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Individual based modeling and parameter estimation for a Lotka–Volterra system

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Abstract

Stochastic component, inevitable in biological systems, makes problematic the estimation of the model parameters from a single sequence of measurements, despite the complete knowledge of the system. We studied the problem of parameter estimation using individual-based computer simulations of a 'Lotka–Volterra world'. Two kinds (species) of particles – X (preys) and Y (predators) – moved on a sphere according to deterministic rules and at the collision (interaction) of X and Y the particle X was changed to a new particle Y. Birth of preys and death of predators were simulated by addition of X and removal of Y, respectively, according to exponential probability distributions. With this arrangement of the system, the numbers of particles of each kind might be described by the Lotka–Volterra equations. The simulations of the system with low (200–400 particles on average) number of individuals showed unstable oscillations of the population size. In some simulation runs one of the species became extinct. Nevertheless, the oscillations had some generic properties (e.g. mean, in one simulation run, oscillation period, mean ratio of the amplitudes of the consecutive maxima of X and Y numbers, etc.) characteristic for the solutions of the Lotka–Volterra equations. This observation made it possible to estimate the four paramters of the Lotka–Volterra model with high accuracy and good precision. The estimation was performed using the integral form of the Lotka–Volterra equations and two parameter linear regression for each oscillation cycle separately. We conclude that in spite of the irregular time course

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of the number of individuals in each population due to stochastic intraspecies component, the generic features of the simulated system evolution can provide enough information for quantitative estimation of the system parameters.

Keywords: Prey–predator interactions; Computer simulations; Continuous space-time; Sphere; Small population

1. Introduction

Simple mathematical models are often used to demonstrate some qualitative features of biological systems and processes. However, they can only occasionally be applied for quantitative description of biological phenomena. Even if an appropriate simple biological system is known or experimentally created, the problem of parameter estimation from, as a rule, strongly perturbed data is difficult to solve. The same problem occurs during analysis of more complex systems. Theoretical studies of the effect of different kinds of perturbations on the kinetics of the system can be now based on computer simulations of interacting individuals within an artificial world created by a computer program. This approach is often called molecular or particle modeling if applied for the description of physical, chemical or biochemical systems, or individual-based simulations if applied for population dynamics studies [1–5]. The modeling consists of: (1) representation of individuals by moving particles in an artificial world specified by a computer program, (2) setting the rules for their movement and interactions as well as for their birth and death, (3) description of the initial state of the world, (4) running the program. The results of the simulations can be analyzed using global (macro-) variables which are defined for the system as a whole. Then, mathematical descriptions of the system can be tested and problem of the parameter estimation can be analyzed. In this way, microparameters concerning individuals and their behavior are defined for the system. Then, by using the results of computer simulations a mathematical model which describes the kinetics of the populations can be studied, relationships between micro- and kinetic macro-parameters included.

This approach was applied for the system of the Lotka–Volterra type of dynamics. The Lotka–Volterra system is the basic example for non-linear oscillations in biology. The differential equations were introduced to describe the interaction between prey and predator populations in ecology, and later they were generalized and analyzed in many different ways [6–8]. Some modifications of the basic 'prey–predator' system were also used for the description of the immune system and in mathematical epidemiology [6,9,10]. The classic Lotka–Volterra equations may also be used for the description of a hypothetical chemical reaction [11,12].

We defined the system as a set of two kinds ('species') of particles moving according to deterministic rules on a sphere. They interacted at the moment of collision and were added (born) or removed ('dying') according to the probabilistic rules. Thus, the system combined deterministic and stochastic kinetic components. As a result, the behavior similar to that obtained in stochastic modeling with fluctuating oscillations of the number of particles in each species and occasional extinction of one of the species was revealed [13,14]. The computer system was designed to provide a simple representation for the interactions described by the Lotka–Volterra equations rather than to describe a particular real biological system of populations.

