

Oscillatory behavior in a lattice prey-predator system

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Using Monte Carlo simulations we study a lattice model of a prey-predator system. We show that in the three-dimensional model populations of preys and predators exhibit coherent periodic oscillations but such a behavior is absent in lower-dimensional models. Finite-size analysis indicate that amplitude of these oscillations is finite even in the thermodynamic limit. This is an example of a microscopic model with stochastic dynamics which exhibits oscillatory behavior without any external driving force. We suggest that oscillations in our model are induced by some kind of stochastic resonance.

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I. INTRODUCTION

Oscillatory behavior in spatially extended systems, which appears in various forms in many branches of physics, is still not fully understood [1]. As an example of such a behavior we can mention periodic oscillations in certain autocatalytic reactions [2]. From the theoretical point of view, the main problem is that inevitable fluctuations should wipe out any coherent behavior in such systems, thus questioning the very existence of periodic oscillations. Indeed, numerical analysis of a certain one-dimensional reaction diffusion model (“Brusselator”) confirms a very strong destructive role of the fluctuations in such systems [3].

Another example of this kind is the oscillatory behavior in prey-predator systems, which is one of the classical problems in population dynamics. In the most transparent way such oscillations were observed for populations of hares and lynxes [4]. The earliest explanation of oscillations in such systems was proposed by Lotka and Volterra [5]. In their model, populations of prey and predators are described by the following set of differential equations:

$$\frac{dx}{dt} = ax - bxy, \quad \frac{dy}{dt} = -cy + dxy, \quad (1)$$

where x and y denote the number of prey and predators, respectively, and a, b, c, d are certain positive constants.

Simple analyses of model (1) indeed reveal the existence of a limit cycle, i.e., populations of prey and predators exhibit periodic (in time) oscillations. However, model (1) has certain drawbacks. In particular, it predicts an unbounded, exponential growth of the number of prey in the absence of predators ($y=0$). To cure this defect one has to introduce additional terms into these equations (environmental capacity) and such terms in general destroy the limit-cycle solutions and asymptotically (i.e., for $t \rightarrow \infty$) the constant solutions are obtained [7,8]. In this respect model (1) might be more precisely termed as structurally unstable.

In principle, one can replace right-hand sides of the above equations by more complicated functions of x and y , and the resulting equations [6] will exhibit both a limit-cycle behav-

ior and remain bounded for $y=0$. It is not clear, however, how these particular functions should be related to characteristics of the populations.

Recently, a lattice model of a prey-predator system was introduced [9]. It was shown that in the steady state this model has two phases: (i) an active phase with a positive fraction of both prey and predators and (ii) an absorbing phase with predators being extinct and prey invading the whole system. For certain values of a control parameter the model undergoes a phase transition of the directed-percolation universality class, which is actually an anticipated property, taking into account the existence of a single absorbing state in the model’s dynamics [10].

An important feature of such a lattice model is that its properties might be studied using controllable techniques, e.g., Monte Carlo simulations, rather than postulated equations. Moreover, such a microscopic model takes into account fluctuations in the system that are completely neglected in models based on differential equations such as Eq. (1). And it is these fluctuations that are responsible for the appearance of the phase transition in this model, since the mean-field approximation, which is equivalent to a certain set of differential equations similar to Eq. (1) (and thus neglects fluctuations), predicts that the active phase is the generic phase of the model for all values of the control parameter, and no transition takes place.

In the present paper we examine the time evolution of densities of prey $x(t)$ and predators $y(t)$ in the above-described lattice model. One might expect that fluctuations, which in our model are caused by the stochastic nature of the dynamics, result in a random and noncorrelated evolution of these densities. And indeed such a behavior is observed, but only in a one-dimensional version of our model. In a two-dimensional model the behavior of these densities is still irregular, but a pronounced peak in a Fourier transform of $x(t)$ and $y(t)$ appears, and for the three-dimensional model very regular periodic oscillations are observed. We argue that these oscillations are induced by a certain kind of stochastic resonance [12] and we suggest an analogy with a certain low-dimensional dynamical system examined some time ago by Gang *et al.* [11].

