PHYSICAL REVIEW E, VOLUME 63, 051909

Coexistence in a predator-prey system

Michel Droz[1,*] and Andrzej Pękalski[2,†]
[1]*Département de Physique Théorique, Université de Genève, quai E. Ansermet 24, 1211 Genève 4, Switzerland*
[2]*Instytut Fizyki Teoretycznej, Uniwersytet Wrocławski, Wrocław, pl. M. Borna 9, 50-204 Wrocław, Poland*

(Received 18 August 2000; revised manuscript received 27 November 2000; published 23 April 2001)

We propose a lattice model of two populations, predators and prey. The model is solved via Monte Carlo simulations. Each species moves randomly on the lattice and can live only a certain time without eating. The lattice cells are either grass (eaten by prey) or tree (giving cover for prey). Each animal has a reserve of food that is increased by eating (prey or grass) and decreased after each Monte Carlo step. To breed, a pair of animals must be adjacent and have a certain minimum of food supply. The number of offspring produced depends on the number of available empty sites. We show that such a predator-prey system may finally reach one of the following three steady states: coexisting, with predators and prey; pure prey; or an empty one, in which both populations become extinct. We demonstrate that the probability of arriving at one of the above states depends on the initial densities of the prey and predator populations, the amount of cover, and the way it is spatially distributed.

DOI: 10.1103/PhysRevE.63.051909 PACS number(s): 87.23.Cc, 82.20.Wt, 87.10.+e

I. INTRODUCTION

The problem of dynamical relations between two, or more, interacting populations already has a long history. It started with the classic papers by Volterra [1] and Lotka [2] describing the fluctuations in the fish catch in the Adriatic. For some time, investigation of the predator-prey systems was the domain of mathematicians and biologists [3]. For an extensive introduction see, e.g., [4]. However, recently it attracted the attention of many physicists. First only homogeneous populations (no spatial dependence) were considered, then it was realized that new, interesting cooperative phenomena could occur in extended systems in which the populations live on a lattice.

Generally speaking, there are two goals in studying the dynamics of the predator-prey system. One is the explanation of the possible oscillations in the temporal evolution of the densities of prey and predators, as well as of the correlations between them. This is the classic problem in the field. The papers by Lipowski and Lipowska [5], Bradshaw and Moseley [6], and Taitelbaum *et al.* [7] are examples of this approach showing different methods and starting points. A modern attempt to explain the recorded correlations between the oscillations of prey and predators has been proposed in [8].

The second problem is the derivation and discussion of the long-time steady states at which a predator-prey system finally arrives. Boccara *et al.* [9] used a probabilistic cellular automata method to model a lattice system in which the prey tries to avoid the predator and the predator moves in the direction of the prey. The predator eats the prey with a given probability and it may die with a given probability. Both species produce just one progeny.

This kind of approach has been continued by Rozenfeld and Albano [10], who added the condition that the species are aware of each other within a given neighborhood. The authors construct a phase diagram showing two phases possible in their model—coexisting and prey only—which they call the absorbing one.

Gerami and Ejtehadi [11] studied a predator-prey system in which the predators (herbivores) move on a square lattice and eat out prey (plant), which grows again after some time. A predator can survive without eating for a certain time and then breed, giving one offspring. The model is solved, via mean-field approximation (MFA) -type differential equations and Monte Carlo (MC) simulations, showing oscillations in the time dependence of the densities of both species and bifurcations in the phase space of the two densities. No attempt is made to discuss the final steady state.

The problem of the final state has been discussed at length in the paper by Maynard Smith and Slatkin [12]. They consider a model with breeding seasons separated by a winter season during which the predator must find prey at a certain minimum rate or starve to death. Young and adult predators have different hunting possibilities and the prey may find cover. The coexistence of prey and predators was possible if the density of predators was well below the carrying capacity of the habitat.

In this paper, we present a lattice model that contains almost all the features found in the papers cited above, plus some that have not yet been considered but are nevertheless important. We use Monte Carlo simulations with sequential updating.

The predators and prey move on a lattice, and in order to survive each species must eat and breed. A certain percentage of lattice sites serves as a cover for prey. Mean-field type theories model the inhibition of population growth by crowding with an ad hoc ‘‘Verhulst factor,’’ but in our model this effect emerges naturally (see below) and we do not need to impose such a term. However, even in the absence of predators, the population of prey stays below the carrying capacity of the system.

