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# Self-organized packs selection in predator-prey ecosystems

Andrzej Pękalski
*Institute of Theoretical Physics, University of Wrocław, pl. M. Borna 9, 50-204 Wrocław, Poland*

Michel Droz
*Department of Physics, University of Geneva, CH 1211 Geneva 4, Switzerland*
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We present a lattice model of a system of predators of five kinds, competing for prey. The predators are grouped in packs and characterized by two parameters—the energy spent on hunting and energy gained by the kill. The success of hunting depends on the actual competition among predators found near a prey. We determine via Monte Carlo simulations the numbers of predators of each kind as a function of time and the distribution of the size of their packs. We show that the ratio of the energy spent by the competing predators determines their fate. The energy gain plays only a secondary role. We show also that the system self-organizes itself into groups of predators living in well defined packs, which size depends on the energy spent. The most preferred size dependence on the energy spent follows a very simple power law. We present also a mean-field-type approach to the problem and we discuss the differences in the results obtained by the two methods, showing in particular, that the simulation approach produces more reliable results.

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## I. INTRODUCTION

The dynamics of interacting species has attracted a lot of attention since the pioneering works of Lotka [1] and Volterra [2]. They showed, in a mean-field like approximation, that simple prey-predator models may have limit cycles during which the populations of both species have periodic oscillations in time. Since then, a lot of activities have been devoted to the study of different classes of prey-predator models. With the rapid development of the field of "complexity" [5,6], it was soon recognized that prey-predator provides simple examples of population dynamic models exhibiting emergent properties or self-organization. It is then natural to study such problems within the framework of statistical mechanics. Moreover, it has been recognized (see [3,4] and references therein) that simple mean-field like approximations were not always sufficient and that is was important to consider extended models. Indeed, the stochastic aspect of the dynamics as well as the use of discrete variables may play an important role [7–9]. These ingredients are included in the so called individual agents based lattice models (IBM). Generally speaking, several generic questions can be asked when studying the dynamics of predator-prey systems. 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. Another one concerns the study of the possible steady states at which a predator-prey system eventually arrives. As a function of the control parameter of the problem, a phase diagram can then be drawn, characterizing the different states (or phases) in which the system can be found. Yet another is the study of a system in its transient regime to see the role of the parameters of the model in determining its fate.

Many different mechanisms, associated with several different control parameters, can be taken into account. For example, the following scenarios in describing population dynamics have been considered in the literature:

(1) seasonal hunting of the predators [10,11],
(2) predating within a certain region [12,13],
(3) predators and prey which may exhibit different strategies, like looking for prey and/or avoiding predators [11,13,14],
(4) including, genetic heritage and accumulation of diseases into the lattice predator-prey models [15].

In this paper, we consider a new aspect of prey-predator dynamics, which is present in all such systems, but has not been yet considered, namely the problem of competitive hunting [16,17]. In the system we consider, one has only one type of prey, which is abundant enough to be always present independently of the hunting abilities of the predators. Populations of predators $P_i$ of several kinds are hunting according to some rules and each predator family is characterized by two properties, its hunting ability $h_i$ and its metabolic rate $m_i$ (a more precise definition of the hunting rules and of $h_i$ and $m_i$ will be given in Sec. II). The predators of family $i$, located at time $t$ at site $\vec{r}$ are hunting in packs of size $n_i(\vec{r},t)$. The problem we would like to approach in this paper is to study the influence of the two above parameters on the dynamics of the system.

The probability distribution of group sizes in a given family is an important element for understanding the evolution of grouping. It may happen that a particular size is selected as the result of a competition between cost and benefits.

We shall find that in the long time limit, for each family of predators a characteristic size is selected. Moreover, these optimal sizes depend upon the metabolic rate $m_i$ as a power law, manifestation of some self-organization in the system.

We are aware that many factors are not present in our model, like, e.g., developing hunting skills by the predators, seasonal hunting, etc. Inclusion of these factors into the model is, of course, possible, however at the cost of increasing the number of its parameters. Such a procedure could be justified, or even desirable, in a biological study. However in order to grasp the most important features of the problem, we have kept the number of parameters minimal.

