

# A history-dependent stochastic predator-prey model: Chaos and its elimination

R. Gerami<sup>1,2,a</sup> and M.R. Ejtehadi<sup>1</sup>

<sup>1</sup> Institute for Studies in Theoretical Physics and Mathematics, PO Box 19395-5531, Tehran, Iran

<sup>2</sup> Department of Physics, Sharif University of Technology, PO Box 11365-9161, Tehran, Iran

Received 12 July 1999

**Abstract.** A non-Markovian stochastic predator-prey model is introduced in which the prey are immobile plants and predators are diffusing herbivores. The model is studied by both mean-field approximation (MFA) and computer simulations. The MFA results a series of bifurcations in the phase space of mean predator and prey densities, leading to a chaotic phase. Because of emerging correlations between the two species distributions, the interaction rate alters and if it is chosen to be the value which is obtained from the simulation, then the chaotic phase disappears.

**PACS.** 87.23.Cc Population dynamics and ecological pattern formation – 05.45.-a Nonlinear dynamics and nonlinear dynamical systems – 82.20.Wt Computational modeling; simulation

## 1 Introduction

The time evolution of systems of interacting species modeling natural ecosystems has attracted wide attention since its first studies by Lotka [1] and Volterra [2]. Various models have been introduced in order to consider different aspects of natural life, including motion, birth and death processes, evolution and extinction [3–5]. Physical motivation for studying such models is that they exhibit interesting features such as chaos and critical phenomena.

A much studied category of such models is that of two interacting species, the so called predator-prey systems [6,7]. However, most of the existing models neglect the effect of time delays on the dynamics of the models. By time-delayed systems we mean such systems that their dynamics is not defined only by knowing their present state, but some information about previous states is required. Time delays are present in many different physical or biological systems, and are particularly able to account for many features of ecological phenomena [3,8,9], although they have not been studied extensively.

In this paper we introduce a new model of the predator-prey problem with history-dependent dynamics. In our model, herbivores and edible plants are the predators and the prey, respectively. The predators stray randomly in a plant-full environment, eating them when they find any, but the eaten plant will regrow after a definite elapsed time. The predators reproduce with a constant rate and die, if they have not eaten anything in a specified length of time. In our model, time delays enter the temporal evolution equations through the terms rep-

resenting plants growth and predators death. Somewhat similar models without such time delays were published before [10,11].

The set of time-delayed equations leads to a rich collection of dynamical behaviors including chaos. As we will show, however, the emerging space correlation of the densities can eliminate the chaotic behavior.

We have studied this model by discrete-time, lattice-based computer simulations, as well as by a mean-field approximation solution. In what follows we describe our model and then present and discuss the results.

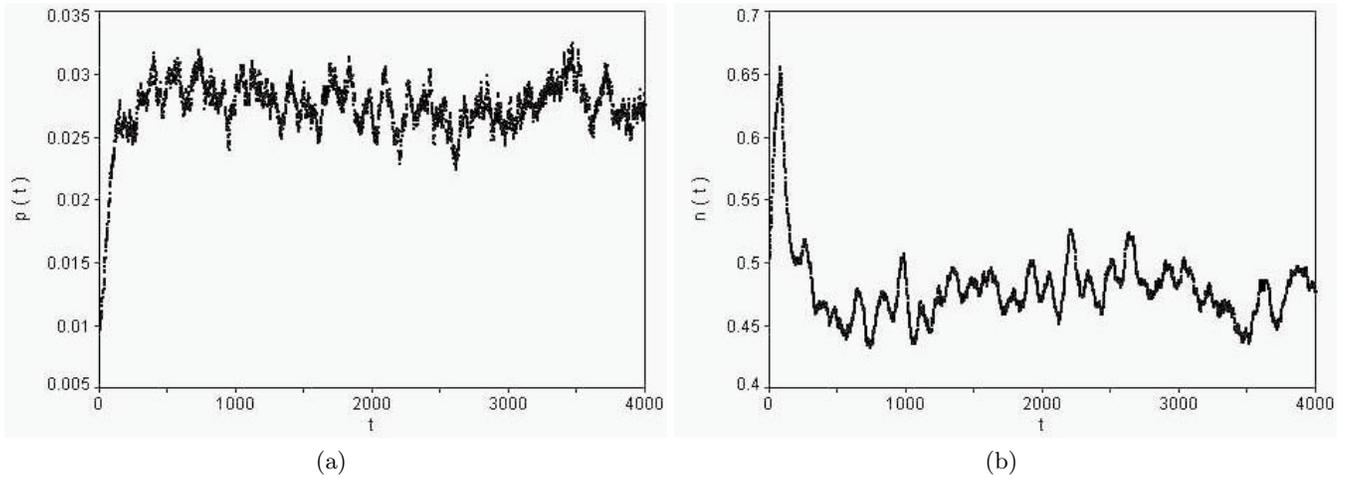
## 2 The model

The ecosystem consists of a(n infinite) square lattice each site of which if not empty, is occupied by either predators or a plant. The predators move randomly to one of the nearest neighbors (two-dimensional free random walk) and do not interact with each other, therefore multiple occupancy of the site is allowed. If a predator enters a site occupied by a plant, it will eat it. However after  $c$  time steps another plant grows at that site.

