

SPATIAL HETEROGENEITY AND LOCAL OSCILLATION PHASE DRIFTS IN INDIVIDUAL-BASED SIMULATIONS OF A PREY-PREDATOR SYSTEM

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Individual-based simulations of a simple prey-predator system of Lotka-Volterra type were carried out on a tessellation of identical squares with discrete time steps. The particles representing individuals moved freely along (roughly) straight lines with constant (on the average) velocity, and changed their movement during a collision with another particle. Individuals were of two types: preys (with free exponential population growth) and predators (with exponential population decrease in the absence of a prey, they attack with probability one and are characterized by zero handling and gestation times). Therefore the system might be also interpreted as a chemical reaction in a gas. For this simple system, a spontaneous generation of complex spatio-temporal pattern was observed with wavy spatial patterns and tendency for preys to form clusters surrounded by predators if the population density was high. The oscillations of the system were investigated at different spatial scales, and the phase lag between the oscillations in different local observation windows was demonstrated. The parameters of the classical Lotka-Volterra equations were estimated and the impact of the migration and the oscillation phase drift on the parameter values was discussed.

Keywords: prey-predator system, individual-based simulations, spatial heterogeneity, oscillation phase drift, parameter estimation

1. Introduction

Pattern formation, patchiness and diffusional instability have been of active interest in chemical, biological and ecological studies since the publication of Turing's paper (1952). The problem has its counterpart in the kinetic patterns if they are studied in areas of different sizes. In particular, a phase shift between the oscillations in different areas and a decrease in their amplitudes have been observed for increasing areas (Durrett and Levin, 1994; Ranta *et al.*, 1997; Wilson *et al.*, 1993). The data of the Canadian lynx from eight Canadian provinces showed that, beside the general

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synchrony in oscillations of that species, there are remarkable shifts in phase of the oscillations between the subpopulations with occasional coincidence between the peak number of lynx in one province and the minimum in the number of lynx in another one (Ranta *et al.*, 1997). This phenomenon is obviously linked to the heterogeneity of the population distribution. A theoretical analysis of the data was performed using a metapopulation model of a single population distributed in the form of patches in a discrete patch state space and changing in discrete time (Ranta *et al.*, 1997). However, similar results were also obtained in individual-based computer simulations of two populations interacting according to the prey-predator scheme (Boccaro *et al.*, 1994a; 1994b; De Roos *et al.*, 1991; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993; 1995).

Mathematical analysis of the systems of interacting and mobile particles based on their smooth density distribution may yield quite different results than computer simulations of discrete individuals, as shown for a spatial version of an evolutionary game (Durrett and Levin, 1994). This was also found for simple systems with Lotka-Volterra type interactions (Boccaro *et al.*, 1994a; 1994b; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993). As opposed to reaction-diffusion equations for two populations with linear growth and death rates and the interaction rate described by a simple bi-linear term (a classical Lotka-Volterra equation) which do not show any diffusional instability (Wilson *et al.*, 1993) (which is in contrast to the system with modified growth, death and interaction rates (Mimura and Murray, 1978; Segel and Jackson, 1972)), individual-based simulations showed spontaneous appearance of irregular patchiness even in the populations with the classic Lotka-Volterra description (Boccaro *et al.*, 1994a; 1994b; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993; 1995). The phenomenon was attributed to different features of the discrete (individuals, space, time) simulations when compared with the smooth mathematical description of the system (Wilson *et al.*, 1993).

Individual-based computer simulations of population dynamics yield data (e.g. time series of the population size) which are in general irregular (and in this respect they resemble experimental data), and therefore the problem of identifying those features of the data which are generic for the system as well as methods for quantitative identification of the system using mathematical models of the population can be studied based on such simulations. Furthermore, the relationship between the estimated parameters and the quantitative rules for particle behaviour and the rules for the observation of the population are of general interest. Studying these issues with individual-based simulations can provide new methods for the evaluation of experimental investigations and field observations.

In our study, a simple individual-based model of the Lotka-Volterra system is discussed using a new approach to modelling particle motions and interactions. The simulation rules were similar to those for gas particles and chemical reactions. We also analyze our simulations using Lotka-Volterra equations for the data collected from observation windows of different surface areas.

2. Computer Model for Interacting Particles

The individual-based model was implemented to investigate the behaviour of a simple predator-prey system. The model has been defined over a two-dimensional tessellation of identical squares (Jędruch and Barski, 1990; Jędruch and Waniewski, 1994). The area of the model is limited and cyclic, i.e. squares at the right and left (and upper and lower) borders of the plane are adjacent to one another (Durrett and Levin, 1994; Wilson *et al.*, 1993). A square may be empty or contain an individual U (prey) or V (predator). No square can contain more than one individual (Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992). However, in some other studies, more than one individual might occupy the same node of the grid (Durrett and Levin, 1994), or the same node may be occupied by an individual (but not more than one) from each of the interacting populations (Wilson *et al.*, 1993).

The state of an individual is specified by a pair of integers, x_p and y_p , specifying the position of the individual in the Cartesian coordinates x - y , and by the pair of real numbers, v_x and v_y , specifying the velocity of the individual in the x and y directions, respectively.

All the transformations in the model are synchronized by a discrete clock.

Particle movement. At each time step, the individuals can move by jumping randomly and consecutively to the both adjacent squares in the x and y directions (the order of directions is chosen randomly) with probability:

$$P_x = \begin{cases} |v_x/s| & \text{if } v \leq s \\ |v_x/v| & \text{if } v > s \end{cases} \quad \text{or} \quad P_y = \begin{cases} |v_y/s| & \text{if } v \leq s \\ |v_y/v| & \text{if } v > s \end{cases} \quad (1)$$

where $v = \sqrt{v_x^2 + v_y^2}$ and s is a constant (here assumed to be 5). If $v \leq s$, then the average Euclidean displacement of a particle is proportional to its velocity v , whereas for $v > s$ the average Euclidean displacement is the same as for $v = s$, which sets up the maximal velocity of one square distance per time step. These rules of movement produce random trajectories distributed around the straight lines, which represents the deterministic continuous movement with velocity (v_x, v_y) . To illustrate the rules some example trajectories are shown in Fig. 1.