The paper is organized as follows. The model is defined in Sec. II. The results obtained by the Monte-Carlo simulation are discussed in Sec. III and compared with the ones obtained by a mean-field like approximation. Finally, concluding remarks are given in Sec. IV.

## II. MODEL

We consider a square lattice of dimensions $L \times L$. Each lattice site could be either empty or occupied by one species (predator or prey). There is just one type of prey on which all predators feed. To make the model as simple as possible (but not simpler, following the advice of Einstein) the prey could not go extinct. It is always, although not on all sites, available to the predators. There are five types of predators and each of them is characterized by two parameters—hunting ability ($h$), which describes its skills at hunting, chasing away competing predators, etc., and by its metabolic rate ($m$) which again encompasses many factors, like energy spent while chasing, breeding, etc. These two parameters are sometimes called by biologists [16] $b$ (benefits) and $c$ (cost).

All animals (predator and prey) are grouped into herds or packs (predators), which are the basic entities we use. Since the prey always exist, the size of prey herds is unimportant. The predators' pack sizes are at the beginning of the simulation given random values between 2 and 10. The groups of animals may move randomly on the lattice and the number of predators in each pack could change in time, depending whether the pack was successful in finding prey and in the competition with other predators. When there are several predators packs around the same prey, there will be a competition in the kill. The packs with the highest $h$ and largest in numbers will have of course the most benefits from the kill. This idea is formalized in Eq. (1).

The algorithm we use has the following form:

(1) A group of animals is randomly selected,

(2) A move to an empty site in the Moore neighborhood (8 sites on the square lattice) is attempted. If not successful, the program returns to (1). Otherwise the move is realized,

(3) After moving all groups of animals we look for predator packs. The new size of the pack of predators $i$ at site $\vec{r}$ is updated according to the formula

$$n_i(\vec{r},t+1) = n_i(\vec{r},t) - I[n_i(\vec{r},t)m_i] + I\left[\frac{\rho_i}{S}\right], \qquad (1)$$

where

$$\rho_i = n_i(\vec{r},t)h_i, \qquad (2)$$

and $S$ is the weighted sum of all predators (at sites $\vec{R}$) participating in the kill of the same prey (at site $\vec{r}_p$) as the pack $n_i$. Formally we may write it as

$$S \equiv S(\vec{r}_p) = \sum_{i=1}^{5} \sum_{\vec{R} \in V(\vec{r}_p)} n_i(\vec{R},t)h_i. \qquad (3)$$

$I[x]$ means taking the nearest integer of $x$ and $V(\vec{r}_p)$ denotes the four sites constituting the neighborhood of $\vec{r}_p$. One can therefore say that the gain in the kill obtained by a given predators pack is proportional to its weighted hunting ability and the size of the pack; the weighting is done with respect to all packs around that prey. The cost of hunting is also proportional to the size of the pack and to the appropriate $m$. It is clear that when there is no prey around a given pack of predators, the last term in Eq. (1) is missing and the size of the pack could only go down.