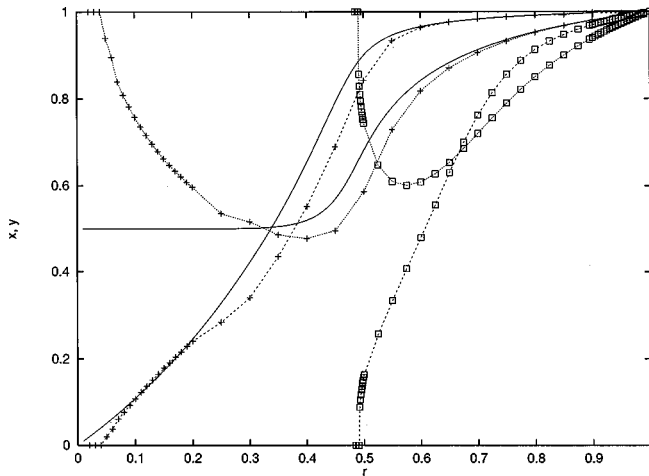


FIG. 1. Steady-state densities of prey (dotted lines) and predators (dashed lines) for the one- (\square) and three-dimensional (+) models as functions of r , as calculated using Monte Carlo simulations [9]. Mean-field results are shown by a solid line.

In addition to offering a model of prey-predator systems, our results are also of somewhat more general interest. They show that, in spatially extended systems, intrinsic fluctuations alone might induce periodic oscillations. This should be contrasted with the standard stochastic resonance setting, where some sort of external periodic perturbation is required.

The paper is organized as follows. In Sec. II we introduce the model and only briefly describe its steady-state properties, which were already described in more detail elsewhere [9]. In Sec. III we present time evolution and a spectral analysis of the density of prey for the one-, two-, and three-dimensional version of our model. Section IV contains the analysis of the standard deviation of density of prey as a function of time. In that section we also suggest a relation with stochastic resonance. Section V contains our conclusions.

II. MODEL AND ITS STEADY-STATE PROPERTIES

In our model a site of a d -dimensional Cartesian lattice of linear size L can be empty, occupied by a single prey, occupied by a single predator, or occupied by a single prey and a single predator. The dynamics of our model is specified as follows:

- (i) Choose a site at random.
- (ii) With the probability r ($0 < r < 1$) update a prey at the chosen site (if there is one; otherwise do nothing). Provided that at least one neighbor of the chosen site is not occupied by a prey, the prey (which is to be updated) produces one offspring and places it on the empty neighboring site (if there are more empty sites, one of them is chosen randomly). Otherwise (i.e., when there is a prey on each neighboring site), the prey does not breed (due to overcrowding).

(iii) With the probability $1-r$ update a predator at the chosen site (if there is one). Provided that the chosen site is not occupied by a prey, the predator dies (of hunger). If there is a prey on that site, the predator survives and consumes the prey from the site it occupies. If there is at least one neighboring site that is not occupied by a predator, the predator

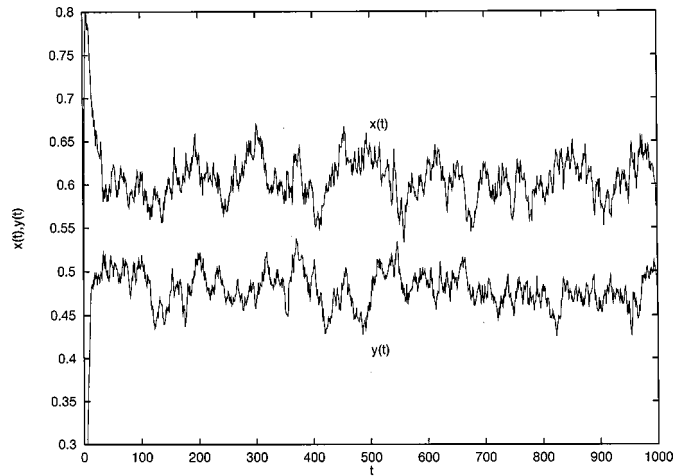


FIG. 2. Time evolution of $x(t)$ and $y(t)$ for the one-dimensional model and $r=0.6$. Calculations were made for the linear size $L=2000$.

produces one offspring and places it on the empty site (chosen randomly when there are more such sites).