When an individual attempts to occupy a square already occupied by another individual, a collision occurs, after which the new velocities of both the individuals are evaluated. The new velocities of the rebounding individuals are computed according to the following formula (it is the formula for elastically rebounding disks in the two-dimensional space):

$$\begin{aligned} v_{1x}(k+1) &= v_{1x}(k) + d(k) \cos(\alpha), & v_{1y}(k+1) &= v_{1y}(k) + d(k) \sin(\alpha), \\ v_{2x}(k+1) &= v_{2x}(k) - d(k) \cos(\alpha), & v_{2y}(k+1) &= v_{2y}(k) - d(k) \sin(\alpha), \end{aligned} \quad (2)$$

$$d(k) = [v_{2x}(k) - v_{1x}(k)] \cos(\alpha) + [v_{2y}(k) - v_{1y}(k)] \sin(\alpha),$$

where v_{1x} , v_{2x} , v_{1y} , v_{2y} denote the respective velocity components of the colliding individuals 1 and 2 in the x and y directions, k and $k+1$ denote respectively the

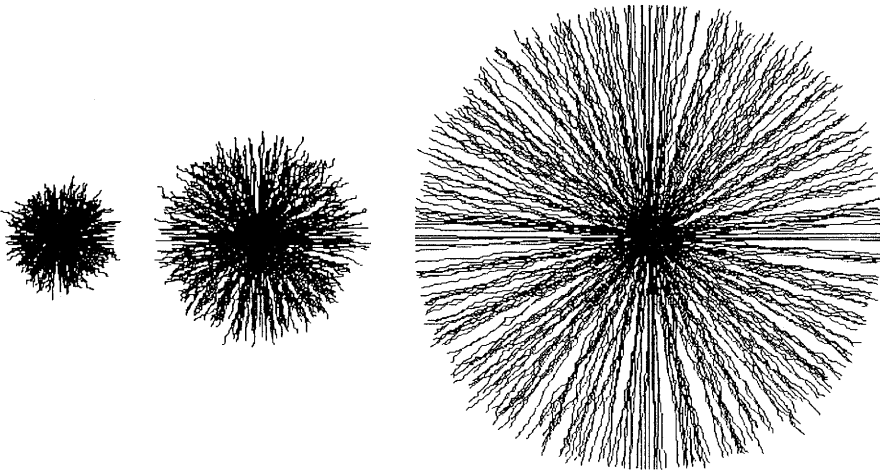


Fig. 1. Example of individual trajectories observed for 180 time steps. The velocities of individuals were equal to 1, 2, and 5 (from the left to the right-hand side), and $s = 5$. For each velocity a set of 360 trajectories was drawn for the directions which differed by 1° .

time steps before and after collision, and α is an angle which is chosen randomly for each collision from the range $(0, 2\pi)$.

The particle migration in other studies was diffusive with random jumps for a given number of lattice spacings per time step (Durrett and Levin, 1994; Wilson *et al.*, 1993), or individuals were stationary, i.e. they did not move at all (Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993) or randomly scrambled (perfect mixing) (Wilson *et al.*, 1993). Special phenomena, such as pursuit and evasion, were also taken into account in cellular automata models (Boccaro *et al.*, 1994b).

Interaction between preys and predators. If a collision of U and V takes place, the individual U is changed to V . This rule may be interpreted as follows: if a predator meets a prey, then it attacks (with probability one) and consumes this prey, and with zero handling and gestation time, gives birth to another predator which has the same position and velocity as the caught prey. A similar rule was also applied in (Wilson *et al.*, 1993). More realistic descriptions of biological phenomena, as predation and predator multiplication or density-dependent birth and death, can also be implemented in individual-based modelling (De Roos *et al.*, 1991; Satulovsky, 1996). It is worth noticing that the implemented interaction rule has also an interpretation of irreversible chemical reaction $U + V \rightarrow 2V$. In fact, Lotka formulated initially his equations for the chemical reaction (Lotka, 1925).

6.37×10^{-10}	4.60×10^{-7}	6.72×10^{-6}	1.50×10^{-5}	6.72×10^{-6}	4.60×10^{-7}	6.37×10^{-10}
4.60×10^{-7}	3.32×10^{-4}	4.85×10^{-3}	1.08×10^{-2}	4.85×10^{-3}	3.32×10^{-4}	4.60×10^{-7}
6.72×10^{-6}	4.85×10^{-3}	7.08×10^{-2}	1.58×10^{-1}	7.08×10^{-2}	4.85×10^{-3}	6.72×10^{-6}
1.50×10^{-5}	1.08×10^{-2}	1.58×10^{-1}	U	1.58×10^{-1}	1.08×10^{-2}	1.50×10^{-5}
6.72×10^{-6}	4.85×10^{-3}	7.08×10^{-2}	1.58×10^{-1}	7.08×10^{-2}	4.85×10^{-3}	6.72×10^{-6}
4.60×10^{-7}	3.32×10^{-4}	4.85×10^{-3}	1.08×10^{-2}	4.85×10^{-3}	3.32×10^{-4}	4.60×10^{-7}
6.37×10^{-10}	4.60×10^{-7}	6.72×10^{-6}	1.50×10^{-5}	6.72×10^{-6}	4.60×10^{-7}	6.37×10^{-10}

Fig. 2. The probability distribution of placing the newly generated individuals U . The parent individual U is placed in the centre square.