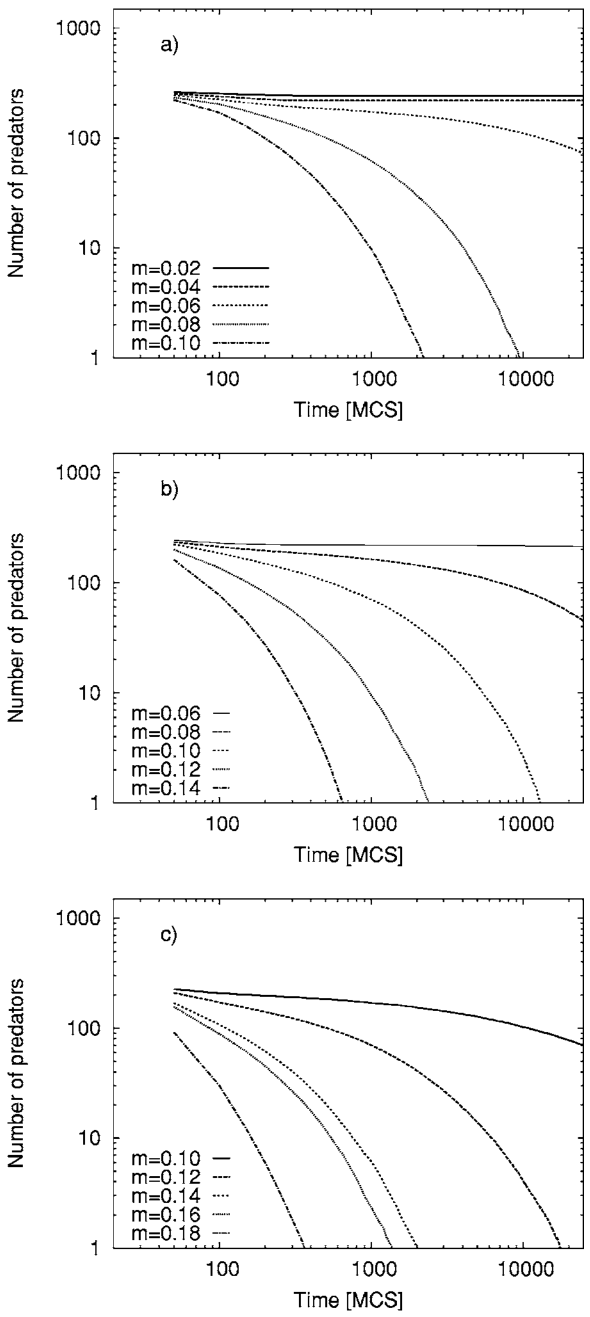

FIG. 1. Time dependence of the number of predators. $h=0.1$, (a) $m=0.02$, 0.04, 0.06, 0.08, 0.10, (b) $m=0.06$, 0.08, 0.10, 0.12, 0.14, (c) $m=0.10$, 0.12, 0.14, 0.15, 0.18.

(4) As usual, after updating, on the average, all packs of predators, one Monte Carlo step (MCS) is completed.

Although simple, this nonlinear model will exhibit complex behavior.