To every predator an *energy* is assigned, indicating the number of steps that it can go without eating anything. As a result, the energy is lowered by one at every time step. Eating a plant raises the energy to the maximum value  $l$ , so that a predator that has not eaten anything in  $l$  steps will die. At every time step each predator reproduces with probability  $b$ . The offspring is positioned at the same site and half of the parent's energy is transferred to it.

These rules are applied in the following order. The predators are first moved in a random sequence. They eat

<sup>a</sup> e-mail: rouzbeh@theory.ipm.ac.ir



**Fig. 1.** Predator and plant mean densities with respect to time for  $l = 20$ ,  $b = 0.02$ ,  $c = 80$ ,  $p(0) = 0.01$  and  $n(0) = 0.75$ . (a)  $p(t)$ , (b)  $n(t)$ .

every plant that they can, after which they reproduce with some probability and finally plant growth occurs. In the case of more than one predator entering a plant site, the early comer eats the plant.

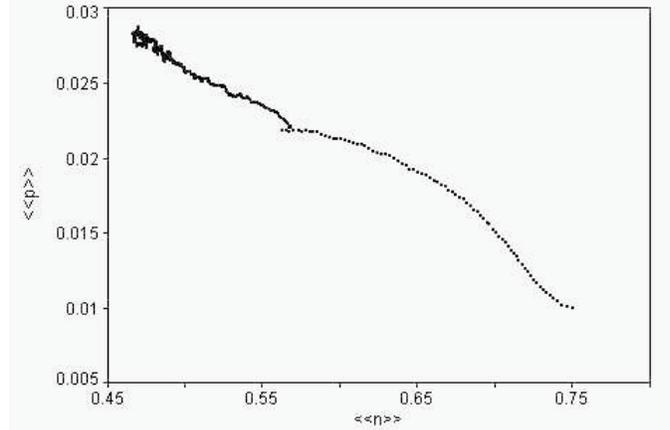
The rules governing the motion of the predators are those that are characteristics of branching diffusion processes, for which the space and time average quantities as well as spatial correlations have been investigated [12]. What we examine in the following sections is the time evolution of the mean spatial densities of predators and plants.

### 3 Fixed points and cluster formation

We first present the results obtained from simulating the model. Simulations are made on a  $M \times M$  square lattice with  $M = 100$  and with periodic boundary conditions. As initial conditions, predators and plants are distributed randomly and the value of  $l$  is assigned to the energy of every predator. The sites that are initially plant-free must be filled with plants in the first  $c$  steps, so a random integer  $\tau$ ,  $0 < \tau < c$ , is assigned to every such site, and a plant occupies that site at the  $t = \tau$ 's time step.

Let  $P(\mathbf{x}, t)$  and  $N(\mathbf{x}, t)$  denote predator and plant respective local densities and  $p(t)$  and  $n(t)$  be their respective spatial mean values, *i.e.*  $p(t) = \langle P(\mathbf{x}, t) \rangle$  and  $n(t) = \langle N(\mathbf{x}, t) \rangle$  (where  $\langle \cdot \rangle$  stands for spatial averaging).  $P(\mathbf{x}, t)$  is an integer number including 0, while  $N(\mathbf{x}, t)$  is either 0 or 1.  $p(t)$  and  $n(t)$  are assumed to be equal to the probability of predators and plants occupying a lattice site (assuming that  $p$  does not become larger than one).