Multiplication of preys. Individuals U can multiply, i.e. at each time step each individual U can be duplicated with probability P_U . The newly generated individuals U are positioned randomly but closely to their parent individuals according to the following algorithm: two times six uniformly distributed random variables are summed and rounded to the closest integers. The resulting two integer numbers added to the position of the parent individual U give the position of the new individual. If these numbers are both zero or the chosen position is already occupied, the procedure is repeated. This algorithm (assuming that there are no other individuals than the parent individual U) leads to the probability distribution shown in Fig. 2. This distribution is obtained using the well-known Laplace formula yielding the probability density function of the sum of uniformly distributed random variables. Thus, the growth of the U population alone would be exponential in the large time scale, until the high density of the population is reached.

Death of predators. Individuals V can die, i.e. they are removed according to the probability P_V per one time step. Thus the V population left alone would die out exponentially.

The rules for U multiplication and V death may also be interpreted within the scheme of chemical reactions: U and V may interact with ‘ghost’ particles A and B , respectively, according to the schemes: $U + A \rightarrow 2U$, $V + B \rightarrow 2B$. The numbers of particles A and particles B are separately kept constant (Jędruch and Waniewski, 1994; Prigogine, 1969).

The computer model has therefore two different interpretations:

1. a much simplified and idealized ecological system of prey-predator interactions,
or
2. a chemical reactions studied at the level of a small number of discrete particles.

The simplicity of the model may help to reveal important factors behind the unexpected observations made for discrete systems of individuals, and observations that cannot easily be interpreted within the mathematical description of the evolution of continuous distribution functions.

3. Evaluation of Computer Simulations with the Lotka-Volterra Model

The system is expected to evolve according to the Lotka-Volterra equations (Edelstein-Keshet, 1988; Murray, 1989):

$$\begin{cases} \frac{du}{dt} = a_U u - b_U uv, \\ \frac{dv}{dt} = -a_V v + b_V uv \end{cases} \quad (3)$$

for $a_U, b_U, a_V, b_V > 0$, where u and v denote the numbers of individuals of U and V species expressed per unit surface area (population densities), respectively. The unit surface area in our calculations is that for a tessellation of 100×100 basic squares.

Writing (3) for the simulated system, we have to assume that the particles are perfectly mixed, i.e. every individual has the same probability to interact with another. Sometimes this approach is called the mean field theory (Durrett and Levin, 1994). Its validity for our simulations will be checked in Section 5.

The following integral form of (3) can be used to estimate the system parameters:

$$\begin{aligned} u(t) &= u(t_0) + a_U F(t) - b_U G(t), \\ v(t) &= v(t_0) - a_V K(t) + b_V G(t), \end{aligned} \quad (4)$$

where

$$F(t) = \int_{t_0}^t u(s) ds, \quad K(t) = \int_{t_0}^t v(s) ds, \quad G(t) = \int_{t_0}^t u(s)v(s) ds.$$

Each of eqns. (4) is a two-parameter linear regression for parameters a and b . We apply (4) for each cycle separately (the cycle stands for the period between the consecutive peaks of u ; estimations with other definitions of the cycle yield essentially the same results), and then calculate the average values of the estimated parameters over all the available cycles (Waniewski and Jędruch, 1999).

4. Computer Simulations

A series of experiments has been made for various initial numbers of individuals, various probabilities P_U , P_V , and various sizes of the tessellation area. All experiments show that the numbers of U and V individuals oscillate with variable amplitudes. The oscillation amplitude strongly depends on the size of the observation window (Fig. 3 and Tab. 1).

Table 1. Simulations of interacting populations on a square of the total surface area of 256 units (1600×1600 tessellation, one surface area unit = 100×100 squares) $a_U = a_V = 0.40 \times 10^{-2}$, and an initial population density of $u = v = 32$ individuals per unit surface area. The simulation was performed for 20000 time units (11 cycles occurred); the results are shown for observation windows of different surface areas. Mean values \pm SD are presented. Description of symbols on p. 187.

Window area	256	64	16	4	1
Descriptive:					
\bar{u}	50 \pm 1	50 \pm 2	50 \pm 2	48 \pm 4	52 \pm 5
\bar{v}	50 \pm 1	50 \pm 1	49 \pm 2	50 \pm 2	50 \pm 5
A_U/\bar{u}	0.71 \pm 0.28	0.81 \pm 0.27	1.08 \pm 0.40	1.66 \pm 0.86	2.09 \pm 1.24**
A_U/A_V	0.99 \pm 0.09	1.06 \pm 0.06	1.02 \pm 0.10	1.05 \pm 0.12	1.11 \pm 0.28
T	1767 \pm 85	1772 \pm 113	1792 \pm 97	1799 \pm 152	1831 \pm 157
φ	0.21 \pm 0.05	0.21 \pm 0.09	0.16 \pm 0.02	0.15 \pm 0.03	0.13 \pm 0.04**
Theoretical:					
$a_U \times 10^2$	0.36 \pm 0.02	0.36 \pm 0.03	0.38 \pm 0.02	0.41 \pm 0.02	0.42 \pm 0.07*
$a_V \times 10^2$	0.36 \pm 0.01	0.36 \pm 0.02	0.36 \pm 0.03	0.38 \pm 0.03	0.41 \pm 0.05*
$b_U \times 10^4$	0.71 \pm 0.03	0.73 \pm 0.04	0.75 \pm 0.06	0.77 \pm 0.04	0.82 \pm 0.13*
$b_V \times 10^4$	0.70 \pm 0.05	0.70 \pm 0.04	0.69 \pm 0.06	0.73 \pm 0.07	0.78 \pm 0.11*

The oscillations have many features characteristic for the solutions of the Lotka-Volterra equations, independently of the size of the observation window (Fig. 3). The extreme values of V follow the extreme values of U . If the amplitudes are small, the oscillations resemble harmonic ones. If the amplitudes of oscillations are large, the peaks are narrow and steep, and the troughs wide and shallow. In small observation windows one of the species can get extinct, while in a deeper trough with a low number of individuals due to random fluctuations; however, the window is soon recolonized. The pattern of oscillations can change a lot if the simulations are done with the same initial dynamic state but different contingent events (adding and removing particles). Nevertheless, these patterns have some generic characteristics which make it possible to recover the parameters of the Lotka-Volterra equations.