A steady-state description of our model is given in terms of densities of prey x and predators y , which might also be regarded as the probabilities that a given site is occupied by a prey or a predator, respectively. Monte Carlo simulations of the above model predict [9] that this model will undergo the phase transition at a certain value of the parameter $r=r_c(d)$. The transition point $r_c(d)$ separates the active phase with $0 < x, y < 1$ and the absorbing phase with $x=1, y=0$. The plot of the steady-state densities x and y as functions of r for the one- and three-dimensional models, based on previous simulations [9], is shown in Fig. 1. Results for the two-dimensional model are not shown but they interpolate between the one- and three-dimensional graphs with the critical point located at $r=r_c(2) \sim 0.11$.

III. TIME EVOLUTION AND SPECTRAL ANALYSIS

Let us ask the following question: What is the time evolution of densities $x(t)$ and $y(t)$ in the active phase of our model? Because the model is driven by stochastic dynamics, the expected answer to this question is that these quantities

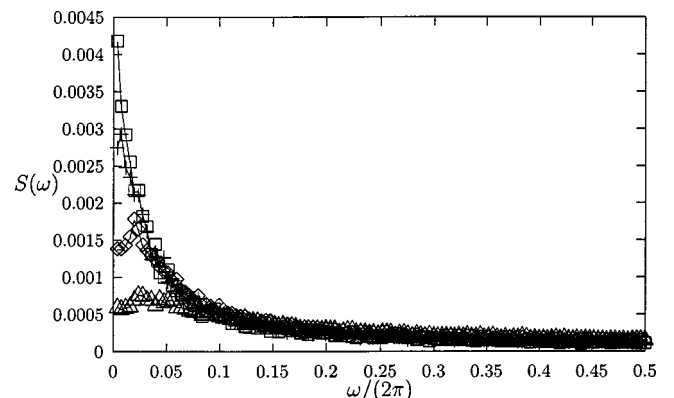


FIG. 3. Power spectrum $S(\omega)$ for the one-dimensional model and $r=0.7$ (\triangle), 0.6 (\diamond), 0.55 (+), and 0.52 (\square). Calculations are made for $L=10^4$.

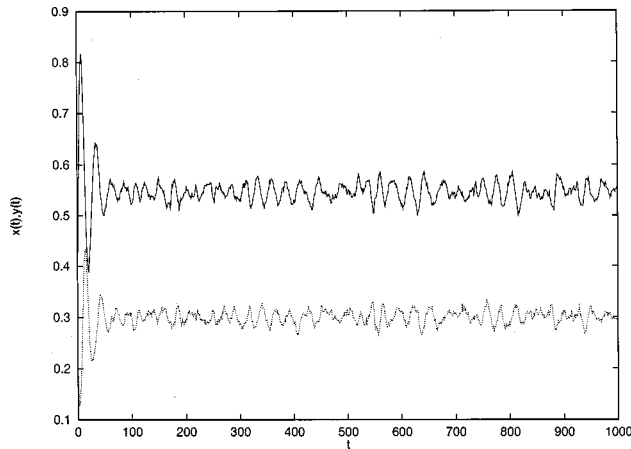


FIG. 4. Time evolution of $x(t)$ (solid line) and $y(t)$ (dotted line) for the two-dimensional model and $r=0.3$. Calculations were made for the linear size $L=200$.

exhibit more or less random fluctuations. Presented below results obtained using Monte Carlo simulations show that these expectations are not always correct.