2. Computer model

The individuals were represented by small spherical caps (of angular diameter 0.004) moving on a sphere of unit radius along arcs of great circles of the sphere with constant angular velocities. This motion is analogous to the motion of particles with constant velocity along straight lines on a plane. The analogy comes from the fact that great circles are geodetics on the sphere, i.e. an arc of the great circle which passes through two points is the shortest pathway on the sphere between these points. The modeling of individual movements is often performed on a square. However, in this case the boundary conditions for the particles must be defined [3,4]. For example, the condition of bouncing (elastically or at random) from the edge of the square or cyclic behavior at the boundary can be applied. In the later the geometry of the surface is in fact that of a torus. The application of a sphere is a solution for the problem: no boundary conditions are necessary and the description of particle movement is relatively simple (comparing e.g. to the motion on a torus).

The movement of individuals within their world is often described as random redistribution over the whole world at discrete time intervals [3], diffusion, i.e. random movement over the lattice with discrete clock [3], or deterministic movement over a lattice with discrete clock [2,4]. In our study we applied continuous in time determininstic movement of particles.

There were two kinds of individuals: X – preys and Y – predators. The same unit mass was attributed to both kinds of particles. At any collision of the particles the new directions and velocities were calculated using the momentum and kinetic energy conservation laws. At the collision of X and Y the particle X was turned into a new particle Y. This interaction rule is probably the simplest interpretation for the Lotka–Volterra equations, although it resembles more a chemical reaction in a gas than any of biological interactions. Nevertheless, it is quite useful for the purpose of this study, because no 'hidden' (i.e. not described by the classic Lotka–Volterra equations) feature of the individuals and their interactions is involved.

The state of each particle was specified by three orthonormal, three-dimensional vectors of real numbers: **r**, **v**, **w**, and by a real number ω. The vectors **r** and **v** specified the position of the center of the particle and the direction of its movement, respectively, while $\mathbf{w} = \mathbf{r} \times \mathbf{v}$ was an auxiliary vector, invariant during the movement of the particle between its consecutive collisions; ω described the angular velocity of the particle.

The movements of all particles can be traced by solution of position and velocity equations. An equivalent, simpler and faster, method was used in our simulations. It was possible to apply this method, because there are no interactions between particles except at the moment of their collision. Free motion along a great circle was described as

$$\begin{aligned} \mathbf{r}(t) &= \mathbf{r}(0)\cos(\omega t) + \mathbf{v}(0)\sin(\omega t), \\ \mathbf{v}(t) &= \mathbf{r}(0)\sin(\omega t) + \mathbf{v}(0)\cos(\omega t) \end{aligned} \tag{2.1}$$

The condition for the collision of two particles A and B was

$$\Theta(t_z) = \Theta_d, \tag{2.2}$$

where $\Theta(t)$ is the angle between A and B at time t, t_z is the collision time, and Θ_d is the angular diameter of the particle. For $\Theta(t)$ the following equations was derived:

$$\begin{aligned} \cos(\Theta(t)) = 0.5[&(\gamma_1 + \gamma_4)\cos(\Psi_A - \Psi_B) + (\gamma_3 - \gamma_2)\sin(\Psi_A - \Psi_B) \\ &+ (\gamma_1 - \gamma_4)\cos(\Psi_A + \Psi_B) + (\gamma_3 - \gamma_2)\sin(\Psi_A - \Psi_B)], \end{aligned} \tag{2.3}$$

where $\gamma_1 = \mathbf{r}_A \cdot \mathbf{r}_B$, $\gamma_4 = \mathbf{v}_A \cdot \mathbf{v}_B$, $\gamma_3 = \mathbf{v}_A \cdot \mathbf{r}_B$, $\gamma_2 = \mathbf{r}_A \cdot \mathbf{v}_B$, $\Psi_A = \omega_A t$, $\Psi_B = \omega_B t$. Numerical solution of equation $\Theta(t) = \Theta_d$ yielded the collision time t_z. The collision time for each pair of particles was found and put to the list of collisions if it was lower than a predetermined limit time. The position of the collision on the list depended on the time of its occurrence. Then the positions of all particles at the time of the first collision were calculated using Eq. (2.1), the new velocities for the colliding particles were calculated, the possible collisions of these two particles with other ones were found as described above and added to the list of collisions if their times were lower than the limit time, and, if the particles were of different kinds, X was turned to Y. Then the program realized the same cycle of operations for the next collision on the list.