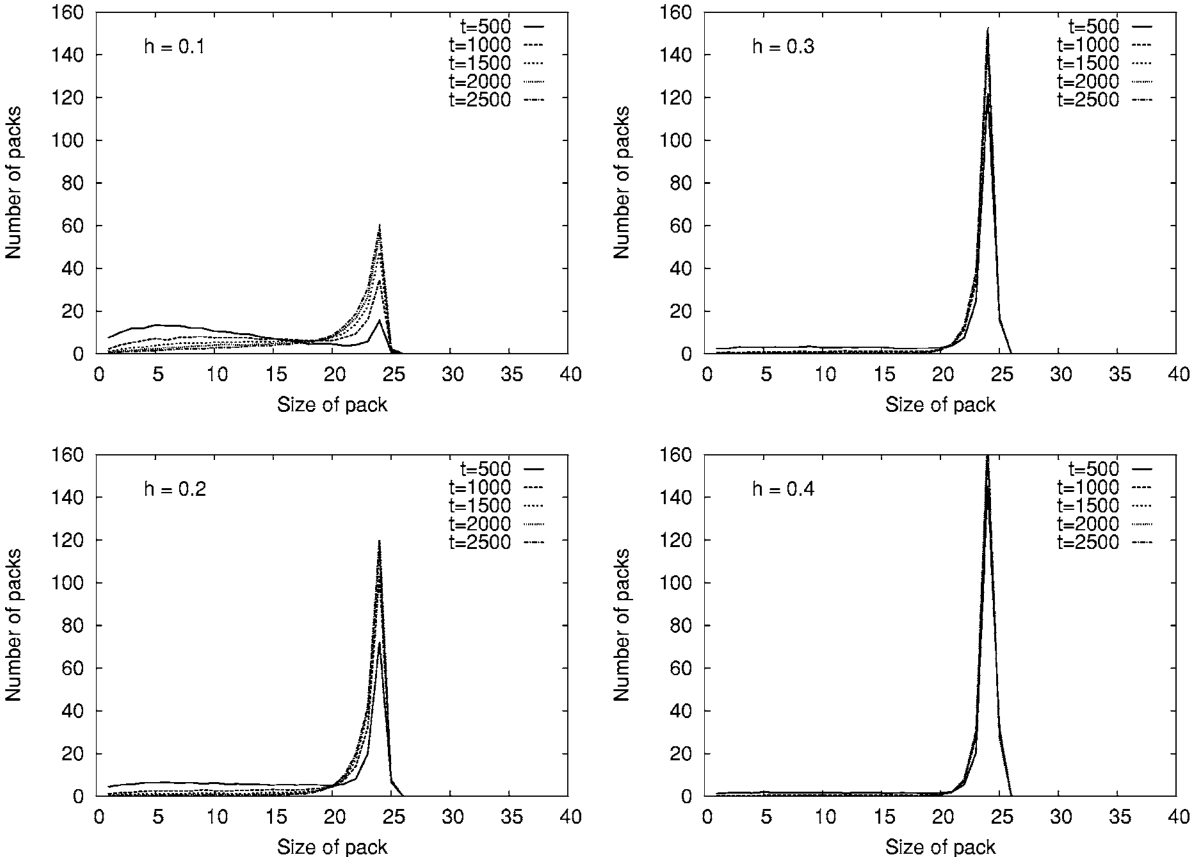

FIG. 2. Distribution of the pack sizes. $m=0.02$. Upper left, $h=0.1$; upper right, $h=0.2$; lower left, $h=0.3$; lower right, $h=0.4$.

The model has the following parameters divided in two groups. The constant group is as follows:

(1) $L=50$, linear size of the system,

(2) $P=5$, five group of predators,

(3) initial concentrations of prey (0.1, i.e., one site out of ten is occupied by prey) and of all predators (0.6).

The variable group is as follows:

(1) $h_i$, hunting ability of predators $i$,

(2) $m_i$, metabolic rate of predators $i$.

For a linear size equal $L=50$, no finite size effects are present (for the range of metabolic rates considered, see below) as checked by investigating the properties of larger lattices. Such a size is a good compromise between computer efficiency and stability of the results. For too small lattice sizes one may face the risk of extinction of population due to statistical fluctuations [18].

We have decided to choose $P=5$ since larger values are rather improbable in view of the biological data [16,19]. On the other hand we did not want to operate on a system where after eliminating one competitor only one or two will be left. We have however checked that taking $P=3$ does not change in any significant way our results. In particular the maxima of the pack size distribution follows the same law (see below) that for $P=5$.

It is clear that the sum of the densities of the predators and prey should be smaller than one, otherwise there would be no room for movements. With the choice we made, the initial concentration of each type of predators is slightly higher than that of prey. This may seem unrealistic but since the number of prey remains unchanged, the density of predators quickly drops below that of prey. Choosing larger concentrations of prey (like 0.2 instead of 0.1) leads to slower extinction of predators with high $m$. Increasing or decreasing the initial concentration of predators does not change the behavior in any significant way since the internal dynamics keeps the system in balance.

We have in general let the system evolve till $2.5\times 10^4$ MCS, although to check the stability we have extended the runs in some cases till $1\times 10^5$ MCS. Averaging was done over 100 independent runs.

We have recorded the following quantities, time dependence of the number of predators of each type and the distribution of the size of the packs at different time moments.