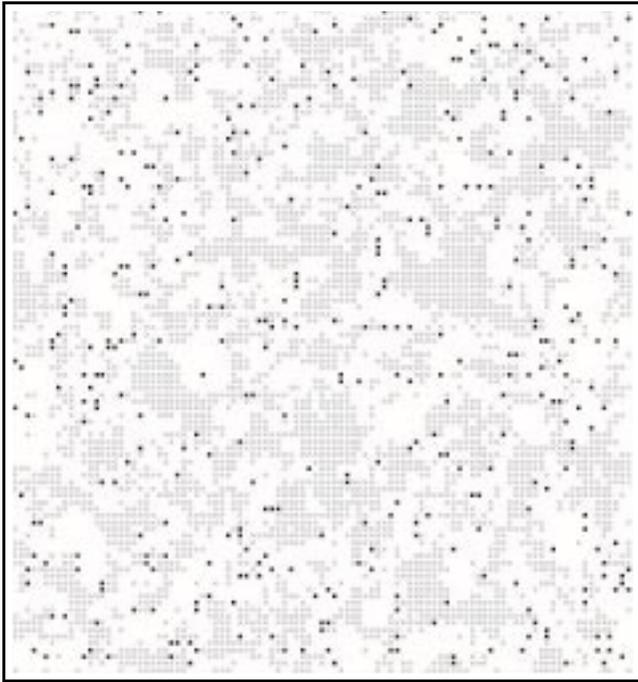
As expected, time evolution of the two species can lead to a stationary state (Fig. 1) in which both  $n$  and  $p$  fluctuate about their (time independent) mean values, and the fluctuations are predominantly anticorrelated (in the sense that when  $p$  goes up,  $n$  comes down and *vice versa*). Therefore by averaging  $n(t)$  and  $p(t)$  over many realizations of



**Fig. 2.** Fixed point in the phase space of expectation values of predator and plant mean densities ( $\langle\langle p \rangle\rangle$ ,  $\langle\langle n \rangle\rangle$ ), for the same parameter set as in Figure 1.

the system we find a fixed point in the ( $\langle\langle p \rangle\rangle$ ,  $\langle\langle n \rangle\rangle$ ) phase space (Fig. 2) (where  $\langle\langle \cdot \rangle\rangle$  represents the expectation value found by averaging over different realizations).

Trivially,  $(n, p) = (1, 0)$  is also a fixed point (*extinction state*). In a wide range of parameters this is unstable, and there exists the just described active oscillatory state with a ( $\langle\langle p \rangle\rangle$ ,  $\langle\langle n \rangle\rangle$ ) stable fixed point. But in a large region in the parameter space of  $l$ ,  $b$  and  $c$ , the point  $(1, 0)$  is stable and there is no non-extinction stationary state. This is the case for sufficiently large  $c$  (low growth rate for the plants), low  $l$  (low energy content of a plant) or low  $b$  (low predator birth rate). Even an unstable fixed point,  $(1, 0)$  can be reached (in transient region) by specific initial conditions that are large  $p(0)$  or large  $n(0)$ . In the latter case, the initially high density of plants increases  $p$  and decreases  $n$  very much and consequently all the predators die of starvation. In the following we consider the non-trivial (non-extinction) stationary state.



**Fig. 3.** Distribution of predators and plants in a  $100 \times 100$  lattice for  $l = 20$ ,  $b = 0.02$ ,  $c = 60$  and  $t = 500$ . Predators are represented by black dots and plants by grey.

Although the predators (plants) have no interaction with each other, the spatial distributions of  $N(\mathbf{x})$  and  $P(\mathbf{x})$  are not uniform in the stationary state. This is due to the rules of the game that are random motion of predators and the laws of birth and death [13]. As a typical pattern, Figure 3 shows the emergence of clusters of predators and plants for  $l = 20$ ,  $b = 0.02$ ,  $c = 60$  and  $t = 500$ , when the system is in its stationary state. Formation of the clusters is characterized quantitatively by the predator or plant autocorrelation functions defined by

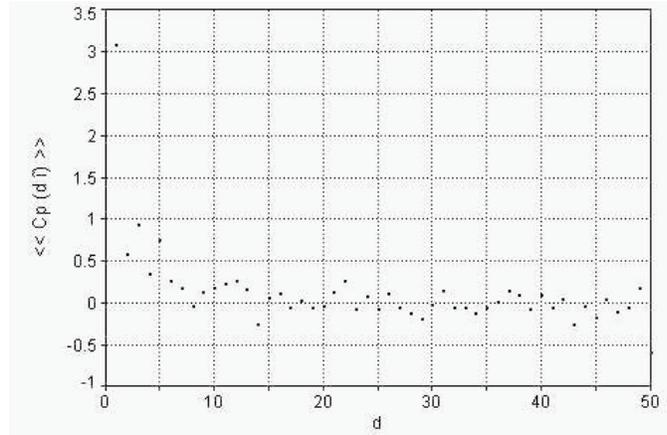
$$C_n(\mathbf{d}) = \frac{\langle N(\mathbf{x} + \mathbf{d})N(\mathbf{x}) \rangle - n^2}{n^2} \quad (1)$$

$$C_p(\mathbf{d}) = \frac{\langle P(\mathbf{x} + \mathbf{d})P(\mathbf{x}) \rangle - p^2}{p^2} \quad (2)$$