To accelerate the analysis of possible collisions the sphere was partitioned into 128 segments of approximately equal surface area, and an appropriate time limit was defined. All collisions between particles within each segment were examined and added to the list of collisions if the time to collision was less than the time limit. Then, the possibility of collisions between particles which occupied each pair of segments within time interval not longer than the time limit was analyzed. If such collisions were not possible for a pair of segments, the equations for the particles from these two segments were not solved.

Otherwise, all collisions with the time to collision less then time limit were found and added to the list of collisions.

Additions of X and deletions of Y were done at random at the moment of each collision, and the exponential probability distributions were assumed as follows:

$$p_X(t) = \alpha_X \exp(-\alpha_X t), \tag{2.4}$$

$$p_Y(t) = \alpha_Y \exp(-\alpha_Y t) \tag{2.5}$$

for the two events, respectively. Thus, for each particle the casting for its multiplication/removal was done with the probability given by the integral of the respective probability distribution over the period $(0, t_z)$, i.e. the probability was $P_X(t_z) = 1 - \exp(-\alpha_X t_z)$ and $P_Y(t_z) = 1 - \exp(-\alpha_Y t_z)$ for the two events, respectively. For the death events this probability follows also from the Poisson process, whereas for the birth events it may be considered as an approximation for the Poisson process if t_z is small and therefore the probability for multiple birth is negligible. The position of the added particle was randomly selected in the vicinity of the 'mother' particle. The angular velocity of the added particle was equal to the value ω_0 attributed to the particles of the initial state (see Section 3), and the direction of its velocity vector was selected at random. The possible collisions of the added particles were evaluated and added to the collision list, and the collisions of the removed particles were deleted from the list of collisions. The procedure of the addition/removal of particles was performed at the moment of each collision just to simplify the computer program (alternatively, one may perform this procedure at a regular short time interval with a constant probability for the events). As shown in additional simulations the applied procedure yields exponential patterns for X growth and Y decay (see e.g. simulations 130 and 132 described in Section 4).

The time of each collision as well as the numbers of X and Y particles were recorded for further analysis.

The method applied provides a simple continuous in time description of the movements of the particles on a continuous two-dimensional manifold. The method is an alternative to the often used discrete network of the positions of particles with discrete time clock.

3. Computer simulation of population kinetics

The initial number of particles were 200 or 400 with equal number of X and Y. The particles were distributed randomly on the sphere, with the same angular velocity, ω_0, and randomly selected direction of velocity vector. An auxiliary run of the computer program was performed with no interaction between X and Y, no additions of X and no deletions of Y, to get the steady

state distribution of particle velocities. Only then the values for the probability distributions parameters, α_X and α_Y (see Eqs. (2.4) and (2.5)), were defined, and the main computer program was run as described in Section 2.

A series of computer simulations were carried out for various values of ω_0 and various values of α_X and α_Y (Table 1). Unstable oscillations with variable amplitudes and time period were observed (Figs. 1 and 2). The Y population changes followed always the X population changes with some time delay. Small fluctuations in particle number around the main trend were observed (Fig. 1, lower panel). Some of simulation runs finished with the extinction of X or Y population, sometimes already after 1–2 cycles. Other simulations continued for long time, until terminated by the operator after 50–70 oscillation cycles. The time course of the simulation depended strongly on the random events in the system (birth of X and death of Y). This is demonstrated in Fig. 2(A) and (B), where two simulations with the same set of microparameters and the same initial state of the system (number of particles in each kind, their positions and velocities) but different setup of the random number generator are shown. However, there was also another factor which influenced the evolution of the system: the initial state (positions and velocities) of the particles. In Fig. 2(C) simulations with the same microparameters and the sequence of the random numbers as for the one in Fig. 2(A) but different initial states of the particles is shown. The oscillations in this simulation formed still another pattern than those shown in Fig. 2(A) and (B).