We shall be interested mainly in discussing the long-time

---

[*] Email address: Michel.Droz@physics.unige.ch

[†] Email address: apekal@ift.uni.wroc.pl

steady state. In particular, we would like to find an answer to the following questions.

(1) What is the role of the initial densities of prey and predators on the chance of reaching a coexisting state?

(2) What is the role of cover and its spatial organization?

(3) How is the fate of the system affected by such details of the model as the habitat size, number of offspring, etc.?

The paper is organized as follows: in the next section we present the model, Sec. III contains the results of the Monte Carlo simulations, and the conclusions are in the final section.

II. THE MODEL

We consider a square lattice of linear size L with periodic boundary conditions. On a cell there may be a predator (e.g., a wolf), a prey (e.g., a rabbit), both of them, or neither. Double occupancy by two animals of the same species is not allowed. Each cell is either covered with grass or a tree is growing on it. Both types of animals move randomly on the lattice, following the blind ant rule, i.e., a direction for a move is randomly chosen, but if the target cell is already occupied by the same species, the move is not realized and there is no second try during one Monte Carlo step (MCS). On a grassy cell, a rabbit eats grass and a wolf eats rabbit if the two are on the same cell. The configuration of the territory, i.e., grass and trees, does not change in time, which means also that the grass is always available to the rabbits on grass sites.

Each animal has to feed at least once every k MCSs. This is realized in our model by attributing to each animal a counter containing just k ''food rations.'' The counter is increased by 1 after each ''meal'' (eating grass by a rabbit or eating rabbit by a wolf) and decreased after completing one MCS. For simplicity, we assume the same value of k for predators and prey. An animal that did not eat for k MCSs dies. Similar, although simpler, ideas of a finite reserve of food characterizing predators has been considered in [11] and, in some sense, also in [12].

If an animal has at least one nearest neighbor of the same species, the pair produces, at most, M offspring. M is the physiological birth rate. In order to breed, apart from finding a partner in its neighborhood, the animal must be strong enough, i.e., it must have at least $k_{\min}$ food rations. Each offspring receives at birth k_{of} food rations (which are not deducted from the parents' stores). The offspring are located, using again the blind ant rule, within the Moore neighborhood [13], which in the case of the square lattice contains eight cells. If the density is high, there is room for only a fraction of M, hence fewer progeny are born. This procedure takes care of the unrealistic unlimited growth of a population found in the classic Lotka-Volterra models (see [4]) and replaces, in a natural way, the phenomenological Verhulst factor.

When an animal moves into a cell with a tree, nothing happens. There is no grass for a rabbit to eat, but a tree makes a shelter against a wolf. Breeding is also impossible on the tree-occupied cell. Hence, such sites make a cover for rabbits, but it is a potentially dangerous one, since the rabbit may die there of hunger. Of course, a wolf may also die of hunger on a tree cell.

The parameters of the model are as follows: linear size of the lattice L, initial densities of both species: prey (rabbits) $c_r(0)$ and predator (wolves) $c_w(0)$, concentration of trees c_t, maximum period of time (MCS) k an animal may survive without eating, the amount of food, $k_{\min}$, needed to be fit for breeding, the amount of food, k_{of}, received at birth, and finally M, the physiological birth rate. To make the model tractable, we have decided on fixing most of the parameters at the following reasonable values: $k=6$, $k_{\min}=2$, $k_{\mathrm{of}}=2$, and $M=4$. We shall therefore investigate mainly the role played by three parameters—$c_r(0), c_w(0)$, and c_t—on the type of the steady state reached by the system, although the role of other parameters will be discussed briefly in the next section. In general, we have used $L=50$.

The territory (distribution of tree and grass cells) is prepared before starting the simulations. The trees are either put randomly or they are organized into a compact cluster making a forest. In the text below, we will refer to the two cases as ''trees'' and ''forest,'' respectively.