A. $d=1$

Such random fluctuations are clearly observed for the one-dimensional model in the entire active phase [i.e., for $1 > r > r_c(1) \sim 0.491$], and an example for $r=0.6$ is shown in Fig. 2. To analyze the time evolution more quantitatively, we calculated the Fourier power spectrum of $x(t)$ and $y(t)$, and the results for $S(\omega) = |x(\omega)|$ are shown in Fig. 3. The spectrum of $y(t)$ is similar to that of $x(t)$ and is not shown. One can see that the spectrum is very broad, which is in agreement with a rather random pattern observed in Fig. 2. The spectrum is calculated using the intervals of 500 Monte Carlo steps, and averaging is made over 100 such intervals. The $S(\omega=0)$ value is not shown.

B. $d=2$

In this case populations of prey and predators also evolve in time rather irregularly (see Fig. 4). Such irregular behavior is reflected in Fig. 5, which shows that the spectrum in this

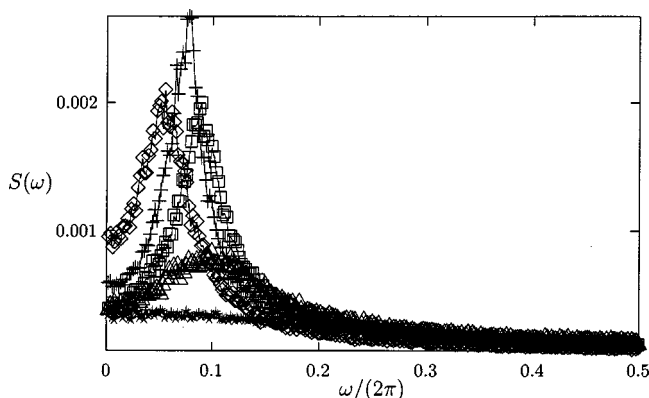


FIG. 5. Power spectrum $S(\omega)$ for the two-dimensional model and $r=0.6$ (\star), 0.5 (\triangle), 0.4 (\square), 0.3 ($+$), and 0.2 (\diamond). The increase of the low-frequency part for decreasing r is related to approaching the critical point at $r \sim 0.11$ (critical slowing down).

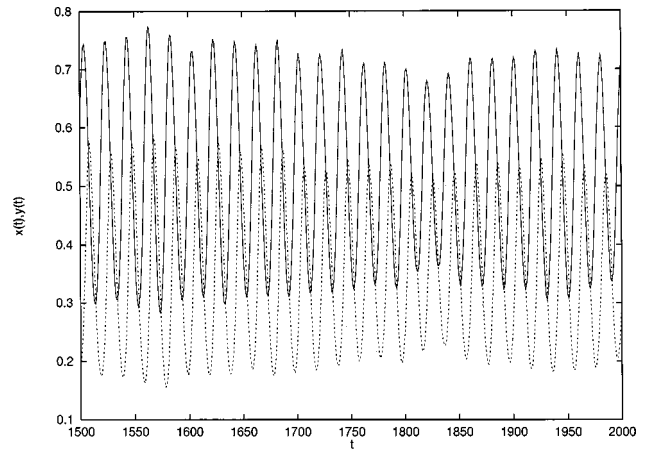


FIG. 6. Time evolution of $x(t)$ (solid line) and $y(t)$ (dotted line) for the three-dimensional model and $r=0.3$. Calculations were made for the linear size $L=30$.

case is also very broad. However, in a certain range of r one can see a pronounced peak in the spectrum at a certain r -dependent frequency. This peak is related to the appearance of a certain slow mode that can also be seen in Fig. 4. Let us also notice that upon approaching $r_c(2)$ (~ 0.11) this peak diminishes and shifts toward lower frequencies. As will be shown below, the behavior of the two-dimensional model is in some sense intermediate between the behavior of the one- and three-dimensional models.