*** $p < 0.05$ and $p < 0.005$, respectively, versus the value for the window area equal to 256, the Student t -test.

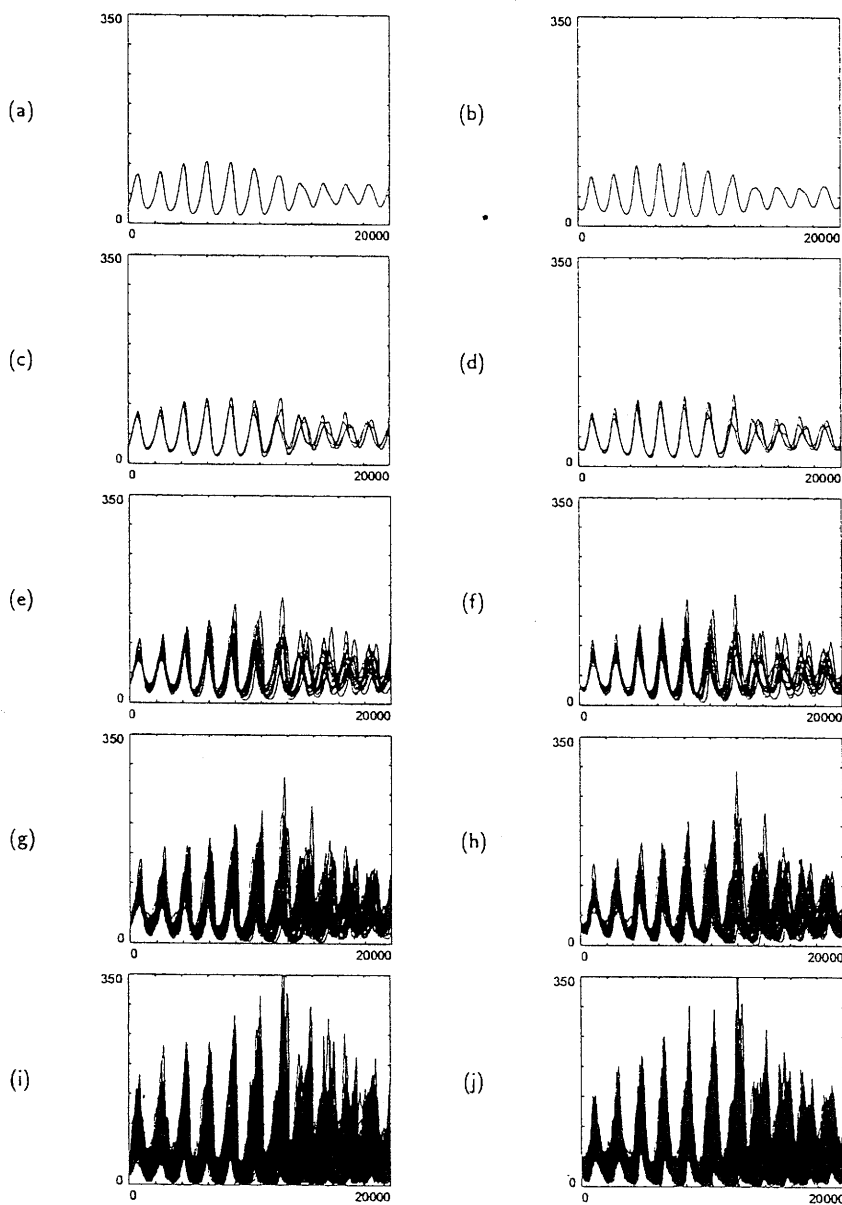


Fig. 3. The density of individuals U (left) and V (right) versus time steps: (a) and (b) in the whole system composed of 1600×1600 elementary squares, (c) and (d) in 4 windows, each composed of 800×800 squares, (e) and (f) in 16 windows, each composed of 400×400 squares, (g) and (h) in 64 windows, each composed of 200×200 squares, (i) and (j) in 256 windows, each composed of 100×100 squares.

Below the results of computer simulations are described and analyzed in detail. The model is defined over the tessellation of 1600×1600 squares. The probabilities of multiplication and death of individuals are $P_U = P_V = 0.004$. The initial state of the system consists of $U = 5192$ and $V = 5192$ randomly positioned individuals having the velocity $v = 1$ and a randomly chosen movement direction. The system evolves over 20000 time steps.

The evolution of the above system was observed in square windows of various sizes. The results are presented in Fig. 3 where the densities of individuals U and V versus time steps for various observation windows are shown: the densities of individuals in the whole model (composed of 1600×1600 squares, Figs. 3(a) and (b)), in 4 windows (each composed of 800×800 squares, Figs. 3(c) and (d)), in 16 windows (each composed of 400×400 squares, Figs. 3(e) and (f)), in 64 windows (each composed of 200×200 squares, Figs. 3(g) and (h)), and in 256 windows (each composed of 100×100 squares, Figs. 3(i) and (j)). As can be seen from Fig. 3, the amplitudes of oscillations decrease if the area of observation increases. The measured coefficients of variation (standard deviation/mean value) for peak amplitudes of individuals U are 0.45, 0.48, 0.57, 0.64 and 0.72 for the windows of the size 1600×1600 , 800×800 , 400×400 , 200×200 and 100×100 , respectively. The same coefficients for individuals V are 0.46, 0.49, 0.57, 0.64 and 0.69, respectively.

The phase trajectories of the system observed in the largest (1600×1600) and the smallest (100×100) windows are shown in Fig. 4. The trajectory from the smallest window strongly fluctuates in the short time scale, whereas the trajectory of the whole system is rather smooth. Both the trajectories look like those drifting slowly over closed trajectories of the Lotka-Volterra system, eqns. (3).