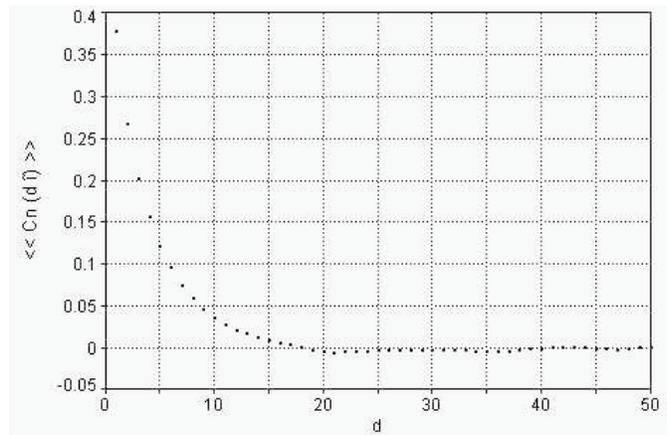
These clusters form separately, since if there is a plant at a site no predators can be at the same site. This is shown by the predator-plant correlation function:

$$C_{np}(\mathbf{d}) = \frac{\langle N(\mathbf{x} + \mathbf{d})P(\mathbf{x}) \rangle - np}{np} \quad (3)$$

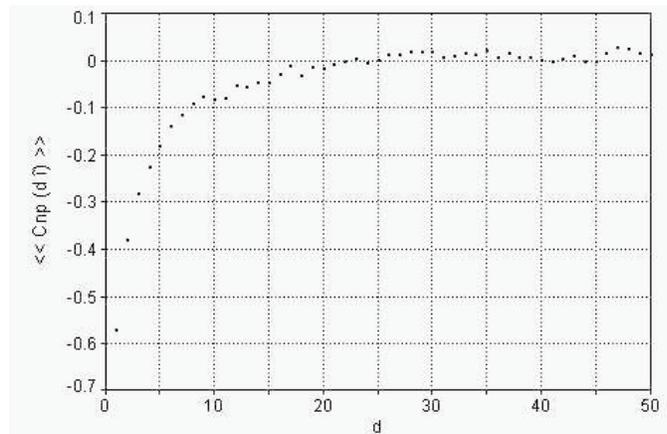
Figure 4 shows  $\langle\langle C_n(\mathbf{d}) \rangle\rangle$ ,  $\langle\langle C_p(\mathbf{d}) \rangle\rangle$  and  $\langle\langle C_{np}(\mathbf{d}) \rangle\rangle$  as functions of  $d$  along the lattice axis, for the same parameter set as in Figure 3. They all vanish as  $d$  increases, but while  $C_n$  and  $C_p$  are positive functions for small  $d$ , representing formation of the clusters,  $C_{np}$  is negative since the probability that a plant occupies a site decreases if there is a predator in the neighborhood. Diffusion of the predators increases the fluctuations in  $C_p$  and  $C_{np}$ . An exponential function best fits to  $C_n$  with correlation length increasing with  $c$ .



(a)

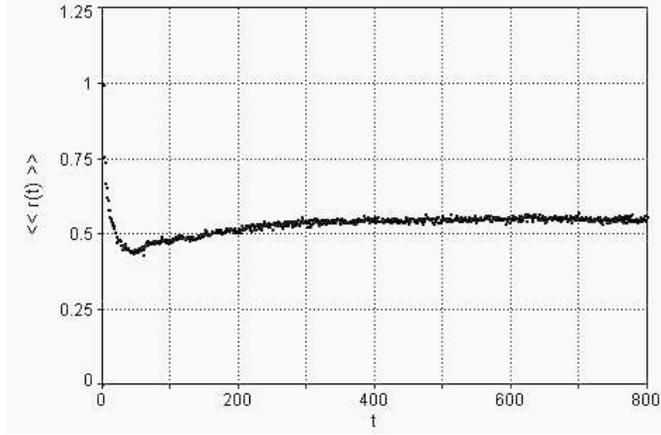


(b)



(c)

**Fig. 4.** Expectation values of (a) autocorrelation function of predators (b) autocorrelation function of plants (c) predator-plant correlation function, as a function of  $d$  along the lattice axis (with unit vector  $\mathbf{i}$ ) for  $l = 20$ ,  $b = 0.02$ ,  $c = 150$  and  $t = 500$ . An exponential function best fits to  $C_n$  with correlation length increasing with  $c$ .