The amplitudes of the oscillations varied a lot during all simulations but some relatively constant characteristic features of the observed patterns were found. Some of them are listed in Table 1 for seven of our simulations. The parameters, which characterized the oscillations, were calculated for each oscillation cycle separately, and the mean values and standard deviations for each of the simulations are shown in Table 1. The oscillation cycle was defined to be from a peak of X to the consecutive peak of X.

The mean values $\overline{X}$ and $\overline{Y}$ of X and Y, respectively, were quite stable with the coefficient of variation (CV = SD/mean) less than 10% (Table 1). In contrast, the amplitudes of oscillations were much more variable, as shown in Table 1 for the amplitude of peak X values, A_X, standardized relative to the mean value of $\overline{X}$: CVs for $A_X/\overline{X}$ were about 50%. The ratio of a peak amplitude of X to the consecutive peak amplitude of Y was about 1 if the generation rate of X, α_X, was equal to the death rate of Y, α_Y (simulations 142, 143, 122 and 140), but decreased significantly if α_X was substantially lower than α_Y (simulations 136 and 141). In simulation 133, with a rather small difference between α_X and α_Y, it was difficult to conclude from the value of $A_x/\overline{X}$ about the differnces in the parameters. However, the ratio $\overline{Y}/\overline{X}$ strongly depended on the ratio α_X/α_Y (Table 1), as predicted by the theory of the Lotka–Volterra equations [10]. The time period T was quite stable with CV within the range of 10–20% (Table 1). The ratio φ of the phase lag between

Table 1
Simulations of interacting populations

	Simulation #						
	142 [a]	143 [a]	122 [b]	133 [c]	136 [b]	140 [c]	141 [c]
Microparameters							
ω_0	2	2	1	1	1	0.5	0.5
α_X	0.250	0.250	0.115	0.115	0.115	0.160	0.115
α_Y	0.250	0.250	0.115	0.140	0.160	0.160	0.160
Initial values							
X_0/Y_0	200/200	200/200	100/100	100/100	100/100	200/200	200/200
Number of cycles							
Calculated	19	17	34	69	9	42	14
$\overline{X}$	158 ± 13	161 ± 14	142 ± 11	173 ± 10	215 ± 15	400 ± 15	397 ± 23
$\overline{Y}$	153 ± 10	153 ± 16	140 ± 11	144 ± 10	136 ± 10	397 ± 16	284 ± 21
$A_x/\overline{X}$	1.03 ± 0.45	1.55 ± 0.87	1.22 ± 0.86	0.71 ± 0.4	41.71 ± 0.6	30.600 ± 0.2	92.28 ± 0.94
A_X/A_Y	1.11 ± 0.17	1.05 ± 0.14	1.07 ± 0.18	0.98 ± 0.16	0.90 ± 0.07	1.02 ± 0.16	0.89 ± 0.04
T	26.8 ± 2.8	28.7 ± 5.1	59.1 ± 8.1	52.4 ± 9.5	55.9 ± 5.4	40.6 ± 3.8	57.6 ± 6.0
φ	0.17 ± 0.06	0.16 ± 0.06	0.17 ± 0.06	0.20 ± 0.07	0.13 ± 0.03	0.21 ± 0.06	0.12 ± 0.03
Estimated							
a_X	0.239 ± 0.022	0.252 ± 0.023	0.117 ± 0.014	0.118 ± 0.022	0.111 ± 0.005	0.158 ± 0.019	0.116 ± 0.004
a_Y	0.269 ± 0.054	0.260 ± 0.045	0.115 ± 0.014	0.144 ± 0.028	0.168 ± 0.009	0.159 ± 0.018	0.158 ± 0.007
$b_X \times 10^3$	1.55 ± 0.13	1.61 ± 0.11	0.83 ± 0.09	0.82 ± 0.16	0.80 ± 0.03	0.40 ± 0.05	0.40 ± 0.01
$b_Y \times 10^3$	1.72 ± 0.29	1.65 ± 0.26	0.81 ± 0.09	0.83 ± 0.15	0.80 ± 0.05	0.40 ± 0.04	0.39 ± 0.02