The dynamics of our model can be decomposed into two phases: diffusion (motion) and reaction (eating and breeding). The two are included in the following algorithm: (i) A cell is randomly chosen. If it is occupied by either animal, then (ii) a direction for a move is randomly determined. If the chosen cell is empty, the move is realized; (iii) if there is grass on the chosen cell then the following holds true: (a) if there are two animals (a wolf and a rabbit), the wolf eats the rabbit and the wolf's counter is increased by 1, (b) if there is a rabbit but no wolf, the rabbit eats grass and the rabbit's counter is increased by 1, (c) if there is a wolf and no rabbit, nothing happens, and (d) a check is made if the animal that is on the cell has enough resources to breed, i.e., whether its counter reads at least $k_{\min}$. If so, one search is made randomly in the nearest neighborhood for a partner. If it is found, the pair produces M offspring. For each of them, an independent search is made for a free cell in the Moore neighborhood. If found, the progeny is put there and it receives k_{of} food rations. If the cell is already occupied, nothing happens and we search for a place for the next baby. (iv) If there is a tree on the chosen cell, nothing happens. (v) After completing as many picks as there are animals at that time, one MCS has been accomplished and the food rations of all animals are decreased by 1.

Most of the simulations were performed on lattices of 50×50 size, although to estimate the size effects we increased it in some cases to 100×100 and 256×256. To find the chances of a population with given initial parameters reaching one of the three possible final states (coexistence, pure prey, or empty), we have averaged over 100 independent runs, choosing a different territory each time, but with the same amount of trees.

III. RESULTS

The main object of our study was the final state attained by a population. As could be expected, we have found three possible states: the coexisting one with prey and predators,

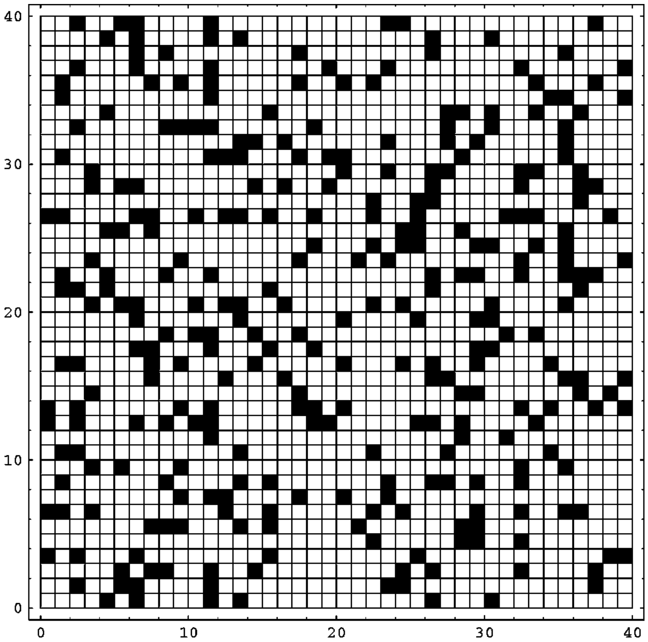

FIG. 1. An example of the distribution of trees (black squares) and grass (white squares) for $c_t=0.1$.

the absorbing one with prey only, and the empty one where no animal survived. Which one is the fate of a given population depends on the parameters characterizing the population and the territory.

Consider first the ‘‘tree’’ case when the trees are distributed randomly over the lattice. One of the possible realizations is shown in Fig. 1. There are indeed very few and small tree clusters. In such a territory, the wolves and rabbits have also been put in a random way. After approximately 100 MCSs, the system arrives at a quasisteady state. If it corresponds to a coexisting state, the densities of wolves and rabbits fluctuate around some ‘‘average’’ values, which do not change in time and which are the same in all coexisting states, irrespective of the initial parameters (see Fig. 2). If that final state is that of prey alone, its density stabilizes, after extinction of the predators, at a level below the carrying capacity of the habitat, which is equal to 1 in our model (see Fig. 3). We have not found periodic oscillations in the time dependence of the prey density in the absence of predators. Similar kinds of curves have been found by Maynard Smith and Slatkin [12] in their nonspatial model. The random oscillations of the two densities, as shown in Fig. 2, are very weakly intercorrelated. Fourier analysis performed on the data showed a wide uniform spectrum.