Figure 5 demonstrates the evolution of the size of U population in windows of decreasing sizes with each smaller window included within the larger ones. At the beginning of the simulation the system was homogeneous and the oscillations in all windows were of the same amplitude and the same phase for a few cycles (Fig. 5, the upper panel). However, the subsystems in small windows then drifted out of phase from other subsystems in windows of the same size, and, at the same time, from the larger subsystems as illustrated in Fig. 5, cf. the lower panel. The drift was rather slow and it took a few cycles to reach the maximum deviation of the phase of the smallest subsystem from those of the larger subsystems.

The differences in the phase of the oscillations observed in small areas within the whole 'world' are related to heterogeneity of the population distribution (Fig. 6). The initially homogenous distribution of both the populations (Figs. 6(a) and (b)) slowly changed and inhomogeneities appeared (Figs. 6(c) and (d)). Strongly heterogeneous distributions were observed later with waves of high and low densities moving through the tessellation (Figs. 6(e)–(j)). Occasionally, clusters of preys arose with almost no predator inside, but instead surrounded by many of them (Figs. 6(g) and (h)).

5. Quantitative Analysis of System Dynamics

The oscillations vary in amplitude, time period, phase, etc. in all windows, but some relatively constant characteristic features of the patterns observed can be found. Some

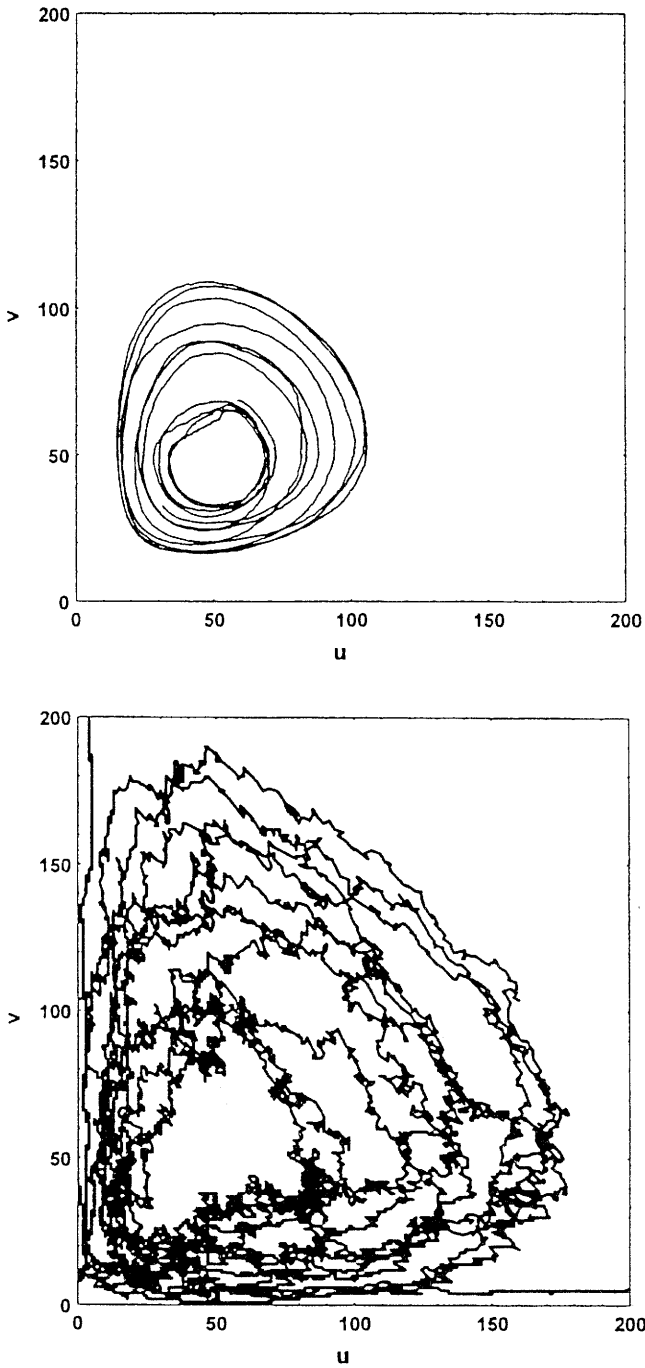


Fig. 4. Phase trajectory of the system observed in the 1600×1600 window (upper panel) and on 100×100 (lower panel) elementary squares.