[a] Simulation finished with the extinction of X.
[b] Simulation finished with the extinction of Y.
[c] Simulation terminated by the operator.

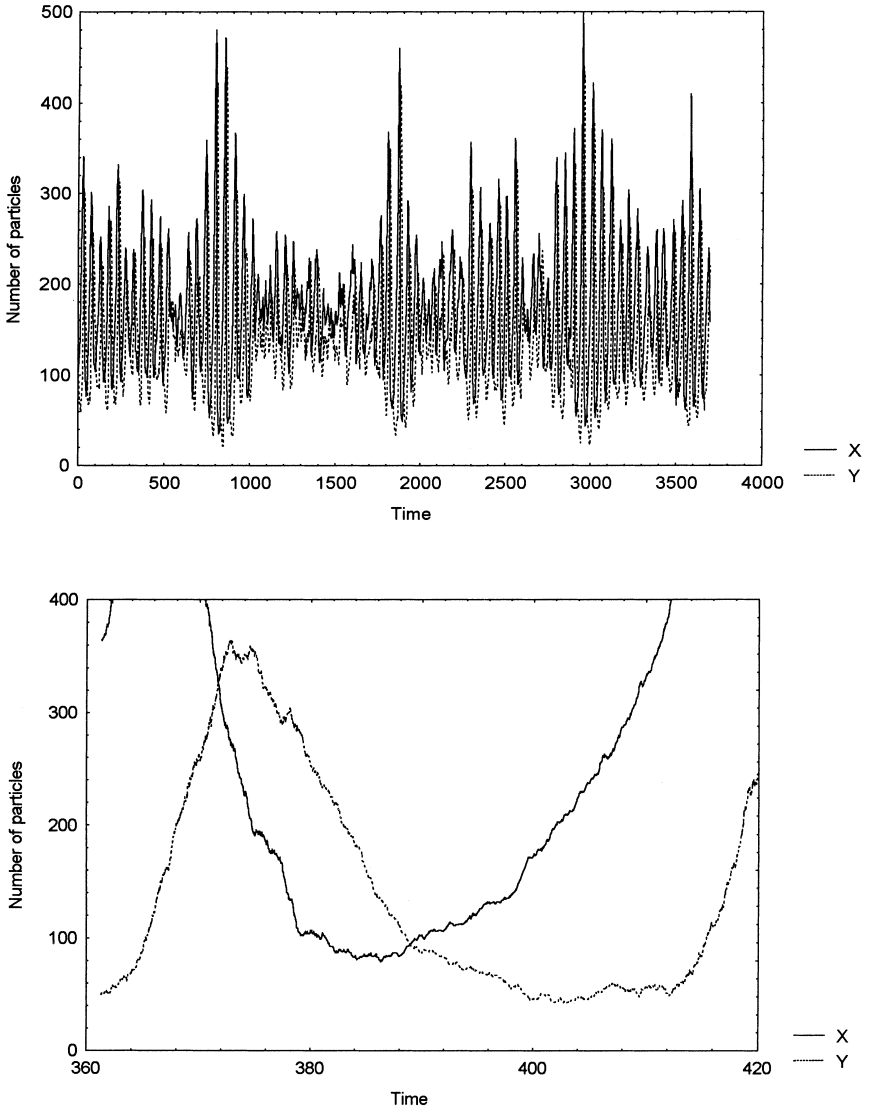

Fig. 1. Time course of the number of X (continuous line) and Y (dotted line) populations during simulation 122. Upper panel: the whole simulation time; lower panel: a short time interval from the simulation.

peak amplitudes of Y and X over the time period was similar in all simulations described in Table 1, but its scattering was higher (CV within the range 25–35%) than that for the time period (Table 1).