## III. RESULTS

In Figs. 1(a)–1(c) the time dependence of the number of each kind of predators is presented. The predators have the following characteristics: $h=0.1$ for all types of them and $m=0.02$, 0.04, 0.06, 0.08, 0.10, respectively for the five types of predators in Fig. 1(a), while in Fig. 1(b), $m=0.06$, 0.08, 0.10, 0.12, 0.14, and finally in Fig. 1(c), $m=0.10$, 0.12, 0.14, 0.15, 0.18. It is clear from the Fig. 1, that the predators with the lowest $m$ are better off than the others. In particular those with the highest $m$ would be eliminated first. By comparing the results presented in Figs. 1(a)–1(c), we conclude that the

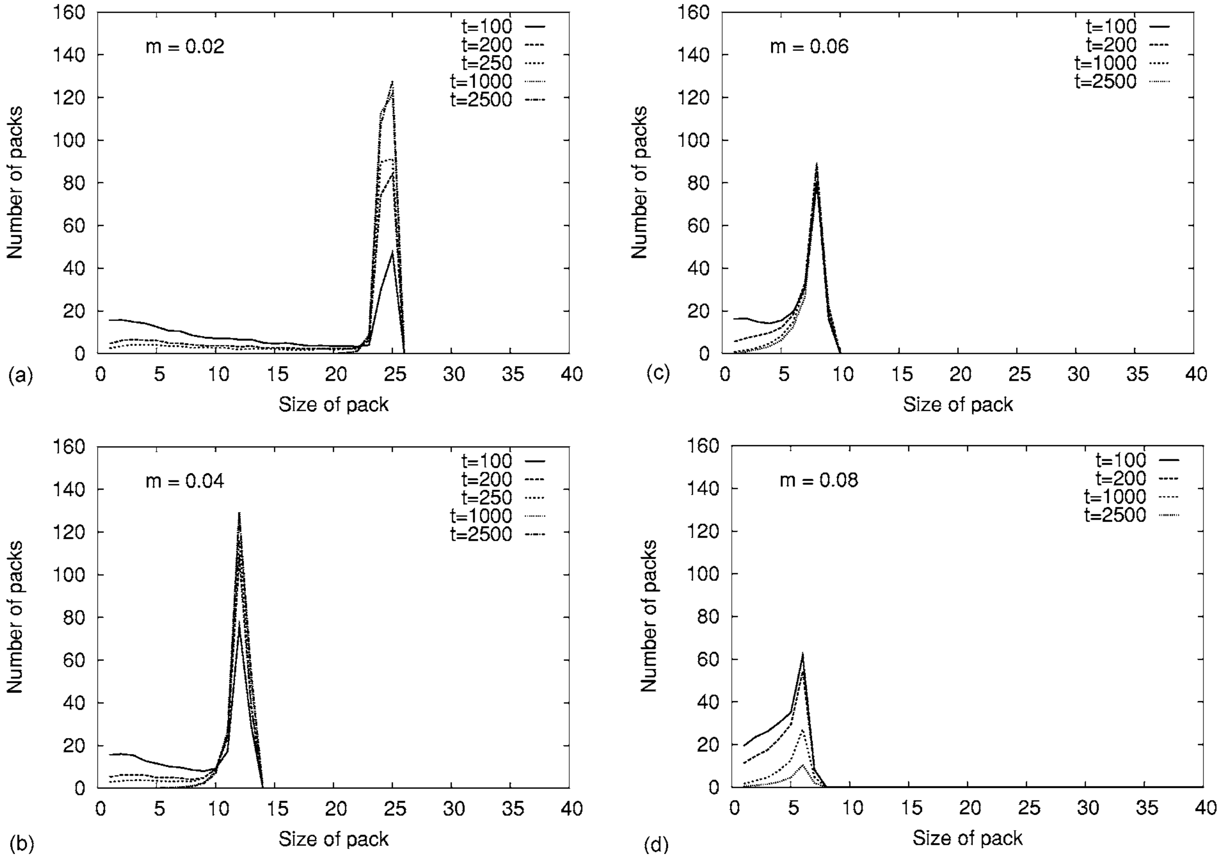

FIG. 3. Distribution of the pack sizes. $h=0.10$. Upper left, $m=0.02$; upper right, $m=0.04$; lower left, $m=0.06$; lower right, $m=0.08$.

survival of predators is essentially governed by two rules. For short times, the survival depends mainly on the respective ratios $\sigma_{ij}=m_i/m_j$ and is only very weakly dependent on the smallest value of $\{m_i\}$. However, for longer times, the decay of survival significantly depends not only on the ratios $\sigma_{ij}$ but also upon the smallest value of $\{m_i\}$.