Initial densities

The chances of a population, starting with a given initial density of wolves and rabbits, to arrive at each of the three possible final states are shown in Fig. 4 for small concentrations of trees ($c_t=0.2$). Since the initial configurations, even for fixed c_t, c_r, c_w parameters, are different, and the evolution is probabilistic, the system may reach different stationary states. It is clear that the prey and predator populations can coexist only if the initial density of the wolves does not exceed that of the rabbits too much. However, if the initial density of the wolves is greater than 0.4, then, as seen in Fig. 4, the empty state is the most probable one. For a large enough initial concentration of predators, increasing the initial density of the rabbits may result in increasing the probability that the system will reach the pure prey state, but not the coexisting one. When increasing $c_r(0)$ for a fixed ratio $c_r(0)/c_w(0)\leqslant 1$, one passes from a coexistence through prey only to an empty state. The probability to reach a given steady state varies continuously as a function of $c_r(0)$. The final distribution of animals is shown in Fig. 5.

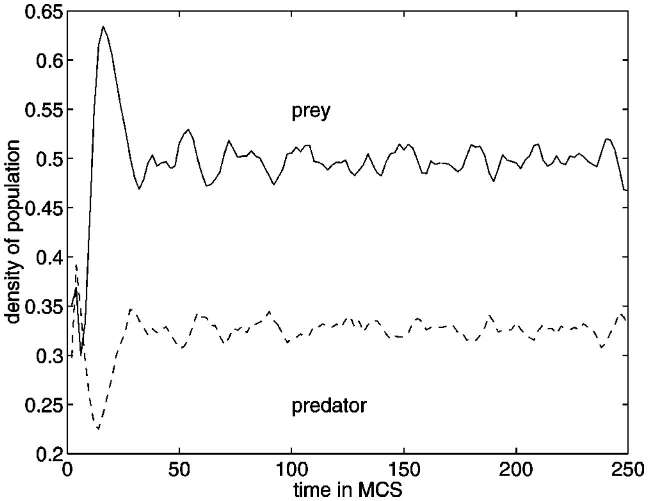

FIG. 2. Time dependence of the densities of predators (dotted line) and prey (solid line) when the final state is the coexisting one. $c_r(0)=0.1$, $c_w(0)=0.1$, $c_t=0.2$, $L=256$.

Cover

The existence of trees is beneficial for the prey since the predators cannot eat them there, but for the very same reason a tree does nothing for the predators. Moreover, the simulations show that in a territory without any trees, the probabil-

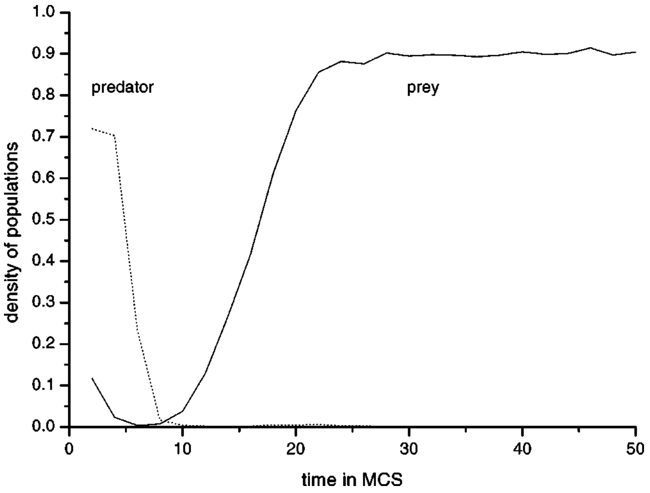

FIG. 3. Time dependence of the densities of predators (dotted line) and prey (solid line) when the final state is prey only. $c_r(0)=0.4$, $c_w(0)=0.5$, $c_t=0.1$, $L=50$.