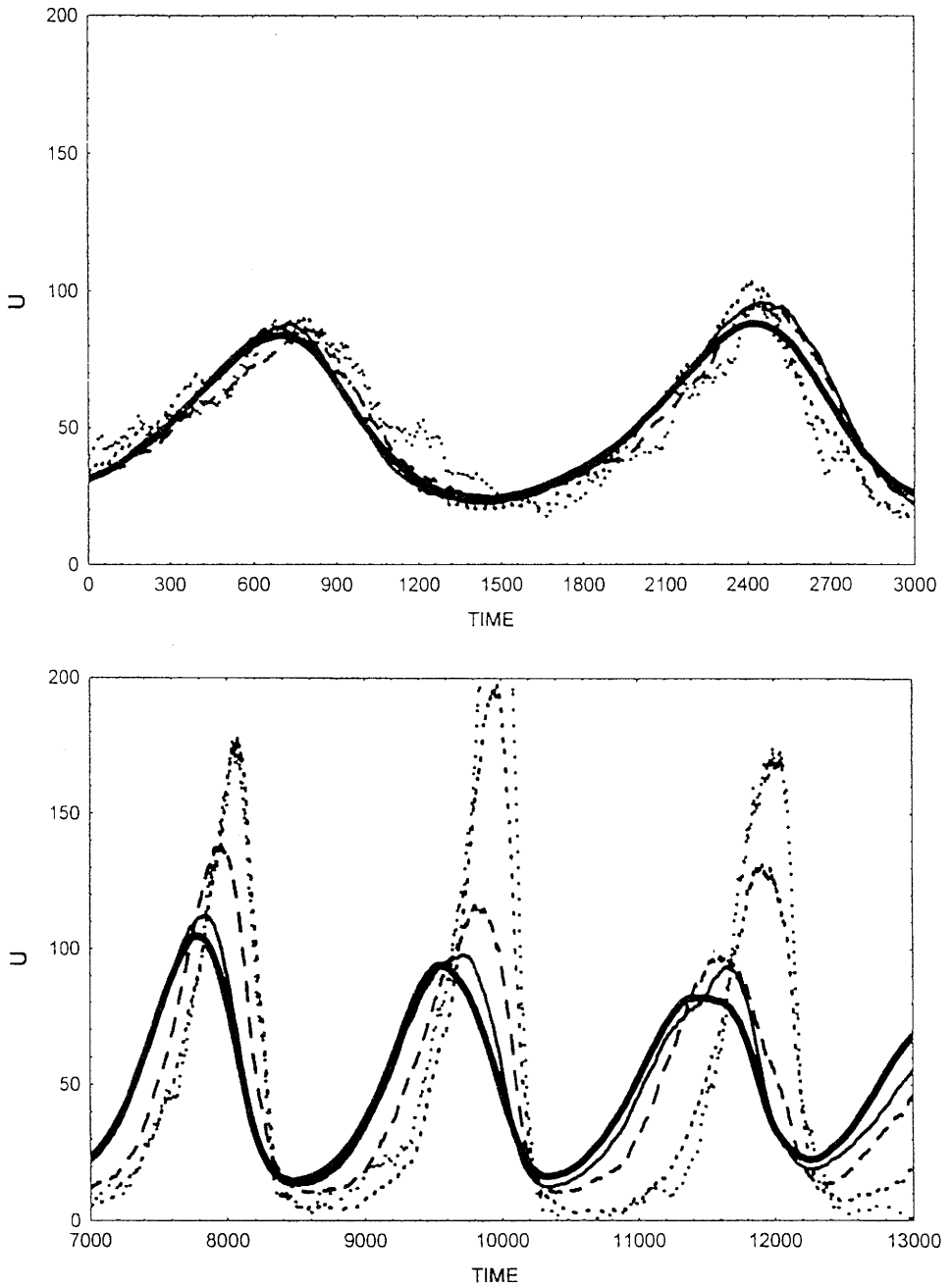


Fig. 5. Oscillations of the system observed in different windows at the beginning (upper panel) and in the middle of the simulation (lower panel).

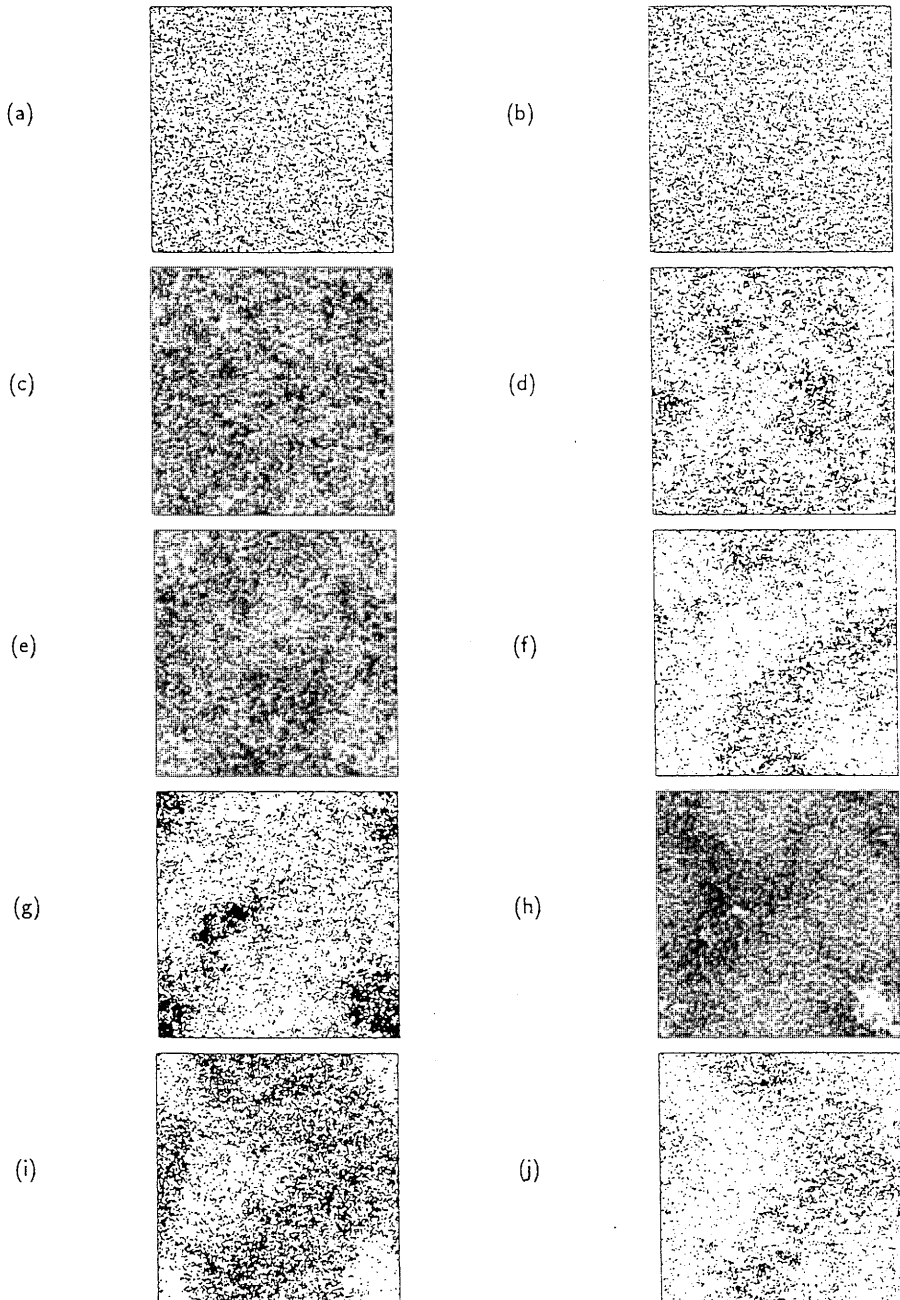


Fig. 6. Distribution of particles U (left) and V (right): (a) and (b) initial, (c) and (d) in step 2300, (e) and (f) in step 7499, (g) and (h) in step 10000, (i) and (j) in step 11884.

of them are listed in Table 1 for each of the five sizes of the observation window (these are the same windows which were selected for Fig. 5). The parameters which characterize the oscillations were calculated for each oscillation cycle separately and the mean values and standard deviations over all available oscillations for each of the observation windows are shown in Tab. 1. The oscillation cycle is defined to be from a peak of U to the consecutive peak of U .