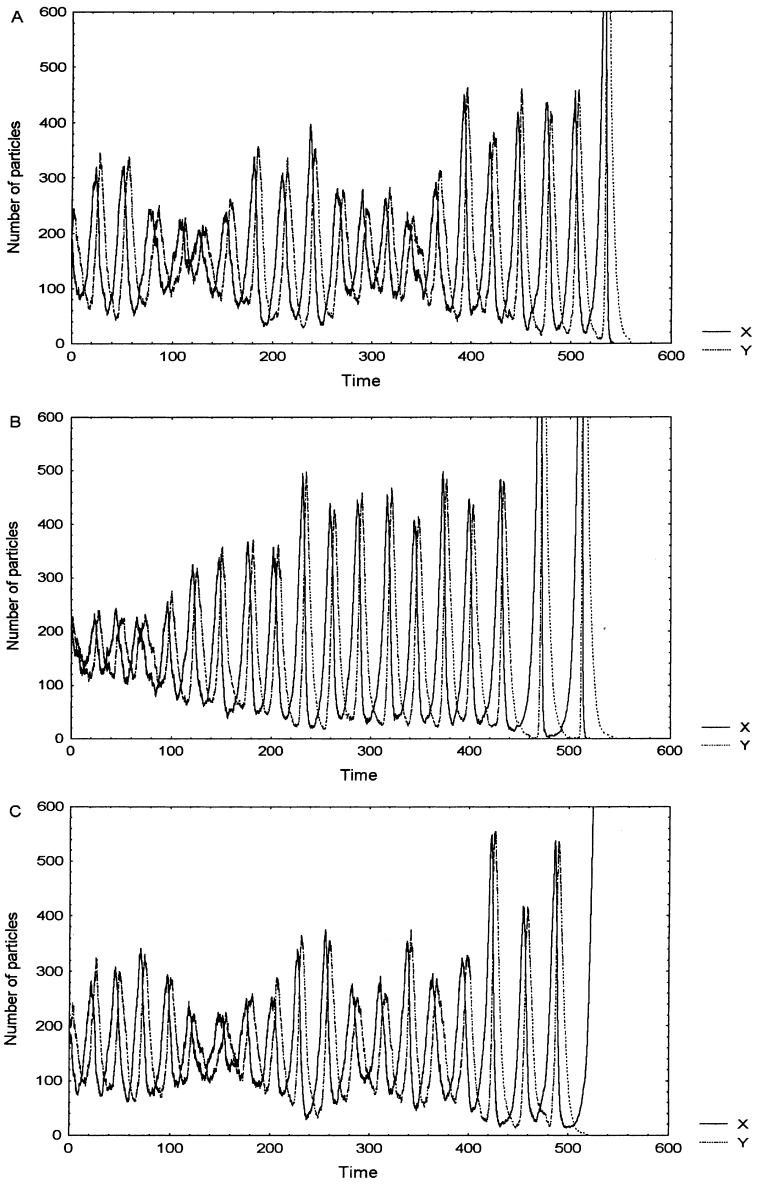

Fig. 2. (A). Simulation 142, see Table 1 for its description. (B). Simulation 143 with the same microparameters and the same initial state of the particles, but with different sequence of random numbers used for stochastic additions of X and deletions of Y, cf. Table 1. (C). Simulation 145 with the same microparameters and the same sequence of random numbers as in simulation 142, but with different initial state of the particles.

