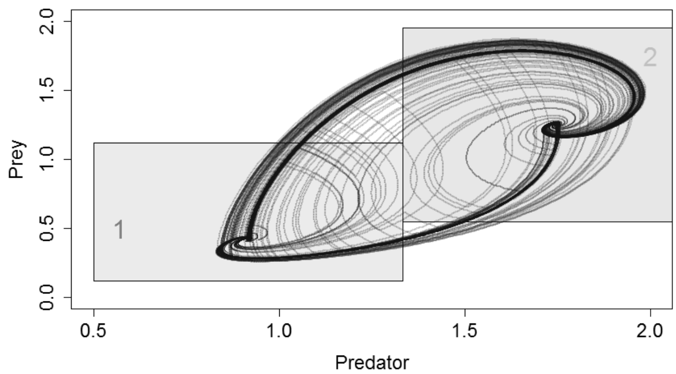

Fig. 7. **Phase plot for Test 2 (c=80, N=500)**

Empirical distributions of the system locations are given by the following histograms (Fig. 8). Two-dimensional distribution is given in Fig. 9.

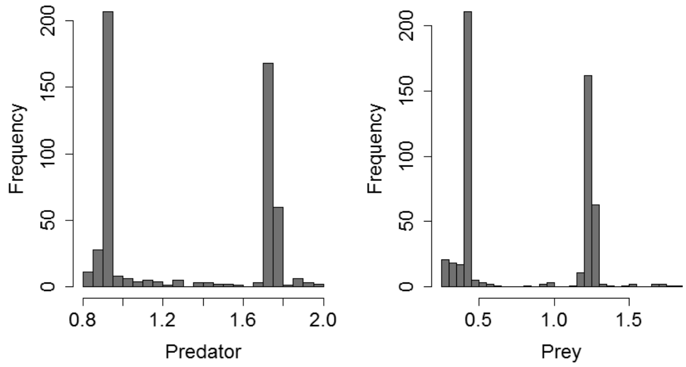

Fig. 8. **Empirical distribution of x_1(left) and x_2(right) at switching moments**

Estimated matrix with transition probabilities is given by

$$\hat{P} = \begin{bmatrix} 0.59 & 0.39 & 0.02 \\ 0.44 & 0.55 & 0.02 \\ 0.44 & 0.56 & 0.00 \end{bmatrix}. \quad (10)$$

Eigen values are λ_1 = 1.0, λ_2 = 0.154 and λ_3 =-0.016. As λ_1 is the only vector with property $|\lambda| = 1$ Markov chain is ergodic. Left eigenvector that corresponds to λ_1 is

$$x_\lambda = [0.51 \quad 0.47 \quad 0.02]^T \tag{11}$$

and defines stationary distribution.

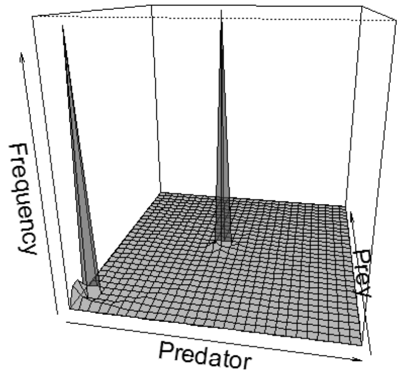

Fig. 9. **Two-dimensional distribution for (x_1, x_2) (c=40, N=2000)**

Results and discussion

Here we describe and discuss the results of modeling. We used Lotke-Volterra predictor-prey equations and modeled it with stochastic switching between the system parameters. Switching moments where assumed to have exponential distribution. We selected two rectangle areas around equilibrium focuses that defined Markov chain states. We studied empirical distribution of the system location and transition probabilities of the Markov chain.

As we can see from Tests 1 and 2, the obtained Markov chains were ergodic with stationary distributions. Markov chain matrices with transitional probabilities can be used as follows. There are two states of the dynamical system and it switches between these states at random. The states are defined as constraints on the number of species: the system is in the state 1/2 if the number of prey is from A to B and the number of predators is from C to D, where A, B, C and D are numbers that define rectangles Π_1, Π_2. Analysis of the Markov chain can be used to obtain transitional probabilities between given states and stationary distribution. For both tests described here stationary distributions show that the system spends approximately the same amount of time in each of the states. That is, approximately half of the time the system spends in state 1 and half in state 2, with minor part of the time the system being observed in intermediate state 3.

Empirical distributions of x_1 and x_2 cannot be described with commonly used theoretical distributions but possess some important graphical features. Qualitatively there are hikes in empirical density around equilibrium states, assuming that there are two small regions where the system stays most of the time. Assumption is confirmed by investigation of empirical two-dimensional distribution of (x_1, x_2).

Conclusions

1. The modeling procedure shows that implementation of stochastic switching into the Lotke-Voltera predator-prey equations leads to the ergodic Markov chain.
2. Empirical distributions of the system location show that there are two regions around equilibrium states where the system is located most of the time.
3. Stationary distribution of the obtained Markov chain shows that for the described tests approximately half of the time the system spends in one of the equilibrium states. Thus, the system is likely to be observed in any of the equilibrium states.

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