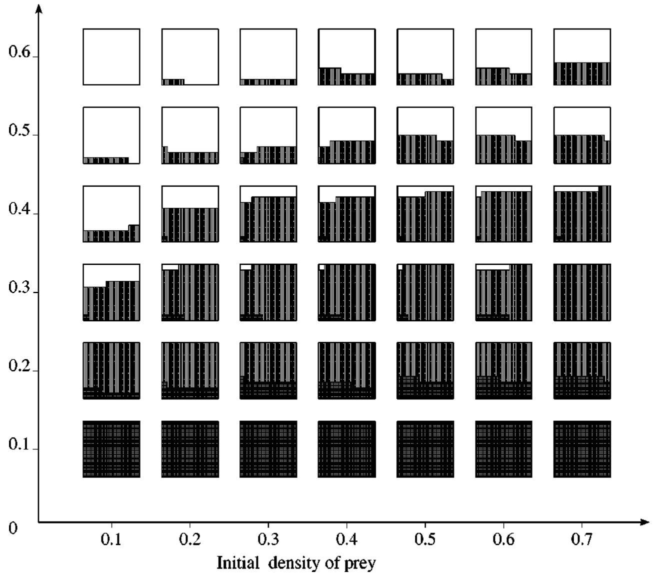

FIG. 4. Phase diagram showing probability of reaching one of the final states starting from a given initial density of predators and prey. Size of the white area corresponds to the probability of the final state with no animals, light gray to the state with prey only, and the dark gray area to the coexisting one (prey and predators). $c_t = 0.2$. The probabilities vary continuously between shown squares.

ity of arriving at the pure prey state never exceeds the probabilities of the remaining states. The pure prey state may become the most probable one, in a rather narrow range of the parameters, if the concentration of trees is $c_t = 0.1$.

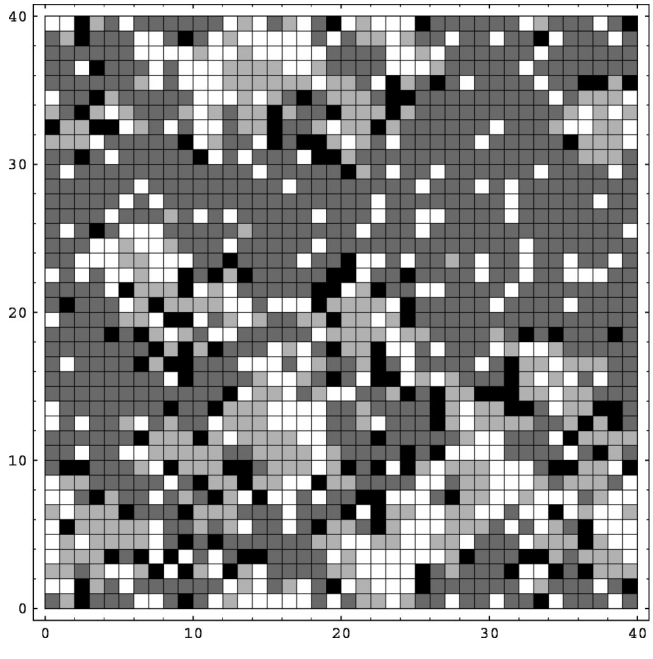

FIG. 5. Typical spatial arrangement of predators and prey in the coexisting state. On white squares there are no animals, on light gray ones there are prey only, on the dark gray ones there are predators, and on the black squares there are predators and prey. $c_w(0) = 0.1$, $c_r(0) = 0.1$, $c_t = 0.1$.

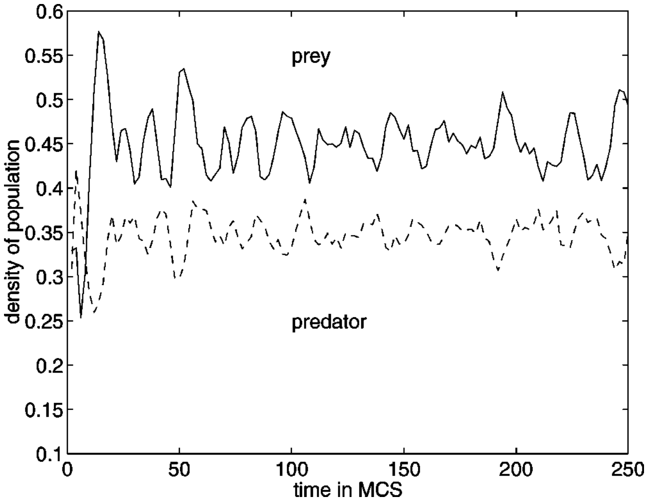

FIG. 6. As in Fig. 2, except that the trees form a compact cluster and the size of the lattice is smaller ($L = 100$), hence the fluctuations are larger.