4. Parameter estimation

It was assumed that the basic features of the system evolution can be described by the Lotka–Volterra equations:

$$\begin{aligned} \frac{dX}{dt} &= a_X X - b_X XY, \\ \frac{dY}{dt} &= -a_Y Y + b_Y XY, \end{aligned} \tag{4.1}$$

where a_X, b_X, a_Y, $b_Y > 0$. To estimate the model parameters the following integral forms of Eq. (4.1):

$$\begin{aligned} X(t) &= X(t_0) + a_X F(t) - b_X G(t), \\ Y(t) &= Y(t_0) - a_Y K(t) + b_Y G(t), \end{aligned} \tag{4.2}$$

where

$$F(t) = \int_{t_0}^{t} X(s)\,ds, \quad K(t) = \int_{t_0}^{t} Y(s)\,ds, \quad G(t) = \int_{t_0}^{t} X(s)Y(s)\,ds$$

were solved as two-parameter linear regression equations for parameters a_X, b_X and a_Y, b_Y, respectively.

The simulated time course of X and Y was not any solution to the Lotka–Volterra equations. However, we assumed that during one (quasi) cycle of the oscillations a solution of the equations may be fitted with a reasonable accuracy. Therefore, the parameters a_X, b_X, a_Y, b_Y were estimated using Eq. (4.2) for each oscillation cycle separately, with the cycle defined as the time interval between two consecutive peaks of X.

One may expect that $b_X = b_Y$ because the disappearance of X particle was linked to the appearance of Y particle. In fact, the average values of these two parameters are very close in all simulations presented in Table 1. Furthermore, they are roughly proportional to the average velocity of particles (see the initial value of ω_0 in Table 1), because the value of $b = b_X = b_Y$ depends mainly on the probability of the interaction (i.e. collision) of particles, and this depends on the velocities of particles. The estimated average values of a_X and a_Y are close to the assumed values of α_X and α_Y, respectively (Table 1). In fact, the expectation time for multiplication of X and deletion of Y was $1/\alpha_X$ and $1/\alpha_Y$, respectively, for the probability distributions described by Eqs. (2.4) and (2.5). On the other hand, the proliferation time of X population (without predators) and life time of Y population (without preys) described by Eq. (4.1) with $b_X = b_Y = 0$ are $1/a_X$ and $1/a_Y$, respectively. The scattering of the parameters estimated for the separate cycles was low with CV within the range 2–20%.

Note that the basic relationships for the average values of X and Y for period time (i.e. $\overline{X} = a_Y/b_Y$ and $\overline{Y} = a_X/b_X$ [10]) are well fulfilled for the values

of the estimated model parameters. This is verified by the values shown in Table 1.

To check the reality of the parameter estimation for the whole system of interacting populations a few additional computer simulations were performed for special arrangements of the system, which make it possible to estimate separately the model parameters (Table 2). With the same microparameters as in simulation 122 (see Table 1) the following initial states and interactions between the particles were defined: (1) no additions of X and no deletions of Y, and normal interactions between X and Y (simulation 129, which described the predation of Y on X without other factors affecting the number of particles), (2) X particles were added to the system according to the same procedure and probability distribution as in simulation 122, but no Y particles were present (simulation 132, which described the exponential development of X population), and (3) there were no X particles in the system, so Y population decreased exponentially because deletions of Y were done in the same way as in simulation 122 (simulation 130, which described dying out of population Y). The model parameters were estimated for these simulations using Eq. (4.2) with all parameters irrelevant for the particular simulations set to zero. The results are shown in Table 2: the parameters estimated separately were very close to those estimated for the whole system.