The mean values of the average density, \bar{u} and \bar{v} , of U and V , respectively, were quite stable and the same in all windows, and the coefficient of variation ($CV = \text{SD}/\text{mean}$) increased with the decreasing window size, but not more than by 10% (Tab. 1). In contrast, the amplitudes of oscillations increased considerably with the decreasing window size, as shown in Tab. 1 for the peak amplitude of u values, A_U , standardized relative to the mean value of \bar{u} , A_U/\bar{u} . The coefficient of variation, CV , for A_U/\bar{u} was over 50% for the windows of small sizes, which was due to a high irregularity of oscillations in those windows. The ratio of a peak amplitude of U to the consecutive peak amplitude of V , A_U/A_V , was about 1 for all windows sizes. This result might be expected for the Lotka-Volterra system with the generation rate of U , P_U , equal to the death rate of V , P_V . The time period T was similar for all window sizes, and CV for T was less than 10%. The ratio φ of the phase lag between peak amplitudes of V and U over the time period was lower for small windows than for large ones, as might be expected for the Lotka-Volterra system with high versus low amplitudes of oscillations.

The simulated time course of U and V did not agree with any solution to the Lotka-Volterra equations. However, we assumed that during one (quasi) cycle of the oscillations a solution to (3) could be fitted to our data with reasonable accuracy. Therefore, the parameters a_U , b_U , a_V , b_V were estimated using (4) for each oscillation cycle separately, with the cycle defined as the time interval between two consecutive peaks of U . The mean (+/- the standard deviation) values of the parameters are shown in Tab. 1.

One might expect that $b_U = b_V$ because in the simulations the disappearance of a U particle due to the interaction with a V particle was linked to the appearance of a V particle. In fact, the average values of these two parameters were very close in the windows of all sizes (Tab. 1). The estimated average values of a_U and a_V were close to each other and to the assumed values of P_U and P_V , respectively (Tab. 1). The scattering of the parameters estimated for the separate cycles was low with CV within the range of 2–20%.

Note that the basic relationships for the average values of u and v for the time period (i.e. $\bar{u} = a_V/b_V$ and $\bar{v} = a_U/b_U$ (Edelstein-Keshet, 1988; Murray, 1989)) were fulfilled for the values of the estimated model parameters (as can be verified based on the values shown in Tab. 1). The formula for the oscillation period for small amplitudes, $T = 2\pi/\sqrt{a_U a_V}$, is also fulfilled for a larger window (low amplitudes of the average density) with the calculated T equal to 1745 time steps.

The values of the estimated parameters for the Lotka-Volterra model depend on the window size (Table 1). The correct (i.e. in agreement with the assumed values for the birth, P_U , and death, P_V , rates), values of a_U and a_V were obtained for the small windows of area equal to one and four units. The estimated values of a_U

and a_V for larger windows were however slightly lower than the assumed values of P_U and P_V , respectively. The same decrease was also found for the interaction parameters b_U and b_V . The observed dependence of the parameters of the Lotka-Volterra equations on the size of the observation windows might be due to the effect of a limited particle migration. In fact, the migration of the particles was rather slow and a particle moving freely could pass about 180 squares per one oscillation cycle. Therefore, the assumption of perfectly mixing might be valid to some extent in the small observation windows but not in large ones. In fact, the tendency to underestimate the values of P_U and P_V by a_U and a_V , respectively, is strong, especially in a window with the area greater than or equal to 16 units (Tab. 1). The reason for the observed decrease in the parameter values with increasing window sizes was the effect of averaging strong oscillations in the subregions which yield milder oscillations and slower apparent rates of microevents (birth, death, predation).

6. Discussion

Spatial heterogeneity and the phase drift between different subareas, as well as the stabilization of the system due to these phenomena, have been observed in our simulations. Similar effects appear for other individual-based simulations of the prey-predator system with different arrangements of the simulation details (Boccaro *et al.*, 1994a; 1994b; De Roos *et al.*, 1991; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993; 1995). Thus, these phenomena are linked more to the presence of discrete individuals within the population and the dynamic, collective enforcement of local stochastic events in such discretized systems, than to specific biological features of individuals and populations. In spite of many irregularities in the observed oscillations, the basic parameters of the system have been estimated with good accuracy.

The description of the space and time in our simulations was attempted to be realistic, i.e. the discretization of space and time was just a tool to organize the simulations and increase their speed, in contrast to a discrete approximation of an *a-priori* assumed differential equation. In fact, the simulated time course of population densities u and v , especially observed in the small windows, was quite similar to the results of simulations of the Lotka-Volterra interactions for particles moving on a (continuous) sphere surface with continuous time (Waniewski and Jędruch, 1999).

The squares of the tessellation were considered to be small and not able to accommodate more than one individual. The average density of the populations was small (50 individuals per 10000 squares), however in clusters it might be much higher.