Let us consider now the case of trees growing on neighboring cells and forming a cluster (the ''forest'' case). For a given concentration of trees, this kind of configuration favors the predators, leaving more open space for hunting and less cover for the prey. In the case of equal, and rather large, initial densities of prey and predators, $c_r(0) = c_w(0) = 0.3$ and $c_t = 0.2$ the chances a population has of ending up as either empty, coexisting, or pure prey states are 0.01, 0.02, and 0.97, respectively, in the case of dispersed trees, and 0.07, 0.81, and 0.12 in the forest. A predator population has a good chance (over 20%) of survival, and hence of realizing the coexisting state, even for very high initial densities of predators and prey [like $c_w(0) = 0.5$ and $c_r(0) = 0.6$] if the evolution takes place in the forest. In contrast, the predator population becomes extinct in the ''tree'' case if $c_w(0) > 0.3$. For compact clusters of trees (or no trees at all), we have found correlations between the time dependence of the two densities, predators (wolves) and prey (rabbits) (see Fig. 6). The role of the concentration of the trees and the way they are arranged are shown in Fig. 7. Here again, the similarity between the situation of no cover and trees grouped in a compact cluster is clearly seen. The forest, after initial penetration of the animals, remains empty, as shown in Fig. 8.

Finite size effects

From a biological point of view, the most interesting case is that of populations living in a small habitat. It is well known [14,15] that populations of small size are very vulnerable and may become extinct because of stochastic fluctuations. This is exactly what we have found in our model. Populations of prey and predators with the initial densities of $c_r(0) = 0.1$, $c_w(0) = 0.2$, and the concentration of forest $c_t(0) = 0.1$ were quite stable on a 50×50 lattice, having an 83% chance of coexistence and a 17% chance of becoming a pure prey state. The same system on a smaller, 20×20, lattice showed quite different behavior: 30% of coexisting states, 14% of the prey only, and 56% of an empty one.

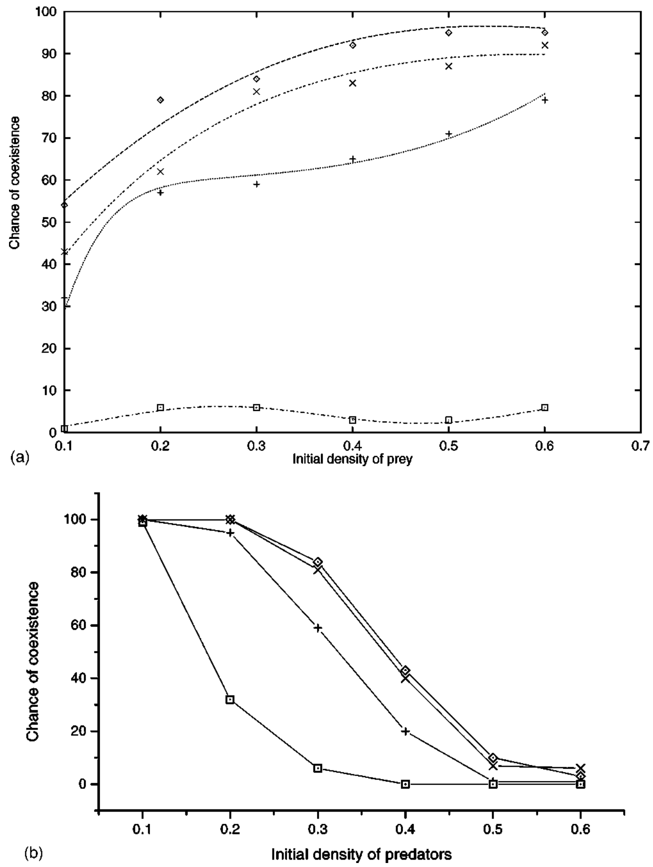

FIG. 7. Chances of reaching the coexisting state versus initial density of predators (a) and of prey (b), for different concentrations and arrangement of trees. If the trees are randomly located and $c_t \geqslant 0.3$, the chances of reaching the coexisting state do not exceed 5%. ◇ (case of no trees), × ($c_f = 0.1$), + ($c_f = 0.2$), and □ (forest and $c_f = 0.2$). Lines are guides to the eye only.

Increasing the number of predators, the probability of arriving at an empty state grows dramatically, and at $c_w(0) = 0.5$ it is above 90% for all initial densities of the prey, on the 20×20 lattice. The important factor is the number of individuals (size of the population) rather than the concentration. Consider two populations with an equal initial number of prey and predators—one on a small and one on a large lattice. The population living on a larger (e.g., 50×50) lattice reached higher densities fairly soon and the stochastic fluctuations left no marked effect, while the one living on a small lattice had no chance for growing (there is not much room for growth) and was easily affected by such fluctuations.