In Figs. 2(a)–2(d) we show the distribution of the pack sizes, at different time moments, for the case when the predators have all the same value of $m$ ($=0.02$) and differ by their hunting ability; $h=0.1$, 0.2, 0.3, 0.4, 0.5. We present four graphs since the fifth one ($h=0.5$) looks very much like the one for $h=0.4$. We observe that, regardless of the value of $h$, there is always a preferred size of the pack, and that it is located at about 24 animals. Hence all competing predators prefer similar sizes of their packs. Initially there is a long tail in the distribution, indicating the presence of smaller packs, but with time the peak at 24 grows up at the expense of smaller packs. The height of the maximum tells us how many such packs, hence indirectly also predators of a given type, exist in the system. It is natural that with growing hunting ability the number of such skillful predators grows too. Predators with no hunting ability at all ($h=0$) are, of course, eliminated quickly.

Figures 3(a)–3(d) show the situation when the competing predators have the same hunting ability ($h=0.1$) but different $m=0.02$, 0.04, 0.06, 0.08, and 0.10. Here also we present four graphs, since the case $m=0.10$, in the scale we use, shows just a small, disappearing in time, bump. Now the preferred pack distribution depends very much on the type of predators. Those with low $m$ hunt in rather well defined and large packs. The peaks are sharp, tall, and practically there are no packs larger than the preferred ones. When the $m$ grows, the most often found size of the pack goes down, becomes smaller and its left-hand tail becomes more thick. All this shows that larger animals, which spent more energy, hunt in smaller groups, which also may become quite small, and that the total number of such predators is smaller than their smaller in size competitors.

In Fig. 4 we present the distribution of the pack sizes for the five types of predators present in the system. The metabolic rates are equal 0.02, 0.04, 0.06, 0.08, and 0.10. As can be seen on the last graph, the predators with the highest metabolic rates disappeared from the system.

Apart from the two cases presented above, constant $m$ and varying $h$ and vice versa, we have also considered the case of predators differing in both parameters. We have attributed the largest $m$ to the predators with the highest $h$. Such a situation could, e.g., correspond to lions (high values of both parameters) and hyenas (low values). Both live in the same ecosystem and feed on similar prey [17]. Lions have larger body size hence they use more energy, but they are also able to chase away hyenas from their kill. While the lions hunt generally in groups of just a few animals, hyenas' packs count 15–20 [16]. In the above case we have found a behavior quite similar to the case when the $h$'s were equal. This demonstrates the crucial role, in determining the dynamics of