C. $d=3$

The most interesting results are obtained for the three-dimensional model. In Fig. 6 we show the time evolution of $x(t)$ and $y(t)$ for $r=0.3$. For this value of r the system exhibits very regular oscillations and the spectrum (Fig. 7) has a very high and sharp peak. Such regular oscillations appear only in a certain range of r . For sufficiently large or sufficiently small r the irregular behavior, similar to that shown in Fig. 2 sets in.

IV. STANDARD DEVIATION AND ITS FINITE-SIZE ANALYSIS

The results shown in the preceding section clearly indicate a qualitative difference in the temporal evolution of the

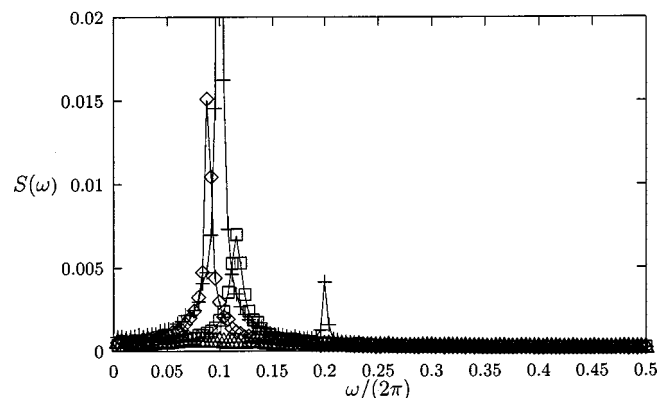


FIG. 7. Power spectrum $S(\omega)$ for the three-dimensional model and $r=0.5$ (\triangle), 0.4 (\square), 0.3 ($+$), and 0.2 (\diamond). Calculations are made for $L=30$. The maximum value of $S(\omega)$ for $r=0.3$ is $S_{\max} \sim 0.12$.

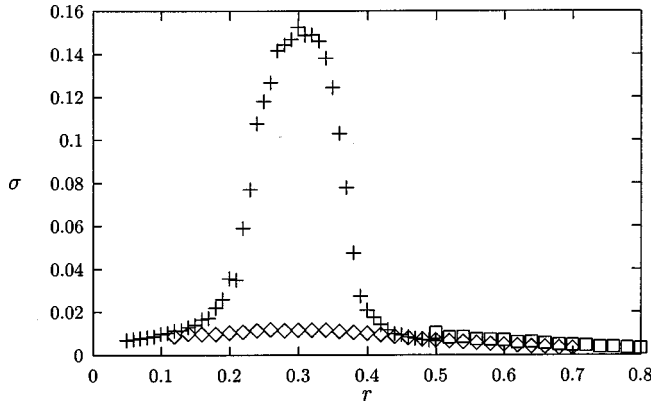


FIG. 8. Standard deviation σ as a function of r for the one- (\square), two- (\diamond), and three-dimensional models ($+$). For $d=1, 2$, and 3 calculations were made for $L=30000, 150$, and 30 , respectively. For each value of r we made runs of 2×10^4 Monte Carlo steps.

one- and three-dimensional models. Pronounced oscillations observed in the three-dimensional case prompted us to ask the following question: What is the amplitude of these oscillations in the thermodynamic limit ($L \rightarrow \infty$)? To answer this question we calculated the standard deviation σ of $x(t)$ for $d=1, 2, 3$ and various system sizes L and values of r . This quantity roughly corresponds to the amplitude of oscillations (or fluctuations) of $x(t)$. The behavior of σ as a function of r is shown in Fig. 8. For $d=1$ the standard deviation σ is only weakly r dependent and is a decreasing function of r . The increase of σ upon decreasing r is an expected behavior, since the largest fluctuations usually occur at the critical point $r_c(1)$ (~ 0.49). For the two-dimensional case, σ is also weakly r dependent, but one can see a small maximum of σ around $r=0.3$. On the other hand, for the $d=3$ case a pronounced maximum around $r=0.3$ is observed. Let us notice that this maximum is not related to the critical point, which in this case is located at a much smaller value of r , namely at $r=r_c(3) \sim 0.05$. On general grounds one expects that the outside critical point correlation length is finite in our model and thus the standard deviation of $x(t)$ [and also of $y(t)$] should scale as $1/L^{d/2}$. Thus, in the thermodynamic limit σ should converge to zero and so should the amplitude of oscillations.