**Fig. 5.** Numerically calculated expectation value of  $r(t)$  as a function of  $t$  for  $l = 20$ ,  $b = 0.02$  and  $c = 60$ , with 0.54 mean value for  $t > 400$ .

## 4 Mean-field approximation

We consider the correlation of the predators and plants within a mean-field approximation. If the probabilities that a site is occupied by a predator or a plant were independent, the density of the eaten plants at every time step would be given by

$$\Delta_- n(t) = n(t)p(t) \quad (4)$$

*i.e.*  $\Delta_- n(t)$  is the probability of that a site is simultaneously occupied by both a predator and a plant. To take into account the just described correlations, we modify this expression, by writing as

$$\Delta_- n(t) = rn(t)p(t) \quad (5)$$

where  $0 < r < 1$  and also can be thought of as a rate. Stronger correlations imply larger clusters which lowers the value of  $r$ . Introduction of  $r < 1$  rate, can also be justified in this way: since predators move randomly, a predator lowers its food-eating chance by repeatedly coming back to the sites which had previously been occupied by itself and it had eaten the plants in them. We show that  $r$  is an important parameter that controls the ability of the system to transit into a chaotic phase.

To calculate  $r(t)$  by simulation, we enumerate the total number of the eaten plants at time  $t$  and divide it by  $M^2 n(t)p(t)$ . Figure 5 represents as a function of time, the value of  $\langle r(t) \rangle$  for  $l = 20$ ,  $b = 0.02$  and  $c = 60$  which indicates that it becomes essentially a constant at about  $\langle r(t) \rangle \simeq 0.54$  in the stationary state. In fact  $\langle r(t) \rangle$  varies slightly as  $a$ ,  $b$  and  $c$  change. The value of  $r$  can also be read from the correlation function (Fig. 4c). Since the probability that a plant is eaten is 1/4 of the probability that a predator and a plant are nearest neighbors, and this probability is equal to the probability of finding a predator and a plant within a unit distance  $\mathbf{i}$ , we have

$$\Delta_- n = rnp = \langle n(\mathbf{x} + \mathbf{i})n(\mathbf{x}) \rangle \quad (6)$$

then

$$C_{np}(\mathbf{i}) = r - 1. \quad (7)$$

From Figure 4c we find that  $C_{np}(\mathbf{i}) \simeq 0.46$  and  $r = 0.54$  in complete agreement with the independently calculated value of  $r$  (Fig. 5).

The time evolution equations will then be

$$n(t+1) = n(t) + r[n(t-c+1)p(t-c+1) - n(t)p(t)] \quad (8)$$

$$p(t+1) = p(t) \left\{ (1+b) - \prod_{t'=0}^{l-1} [1 - rn(t-t')] \right\}. \quad (9)$$

The second term on the right-hand side of equation (8) is  $\Delta_- n(t)$  and the first is  $\Delta_+ n(t) = \Delta_- n(t-c+1)$ , the density of the plants eaten at time  $(t-c+1)$  which will grow again after  $c$  steps at time  $t+1$ . The second term on the right-hand side of equation (9) is the probability of a predator not eating anything in each of the past  $l$  steps. At any time, a predator does not eat a plant with a probability

$$\frac{p(t) - rn(t)p(t)}{p(t)} = 1 - rn(t) \quad (10)$$

*i.e.* the ratio of density of those predators who do not eat to the total predators density.

## 5 Solution of the mean-field equations

In order to find the possible solutions of this set of equations, we numerically compute  $p(t+1)$  and  $n(t+1)$ , knowing the values of  $p$  and  $n$  at the earlier times. By repeatedly doing this, we can find all the possible trajectories in the  $(p, n)$  phase space. However, because of the existence of time delays, it is not sufficient to know only  $p$  and  $n$  at time 0 in order to initiate these equations. Therefore, to overcome this difficulty we rewrite these equations as

$$n(t+1) = n(t) + \frac{1-n(0)}{c} - rn(t)p(t) \text{ for } t < c \quad (11)$$

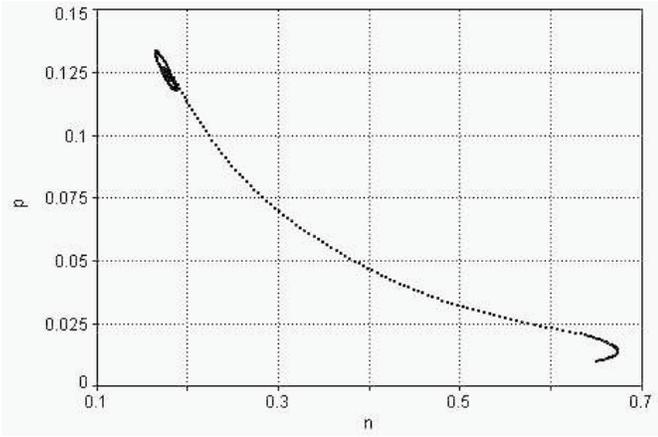
$$p(t+1) = p(t)(1+b) \text{ for } t < l. \quad (12)$$