Taking lattices bigger than 50×50 does not change the general trends, although when the initial density of predators is high and that of prey is low, coexistence becomes more likely as the lattice grows. Analyzing the fluctuations around average densities for different lattice sizes, from $L = 20$ to $L = 256$, convinced us that they decrease approximately as $1/L$.

Other parameters

For simplicity, we have assumed the same numerical values for the parameters characterizing the prey and the predators, although this is clearly not very realistic. The physiological birth rate, i.e., the maximum number of offspring a pair may have, is an important parameter. Lowering it from $M = 4$, taken in the simulations, to $M = 3$ resulted in the almost total elimination of the predators; the only available final states were prey or empty. Increasing M to 5 did not change anything at lower initial densities, but greatly increased (by a factor of 4 at least) the chances for coexistence. A higher reproduction rate for both populations favors the predators, while lowering it below a certain threshold leads to extinction of the predators or of both species.

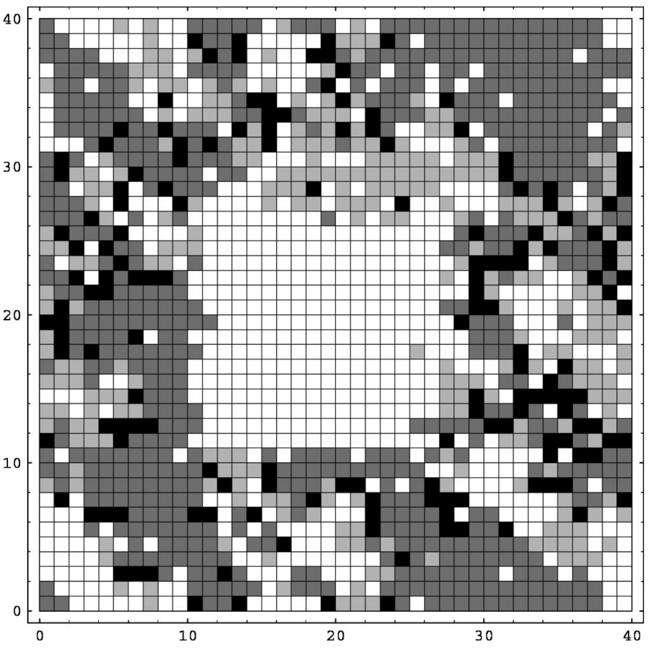

FIG. 8. As in Fig. 5 but for the ''forest'' case.

The same effect of elimination of the predators has an increase of the food reserves needed to breed. A decrease from $k = 6$ to $k = 5$ favored the prey and resulted in a smaller probability for an empty state and a larger one for a state with prey only.

Since the food rations are decreased after each MCS, lowering the amount of food received at birth from $k_{\mathrm{of}} = 2$ to $k_{\mathrm{of}} = 1$ kills most of the progeny and it results in the extinction of both populations. Raising k_{of} to a higher value permits the newborn to survive without eating for several MCSs and produces offspring. This may lead to quite an unrealistic situation when the predators are still alive after eating out the prey.

IV. CONCLUSIONS

We have presented a lattice model of prey and predators that move randomly on a territory containing either grass or tree. On a grass cell, prey eat grass and predators eat prey, while on a tree cell, the prey is safe from the predator but finds no food. To survive, each animal has to eat at least once every k MCS. An animal may breed, provided it finds a partner in the neighborhood and it has enough food reserves. The offspring are located in the neighborhood of the parents, which do not die after giving birth, hence we have a system with overlapping generations.

A real ecological system is of course very complex and contains many important factors, out of which the present model considers only a few, namely spatial inhomogeneity of the habitat, limited ability of the animals to survive without eating, and their mobility. The inhomogeneity is realized here by dividing the territory into two, nonoverlapping, regions, one providing food and a mating ground for prey and predators, and the second providing cover for prey. As in the real world, here also reproduction and finding food are related. In order to mate, an animal must have energy resources above a certain level. To maintain this state, it has to gather food and avoid (especially predators) ‘‘cover’’ cells. By imposing a limited time of survival without eating, we force the animals to move, otherwise an animal will die and liberate the cell on which another animal may move. In our model, as in nature, animal mobility is necessary for catching food and mating. The age of the animals is not considered here explicitly, but denying the reproduction power to newborns has an impact on the dynamics, as with the different hunting skills in the model of Maynard Smith and Slatkin [12].