Finite-size data, which we present in Figs. 9 and 10, show that in the three-dimensional case this argument is false. In Fig. 9 we plot the standard deviation σ as a function of $1/L^{d/2}$. If the above argument about the asymptotic scaling of σ were correct then σ should linearly approach zero for $L \rightarrow \infty$. Our data show that this is indeed the case for $d=1, 2$, and we expect that for $d=1, 2$ such a scaling holds for arbitrary r in the active phase. However, the behavior of $d=3$ is different. Although for $r=0.5$ the scaling seems to hold, it is clearly violated for $r=0.3$ where σ does not even converge to zero. It means that for $d=3$ and r presumably within a certain vicinity of 0.3 , the amplitude of oscillations remains finite in the thermodynamic limit. To our knowledge, this is the first example of oscillatory behavior in a microscopic model with stochastic dynamics and without external periodic force.

An additional indication of anomalous behavior can be seen in Fig. 10, where we present the same data as in Fig. 9

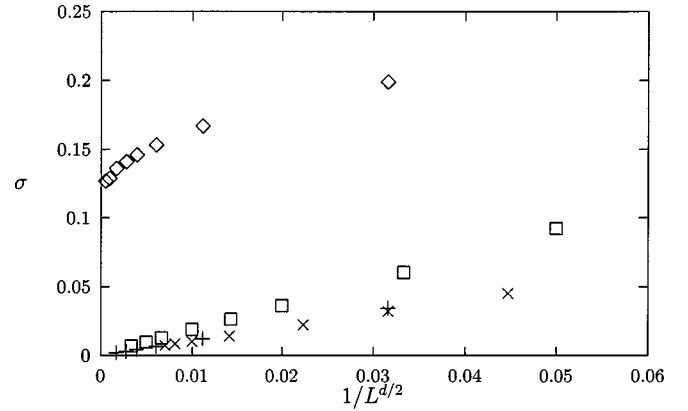


FIG. 9. Standard deviation σ as a function of $1/L^{d/2}$ for (a) $d=3$ and $r=0.3$ (\diamond), (b) $d=3$ and $r=0.5$ ($+$), (c) $d=2$ and $r=0.3$ (\square), and (d) $d=1$ and $r=0.6$ (\times).

but in the double-logarithmic scale. All the data, except $d=3$ and $r=0.3$, approximately follow the solid line of slope $1/2$ that confirms the scaling $\sigma \sim 1/L^{d/2}$. However, for $d=3$ and $r=0.3$ one observes a strong deviation from the expected scaling, and most likely (in agreement with Fig. 9) the standard deviation will remain finite for $L \rightarrow \infty$. Let us also emphasize that simulations for $d=3$ and $r=0.3$ were rather extensive: we made runs of 5×10^4 Monte Carlo steps for systems of linear size up to $L=150$.

To suggest some explanation of our results, let us first examine our model using the mean-field approximation. From the above-stated dynamical rules, after neglecting some correlations, one can easily derive the following mean-field equations [9]:

$$\frac{dx(t)}{dt} = rx(t)[1 - x(t)^{2d}] - (1-r)x(t)y(t), \quad (2)$$

$$\frac{dy(t)}{dt} = (1-r)x(t)y(t)[1 - y(t)^{2d}] - (1-r)[1 - x(t)]y(t). \quad (3)$$

These equations are very similar to Eq. (1), except that they contain some ‘‘environmental capacity’’ terms. Although we did not succeed in solving Eqs. (2) and (3) analytically, these equations can be easily solved numerically. First, equating to zero the left-hand sides of Eqs. (2) and (3), we obtain the so-called steady-state equations, and the solutions x and y of these equations for $d=3$ are shown in Fig. 1.