We drop the  $rn(t-c+1)p(t-c+1)$  term from equation (8) for  $t < c$ , and add the term

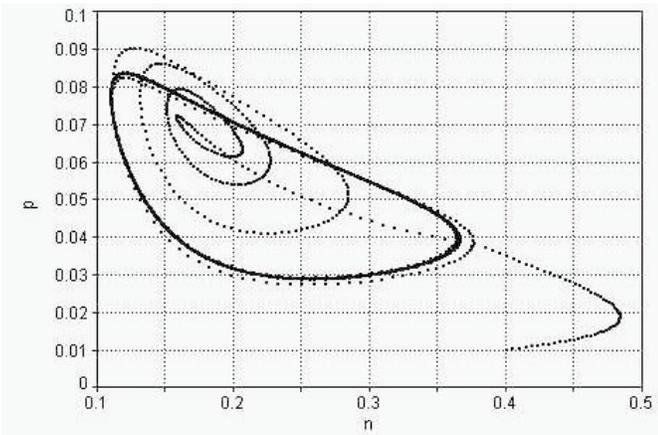
$$\frac{1-n(0)}{c} \quad (13)$$

to take into account growing of the plants in the initially plant-free sites. Also, we eliminate the second term in equation (9) for  $t < l$  because of the initially full energy of all the predators.

As in the case of the simulations,  $(1, 0)$  is a trivial fixed point, which is unstable only for sufficiently low  $l$ , low  $b$  or high  $c$  and long-time behavior of the solutions does not depend on the values of  $n(0)$  and  $p(0)$ . Here, we do not consider that range of the parameters for which extinction occurs. In order to find a fixed point (Fig. 6) we assume that  $n$  and  $p$  are constant for a long time, that is  $n(t') = n^*$



**Fig. 6.** A fixed point in  $(p, n)$  phase space, derived from mean-field equations, for  $l = 20$ ,  $b = 0.02$  and  $c = 38$ .



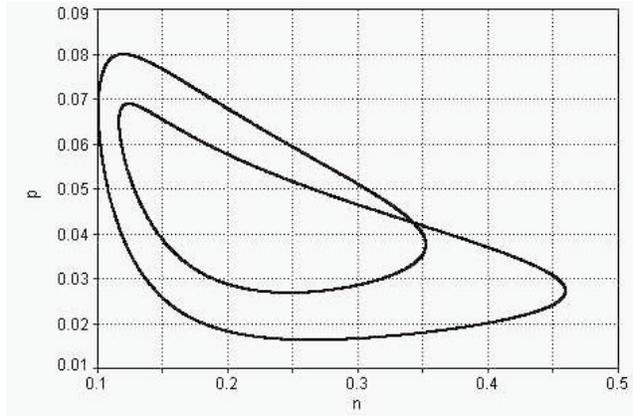
**Fig. 7.** A limit cycle in  $(p, n)$  phase space, derived from mean-field equations, for  $l = 20$ ,  $b = 0.02$  and  $c = 67$ .

for  $t - l \leq t' \leq t$  and  $p(t - c + 1) = p(t) = p^*$ . This leads to

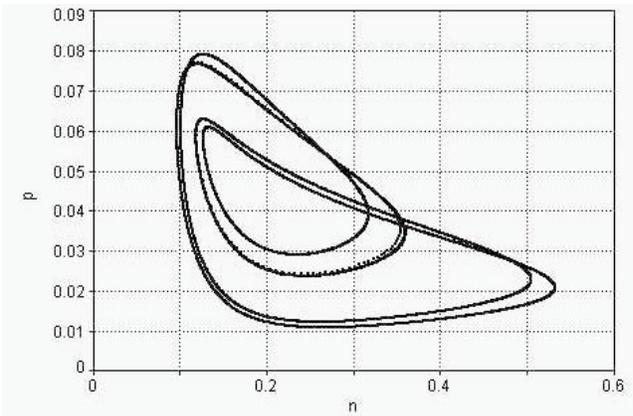
$$n^* = \frac{1}{r} [1 - (1 + b)^{1/l}] \tag{14}$$

(which is independent of  $c$ ) but no explicit expression for  $p^*$ . However, interestingly, as we have checked numerically, there also exists a unique  $p^*$  and the fixed point (specially its  $p$ -coordinate) is uniquely determined by the parameters and independent of initial conditions.