5. Discussion

The Lotka–Volterra deterministic model, Eq. (4.1), with its rather unique mathematical features, such as neutral stability of the steady state and closed

Table 2
Model parameters from test simulations

	Simulation #			
	122	129	132	130
Assumed				
α_X	0.115	0.000	0.115	0.000
α_Y	0.115	0.000	0.000	0.115
Initial values				
X_0/Y_0	200/200	399/1	30/0	0/400
Estimated				
a_X	0.117		0.106	
a_Y	0.115			0.110
$b_X \times 10^3$	0.83	0.81		
$b_Y \times 10^3$	0.81		0.81	

orbits, was often criticized as being not enough realistic to describe real biological systems [10]. However, stochastic modeling of the Lotka–Volterra interactions in small populations revealed unstable oscillations and occasional extinction of one of the species [14]. These features of the evolution of the Lotka–Volterra system resemble more the kinetic patterns of interacting populations observed in biological systems than the evolution described by the determininstic model. Our individual-based modeling yielded the results of the same type as those from the stochastic modeling, which is not surprising because of the stochastic component (prey birth and predator death) included in our computer Lotka–Volterra world. However, there was also another factor of stochasticity of the observed oscillation patterns which came from irregular sequence of particle collisions and X–Y interactions. In spite of the determininstic character of these events, their irregularity resulted in 'stochastic' dependence on the initial microstate of the particles (Fig. 2). Both of these factors might have so substantial impact on the evolution of the system because of low number of particles in the system. With the increasing average number of particles the oscillations are more regular (compare for example the simulations for a few thousands of particles in Ref. [3]). Also the mean time to extinction of a population increases substantially with the increased average number of X and Y as shown in stochastic simulations described in Ref. [13]).

The scattering of the parameters, which described the oscillations (amplitudes, average values of X and Y per cycle, time period, phase lag between Y and X), depended on the considered parameter and was highest for the peak amplitudes of X and Y (Table 1). Nevertheless, the kinetic patterns of the evolution of X and Y populations revealed some features which are characteristic for the determininstic model. The parameters of the Lotka–Volterra model were estimated with high accuracy and precision (Table 1). The result of our study shows that in spite of usually observed stochasticity of the kinetic patterns of interacting populations evolution, the kinetic parameters as suggested by deterministic models of interaction may be, at least in principle, estimated and used for further analysis of the system.

The irregular kinetic patterns which resemble real population data were obtained in the present study using very simple, partly deterministic and partly stochastic, rules for the behavior of the individuals. The deterministic rules for the motion of individuals do not reflect real motion of biological organisms. However, the feature of the motion, which is important at this level of modeling, is the frequency of encounters between individuals and not their behavior between encounters. Note also that diffusion like phenomena (e.g. spreading of the population) can be modeled using the deterministic rules for particle motion.

The rules for the particle motion and interaction resemble more a physico–chemical than a biological system. The motivation for this arrangement was that the system provides a simple and 'transparent' interpretation for the

Lotka–Volterra model. This simple interpretation was possible because the model in fact may be used also for the description of a chemical reaction. Note however that other features of the particles, as death and multiplication, are characteristic for biological individuals. It is interesting that the population dynamics for this simple and rather artificial system of interacting particles is so similar to that observed in real biological populations.

The application of sphere as a 'life stage' for populations can be quite simple as shown in the present study. The sphere may represent the whole Earth in some biological or ecological problems. There are species which are distributed over most of the planet surface, and some individuals (albatrosses or whales, for example) can move around the whole globe. Other individuals spend their life on a restricted area; this situation can be modeled by an appropriate adjustment of particle velocity and life time as well as the initial distribution of the individuals. Numerous modifications of the presented system may be useful in other models, e.g. random walk on a sphere should also use arcs of great circles, etc. Some disadvantage of continuous space–time modeling of many particles is its relative computing slowness comparing to a discrete space–time model with a similar number of particles.

The Lotka–Volterra model is one of the simplest examples of interacting populations and, at the same time, is easy to reproduce in individual based computer modeling. Therefore, we could carry out both the computer simulations and the estimation of the parameters for the deterministic mathematical model for macrovariables and find some relationships between micro- and macro-parameters. However, the individual based modeling may be even more interesting if applied for the description of the behavior of the individuals and the rules for their interactions with no obvious (or: without any) mathematical description for macrovariables by differential equations, as for example for strongly heterogeneous populations [5]. Computer simulations of artificial worlds can be of a great help in such cases and can provide theoretical framework for more mathematically oriented models.

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