Numerical analysis indicates [9] that time-dependent solutions $x(t)$, $y(t)$ of Eqs. (2) and (3) asymptotically (for infinite time) always approach the steady-state solutions. Since these mean-field equations include the ‘‘environmental capacity’’ terms $[1 - x(t)^{2d}]$ and $[1 - y(t)^{2d}]$, the absence of limit-cycle solutions is an expected feature. However, for small r an approach to the steady state proceeds through many oscillations and the system resembles a weakly damped two-dimensional oscillator.

In our opinion, this quasioscillatory behavior suggests a certain mechanism that can explain the origin of such regular oscillations. First, let us notice that noise, which is an intrinsic feature of the dynamics of our model, is clearly neglected in the mean-field approximation (2), (3). In our opinion,

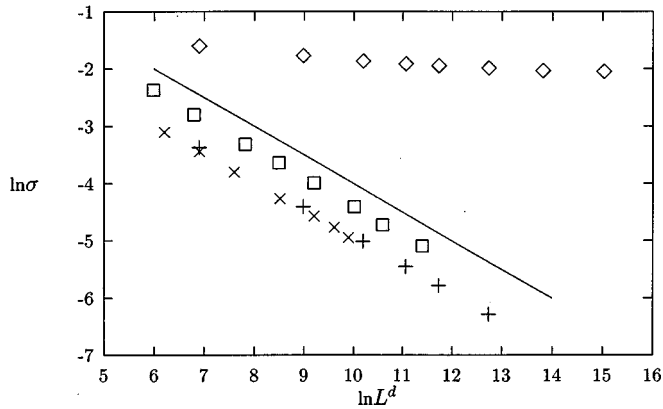


FIG. 10. Standard deviation σ as a function of L^d in a double logarithmic scale for (a) $d=3$ and $r=0.3$ (\diamond), (b) $d=3$ and $r=0.5$ ($+$), (c) $d=2$ and $r=0.3$ (\square), and (d) $d=1$ and $r=0.6$ (\times). The solid line has slope $1/2$.

when coupled to the nonlinear oscillator, Eqs. (2) and (3), this noise might, through some sort of stochastic resonance, lead to the observed regular oscillations.

One indication of a resonatory mechanism is shown in Fig. 7, where for $r=0.3$ one can see a second peak of $S(\omega)$ at approximately twice the frequency of the main peak. Presumably, with more accurate calculations of the spectrum one could also see higher-order harmonics. Another indication is in our opinion the very shape of σ as a function of r for $d=3$ in Fig. 8. Let us notice that σ is a measure of fluctuations of $x(t)$ and thus might be regarded as a response of our system to the noise. From Fig. 8 it is clear that the maximum of the response ($r \sim 0.3$) does not coincide with the maximum of the noise (which most likely occurs at critically, i.e., at $r=r_c \sim 0.05$), which is also a characteristic feature of resonatory systems.

An idea that random noise coupled to some low-dimensional autonomous system might lead to oscillatory behavior is not new. Some time ago Gang *et al.* [11] studied a certain two-dimensional dynamical model with a point attractor. In its parameter space their model is located close to the region with limit-cycle attractor, and as a result some transient oscillations are observed. Qualitatively their model is thus very similar to the system (1), (2). Gang *et al.* showed that when such a system is perturbed by a random noise, coherent oscillations are observed, caused by some kind of stochastic resonance. It might be interesting to examine the behavior of the system (2), (3) subjected to random noise. However, since this system is only a low-dimensional approximation, it is by no means obvious that it will correctly describe the behavior of our microscopic model.