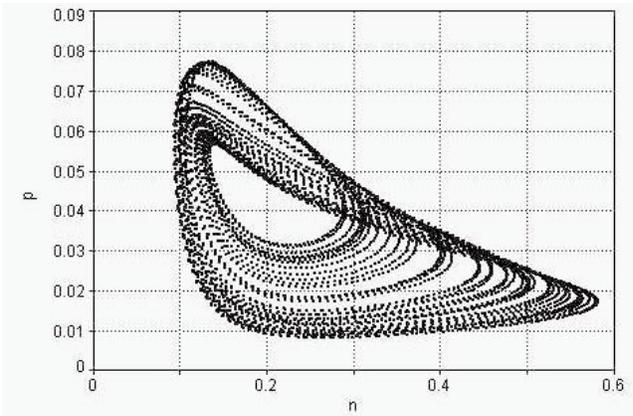
Although  $r$  is obtained definitely from simulation, we assume it to be variable. It is easily seen that the dynamics of the equations depends critically on the value of  $r$ . We temporarily assume  $r = 1$  which means neglecting the correlations and clustering. For every  $l$  and  $b$  the fixed point is stable for low  $c$ . As  $c$  is increased, the fixed point eventually loses its stability through a Hopf bifurcation and turns to a limit cycle (Fig. 7). As  $c$  is increased further, more bifurcations occur which lead to the chaotic phase (Fig. 8). Figure 9 represents the bifurcation diagram, which is the Poincare maps for constant  $l$  and  $b$  and varying  $c$ , obtained from the intersection of trajectories in the phase space with the vertical line  $n = n^*$ . Figure 10 is the same graph for the same set of parameters except



(a)



(b)

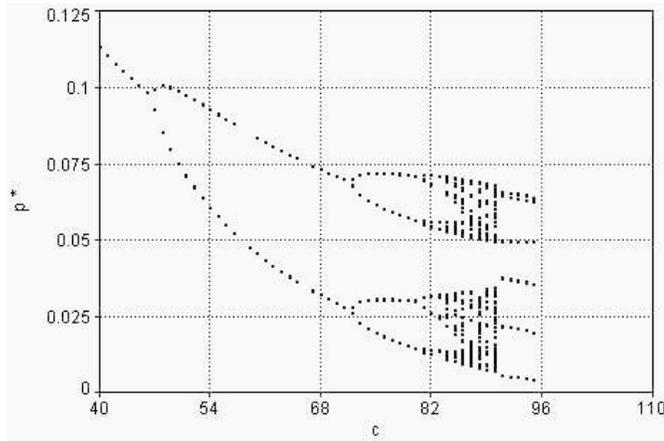


(c)

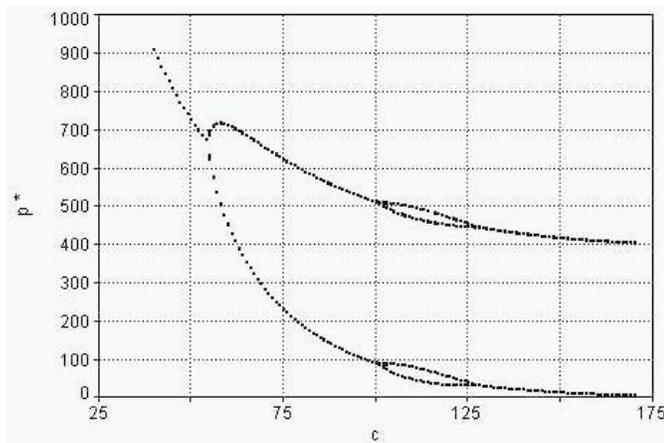
**Fig. 8.** Long-time behavior of other possible solutions of mean-field equations, as  $c$  is increased with other parameters constant (transients have been omitted): (a) two cycles for  $c = 75$  (b) four cycles for  $c = 82$  (c) chaos for  $c = 84$ , in this case the total area is filled in the long times.

that  $r = 0.48$  (see below), in which the chaotic regime has been eliminated.

We found that the time-evolution equations with a realistic value of  $r(l, b, c)$  which is obtained from the simulation, do not exhibit a chaotic behavior. This is similar to what occurs in the simulation which always there exists a stationary state. However, setting  $r = 1$



**Fig. 9.** Bifurcation diagram: intersection points of trajectories in the phase space with vertical line  $n = n^*$ , for the same  $l$  and  $b$  as Figure 7 and  $r = 1$ .