The choice of the tessellation's shape is important for many applications of cellular automata. For example, modelling two-dimensional phenomena described by the Navier-Stokes equation should be done on a hexagonal tessellation, but a square tessellation is enough for the description of diffusion (Rothman and Zalesky, 1997; Weimar, 1996; Wolfram, 1986). Modelling the so-called excitable media with cellular automata needs an isotropic (semi-random) lattice, otherwise the shape of the obtained spatial patterns reflects the shape of the tessellation (Markus and Hess, 1990;

Schepers and Markus, 1992; Weimar, 1996). In our model, the particle movement was generally isotropic (Fig. 1), and therefore the square tessellation was not reflected by the particle distribution (in fact, the distribution was highly irregular, Fig. 6). Moreover, no regularity of the particle distribution was observed in the simulations of the Lotka-Volterra system on square tessellations in other studies (Boccaro *et al.*, 1994a; 1994b; De Roos *et al.*, 1991; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993; 1995).

The simulation model was simple and designed to match exactly to the simple version of the Lotka-Volterra equations. Therefore the assumptions for the particle movement and interactions were oversimplified from the biological point of view, and might be as well interpreted as the rules for chemical reactions in a gas. Nevertheless, this simplified background can be useful as a reference for more complex and biologically realistic simulations.

An attempt to generalize (3) for the description of spatio-temporal patterns is to add a diffusion term to those equations. In fact, the individual-based modelling of the Lotka-Volterra interactions was compared with the adequate reaction-diffusion (R-D) equations in (Wilson *et al.*, 1993), and a general disagreement was found. Similar results, contrary to the R-D equations, were obtained in our simulations as well as in a few other studies (Boccaro *et al.*, 1994b; De Roos *et al.*, 1991; Satulovsky, 1996; Satulovsky and Tome, 1994; 1997; Tainaka and Fukazawa, 1992; Wilson *et al.*, 1993; 1995). It is well-known that a non-trivial spatial distribution may arise in some population models with diffusion, including the prey-predator system, if the local population dynamics is complicated enough, but not in simple systems as simulated in our study (Mimura and Murray, 1978; Segel and Jackson, 1972). These classical results about pattern formation in the (complex) prey-predator system were generalized for more sophisticated systems than the Lotka-Volterra R-D equations, including discrete-time models with integro-difference equations (Neubert *et al.*, 1995), environmental heterogeneity with diffusion along an environmental gradient (Pascual and Caswell, 1997), and diffusion-advection transport (Malchow and Shigesada, 1994).

However, the R-D equations are not necessarily a good description for individual-based simulations. The simulations are performed on this spatial scale where the size of the discrete individuals is taken into account. Therefore, there is an upper limit on the population density, and this is quite different from the continuous description with no upper limit on the local density. The effective mobility of individuals depends on the local population density in simulations with limitations on the number of individuals per one site, and the respective diffusion coefficients in R-D equations should also be density-dependent. Mathematical analysis of the R-D equations with density-dependent diffusion coefficient showed that the segregation processes are possible in such systems (Witelski, 1997). Another factor is a limited velocity of the particles in the individual-based simulations, which is in contrast to the no-velocity limit assumed implicit in the R-D equations. This problem can be addressed with the correlated random walk approach and the reaction-telegraph equations (Hillen, 1996). Furthermore, the predator-prey interactions and the prey multiplication in the individual-based simulations are in fact non-local phenomena because they involve particles from two different cells. Some degree of time delay due to the discrete

clock can also contribute to the disagreement between the individual-based simulations and the local in time and space R-D equations. The non-local in space and time diffusive Lotka-Volterra systems have more bifurcations of the steady state solution than the respective local equations (Gourley and Britton, 1996). Therefore the contradiction between the individual-based simulations and the simple R-D equations for the Lotka-Volterra interactions does not seem so surprising. There are many features of the individual-based simulations which may yield, under some specific conditions, the departure of the system from the dynamics which might be expected from the R-D equations. Different factors are important for the systems with different descriptions of the particle behaviour and, furthermore, different factors may come to play for different parameters for the same qualitative particle behaviour. Further studies are necessary to check which spatio-temporal equations might provide a good description for the simulated data. Different mathematical descriptions may also be necessary for different parameter ranges of the simulations.

Three kinds of drift were observed in our simulations:

1. The drift in the phase space of the system between different closed orbits of the Lotka-Volterra equations. The observed pattern was much more realistic than closed, structurally unstable orbits of (3).
2. The drift of population density in the simulated space, which created fuzzy but easily notable waves (Fig. 6).
3. The drift of oscillation phase in local observation windows, which resulted in the decreased oscillation amplitude in the larger observation windows due to averaging over a few smaller windows with a different oscillation phase.

The wavy space patterns and local oscillation drift were of course two aspects of the same phenomenon. The reason for these patterns was in the increased complexity of the system, in spite of the homogeneous initial distribution of the particles, due to interactions between preys and predators. This phenomenon is not expected from the possible continuous description of the simulated populations by the reaction-diffusion equations. The most probable explanation for the disagreement between the continuous model and our simulations is the discrete description of individuals. Local irregular interactions between individuals might be enhanced by the interaction rules and result in the loss of the homogeneity of the initial space distribution with a randomly arising pattern of a new distribution. The pattern then oscillated in a fuzzy, irregular way in a small space scale. However, the regularity increased with the increasing scale. At any scale, the values of the parameters of the Lotka-Volterra equations estimated for the time oscillations of the average population densities were close (Tab. 1). Some impact of the observed space and time patterns on the estimated parameters could also be noted. For other parameters of the simulated system, the description of the results by the Lotka-Volterra equations might however not be so good as in the case shown in the present paper. The possible patterns in the system and their relationships to the mathematical description should therefore be further studied.

In summary, the appearance of spatio-temporal patterns in individual-based simulations has been observed in contrast to the predictions from the continuous description by reaction-diffusion equations. The pattern was not regular, but fuzzy and random. However, using averaging over oscillations, some generic features resembling those for the solutions to the Lotka-Volterra equations could be found. Furthermore, the parameters of the equations could be estimated at different space scales (observation windows of different sizes). The values of the parameters were similar for all window sizes, but small differences reflected the effects of limited particle migration and of averaging over the patterns of smaller scale than the size of the window.

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