V. CONCLUSIONS

In the present paper we examined the time evolution of densities of prey and predators in a certain lattice model. As our main result we have found that for the three-dimensional case these densities might exhibit very regular periodic oscillations. We presented numerical evidence that the amplitude of these oscillations is nonzero, even in the thermodynamic limit.

Is it possible to suggest a certain general feature of our model that would be responsible for the existence of such oscillations? As far as the steady-state properties of the model are concerned the model has two phases: active and absorbing. Since the absorbing state is unique (all sites being occupied by prey), as expected, the transition between them belongs to the directed-percolation universality class. However, a closer look at the dynamics shows that there is yet another absorbing state in this model: all sites being empty. But this absorbing state is very unstable and the model almost never ends up in this state (a single prey will invade the whole system in the absence of predators). Although this absorbing state is irrelevant as far as the critical properties are concerned, this state might, in our opinion, affect the off-critical dynamical properties of our model: First let us notice that empty sites are likely candidates for becoming occupied. Thus, when large clusters of empty sites can be formed, large fluctuations of densities are likely to happen too. Such large clusters can form for neither large r (almost all sites occupied by prey and predators) nor for small r (for r only slightly larger than r_c almost all sites are occupied by prey) making the intermediate regime of r the only possibility. Let us also notice that this percolative argument explains the absence of oscillations for the $d=1$ case (there is no percolation in $d=1$, except for all sites being empty). But to make this argument more convincing it would be necessary to examine in detail the percolative properties of our model. Since the present model might be one of the simplest models exhibiting such oscillations, explaining its properties would be very desirable, especially because a similar mechanism might be responsible for oscillations in other spatially extended systems.

Finally, we would like to make a very qualitative comparison of our results with experimental data on the oscillatory behavior in prey-predator systems. Although some oscillatory behavior can be seen, these data (see, e.g., [6]) clearly show that these oscillations are very irregular. In our opinion, qualitatively, these data are more similar to our $d=2$ results rather than to $d=3$. But this might not be very surprising, since the “world” of prey-predator systems for which these data were collected is basically two-dimensional. Since some populations develop rather three-dimensional connections between individuals (e.g., fishes), it would be interesting to check whether oscillations in such populations are more regular.

[1] G. Nicolis and I. Prigogine, *Self-Organization in Nonequilibrium Systems* (Wiley-Interscience, New York, 1977); Y. Kuramoto, *Chemical Oscillations, Waves and Turbulence* (Springer, Berlin, 1984).

[2] I. Prigogine and R. Lefever, *J. Chem. Phys.* **48**, 1695 (1968).

[3] F. Baras, *Phys. Rev. Lett.* **77**, 1398 (1996); J. Dethier, F. Baras, and M. Malek Mansour, *Europhys. Lett.* **42**, 19 (1998).

[4] J. T. Tanner, *Ecology* **56**, 855 (1975).

- [5] A. J. Lotka, Proc. Natl. Acad. Sci. USA **6**, 410 (1920); V. Volterra, *Leçon sur la Théorie Mathématique de la Lutte pour la Vie* (Gauthier-Villars, Paris, 1931).
- [6] T. G. Hallam, in *Mathematical Ecology*, edited by T. G. Hallam and S. A. Levin (Springer-Verlag, Berlin, 1986).
- [7] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, 1988).
- [8] N. S. Goel, S. C. Maitra, and E. W. Montroll, Rev. Mod. Phys. **43**, 231 (1971).
- [9] A. Lipowski and D. Lipowska, Physica A (to be published).
- [10] H. K. Janssen, Z. Phys. B **42**, 151 (1981); P. Grassberger, Z. Phys. B **47**, 365 (1982).
- [11] H. Gang, T. Ditzinger, C. Z. Ning, and H. Haken, Phys. Rev. Lett. **71**, 807 (1993).
- [12] L. Gammaitoni, P. Hänggi, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998).