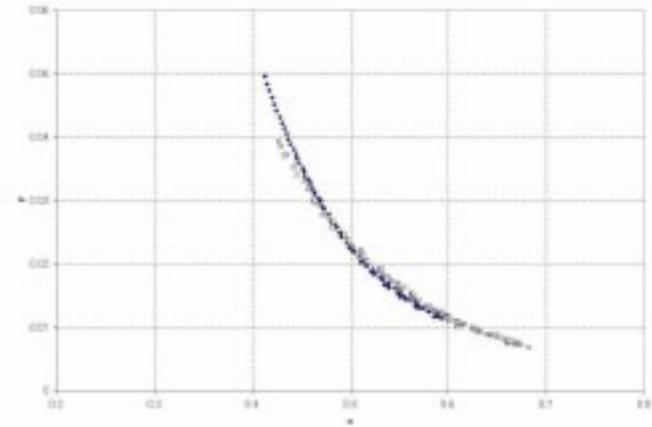
**Fig. 10.** The same as Figure 9 but with  $r = 0.48$ .

artificially, can produce a chaotic behavior. This has an interesting interpretation: formation of the clusters and emergence of correlations removes the chaotic regime.

Finally, Figure 11 offers a comparison between the mean-field results and those of the computer simulations. Here, the fixed points in  $(\langle\langle p \rangle\rangle, \langle\langle n \rangle\rangle)$  phase space derived from simulation and the time-average of  $(p, n)$  obtained from the mean-field equations are shown with  $l = 20$ ,  $b = 0.02$ , and varying  $c$  from 65 to 150.  $r$  is chosen so that the two curves best coincide and that occurs if  $r \simeq 0.48$ .

## 6 Conclusion

We have introduced and studied a model for the predator-prey problem with time delay in which the prey are edible plants and the predators are herbivores. The model is defined algorithmically through a series of rules that are i) random-walk motion of the predators; ii) growth of the eaten plants after a time delay, and iii) death of those predators not having eaten anything in a specified length of time. Both rules ii and iii generate history dependence in the mean-field equations. Simulation of the model on a lattice yields stationary states with fixed points in the



**Fig. 11.** Comparison of simulation and mean-field results: black squares are numerically calculated fixed points in  $(\langle\langle p \rangle\rangle, \langle\langle n \rangle\rangle)$  phase space. White squares are time average of  $p$  vs. time average of  $n$  derived from mean-field equations.  $r$  is chosen to be 0.48 which best coincides two curves.

phase space of  $(\langle\langle p \rangle\rangle, \langle\langle n \rangle\rangle)$  as well as a trivial  $(1, 0)$  fixed point.

In such stationary states, the predators and the prey are distributed in separately-formed clusters and hence producing non-zero autocorrelation as well as correlation functions. Such correlations are taken into account in the mean-field equations by introduction of a rate  $r < 1$  in the expression of the eaten plants density. These equations have chaotic solutions for  $r$  nearly 1, but there is no chaos if  $r$  is lowered to its true value obtained from the simulation.

The authors offer their special thanks to N. Hamedani, V. Shahrezaei, H. Seyed-Allaei and S.E. Faez for invaluable discussions and to M. Sahimi, A. Erzan and A. Aghamohammadi for carefully reading the manuscript and useful comments.

## References

1. A.J. Lotka, Proc Natl. Acad. Sci. U.S.A. **6**, 410 (1920).
2. V. Volterra, Mem. Accad. Nazionale Lincei **26**, 31 (1926).
3. J.D. Murray, *Mathematical Biology* (Springer Verlag, N.Y., 1993).
4. Z. Csahok, T. Vicsek, Phys. Rev. E **52**, 5297 (1995).
5. T.J.P. Penna, J. Stat. Phys. **78**, 1629 (1995).
6. N. Boccara, O. Roblin, M. Roger, Phys. Rev. E **50**, 4531 (1994).
7. J. Satulovsky, T. Tome, Phys. Rev. E **49**, 5073 (1994).
8. J. Faro, S. Velasco, Physica D **110**, 313 (1997).
9. V. Mendez, J. Camacho, Phys. Rev. E **55**, 6476 (1997).
10. W.F. Wolff, in *Ecodynamics - Contributions to Theoretical Ecology*, edited by W. Wolff, C.J. Soeder, F.R. Drepper (Springer, Berlin-Heidelberg, 1988) pp. 285.
11. I. Mroz, A. Pekalski, Eur. Phys. J. B **10**, 181 (1999).
12. K.B. Althreya, P.E. Ney, *Branching Processes* (Springer, Berlin, 1972).
13. M. Meyer, S. Havlin, A. Bunde, Phys. Rev. E **54**, 5567 (1996).