The MC simulations show that there are three possible final states into which the dynamics will lead the populations: coexistence of prey (with density about 0.50) and predator (with density about 0.32), prey only (with concentration about 0.90), and an empty state in which both populations are extinct. The coexisting state is realized only if the parameters characterizing the populations are within a certain, rather restricted, range. A population may die out if the birth rate is too low, getting food requires a very long time, or there are too many enemies. The size of the predator or prey population may fall below a safe number. This is the situation found in nature [12,16].

The initial density of predators cannot be too large, although for smaller densities it may be greater than the density of the prey. However, the knowledge of the initial densities is not enough to define completely the initial state. Indeed, different initial states characterized by the same values of $c_r(0)$ and $c_w(0)$ can correspond to quite different microscopic configurations. Two such configurations can evolve in very different ways and approach different stationary states. Accordingly, the stationary phase diagram acquires a probabilistic character, giving the probabilities of reaching a particular type of stationary states, starting from an initial state defined in terms of $c_r(0)$ and $c_w(0)$.

As Maynard Smith and Slatkin [12] found in their own model, the existence of cover may lead to extinction of the predators, but it does not increase the chance of coexistence. The way in which the cover (here trees) is organized also plays a role. If the trees are scattered around all the territory, thus offering many shelters for the prey, the predators have fewer chances than when all (or most) of the trees are grouped in a compact cluster (a forest). When the initial density of predators exceeds 0.4, the prevailing final states are either prey only or empty state.

ACKNOWLEDGMENTS

A.P. is grateful for the hospitality he received at the Département de Physique Théorique de l’Université de Genève, where a large part of this work was done, and he acknowledges useful discussions with Marcel Ausloos and Nicolas Vanderwalle. M.D. is grateful for the hospitality he received at the Institute of Theoretical Physics of the University of Wrocław, where this work was completed. This work was partly supported by the Swiss National Foundation. We are grateful to Jérôme Magnin for his help.

---

[1] V. Volterra, *Leçon sur la Théorie Mathèmathique de la Lutte pour la Vie* (Gauthier-Villars, Paris, 1931).
[2] A. J. Lotka, Proc. Natl. Acad. Sci. U.S.A. **6**, 410 (1920).
[3] R. Durrett and S. A. Levin, Philos. Trans. R. Soc. London, Ser. B **343**, 329 (1994); R. Durrett, in *Asymptotic Problems in Probability Theory: Stochastic Models and Diffusions on Fractals*, edited by K. D. Elworthy and N. Ikeda, Pitman Research Notes 283 (Longman, Essex, England, 1992).
[4] J. D. Murray *Mathematical Biology* (Springer Verlag, Berlin, 1993).
[5] A. Lipowski and D. Lipowska, Physica A **276**, 456 (2000).
[6] A. T. Bradshaw and L. L. Moseley, Physica A **261**, 107 (1998).
[7] H. Taitelbaum, Z. Koza, Y. Yanir, and G. H. Weiss, Physica A **266**, 280 (1999).
[8] A. Blasius, A. Huppert, and L. Stone, Nature (London) **399**, 354 (1999).
[9] N. Boccara, O. Roblin, and M. Roger, Phys. Rev. E **50**, 4531 (1994).
[10] A. F. Rozenfeld and E. V. Albano, Physica A **266**, 322 (1999).
[11] R. Gerami and M. R. Ejtehadi, Eur. Phys. J. B **13**, 601 (2000).
[12] J. Maynard Smith and M. Slatkin, Ecology **54**, 384 (1973).
[13] B. Chopard and M. Droz, *Cellular Automata. Modeling of Physical Systems* (Cambridge University Press, Cambridge, 1998).
[14] M. L. Shaffer, Bioscience **21**, 131 (1981).
[15] R. Gomulkiewicz and R. D. Holt, Evolution (Lawrence, Kans.) **49**, 201 (1996).
[16] I. Hanski, A. Moilanen, and M. Gyllenberg, Am. Nat. **147**, 527 (1996).