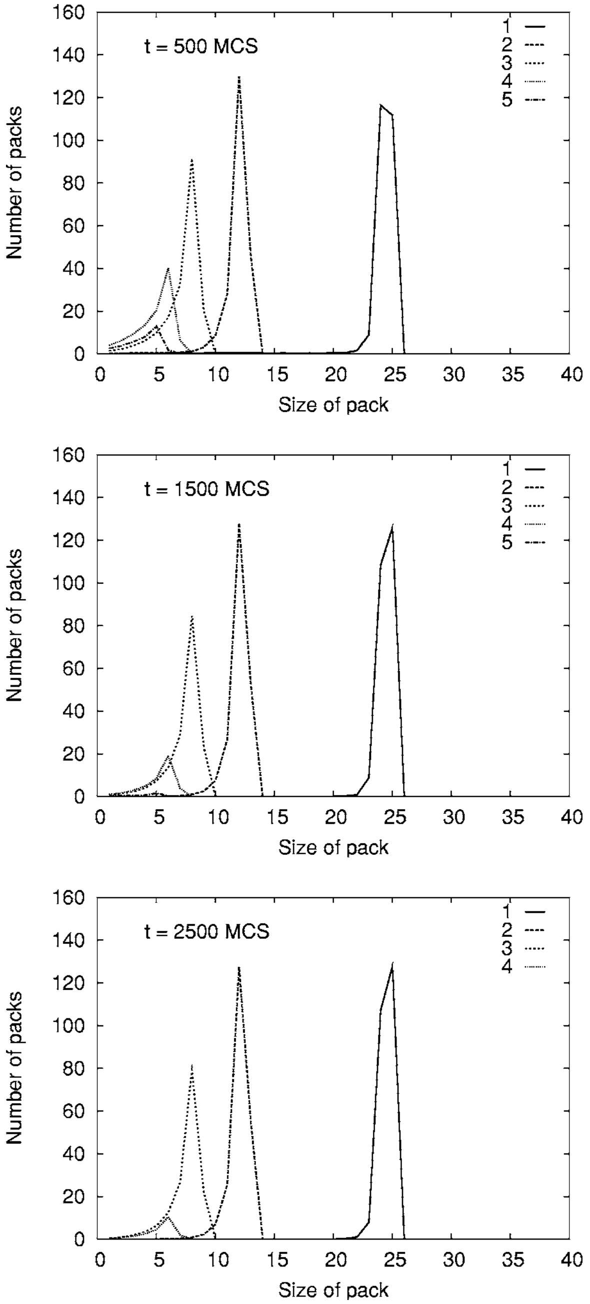

FIG. 4. Distribution of the pack sizes of the five types of predators (marked by $1,2,\ldots,5$) for three time moments. Top $t=500$ MCS, middle $t=1500$ MCS, and bottom $t=2500$ MCS. $h=0.10$.

competing predators, played by the ratio of their $m$, or energy spent.

Finally, in Fig. 5 we present the dependence of the size of the preferred pack ($p_s$) on the values of $m$. It shows a power-type behavior, which could be very well fit by the equation

$$p_s = \frac{0.49 \pm 0.01}{m}. \tag{4}$$

The explanation of this kind of power-law behavior, as well as the stronger dependence of the dynamics of the system on $m$ than on $h$, could be found in the structure of Eq. (1), which determines the dynamics. The interplay between two opposite factors involving size of the herd, growth because of a better chance to catch prey (proportional to the size of the herd), but decrease due to energy spending (also proportional to the size), produces the effect of appearing of a rather sharp maximum for the pack size. The power law character of the dependence extends over two decades. Because of the restricted size of the system we have shown packs up to size of 500. The presented data should be sufficient to make our point, that the dependence has indeed a power type character.

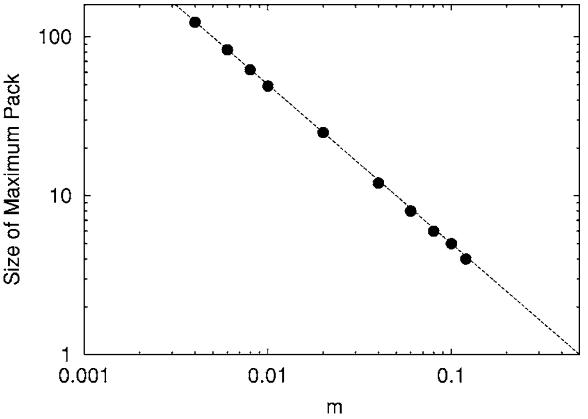

FIG. 5. Preferred size of the pack versus $m$ on a doubly logarithmic scale. Solid line is a fit [see Eq. (4)].

Although in our model there are no direct interactions among the predators packs, the predators of the same type have a tendency to move within an area in which they are in majority (see Fig. 6), hence one could say that the predators of one type try to avoid other types.

It is also possible to treat the problem analytically within a mean-field approach (MFA), in which the system is supposed to be spatially homogeneous. Denoting by $n_i$ the size of a pack of predators of type $i$, one can write the following set of difference equations

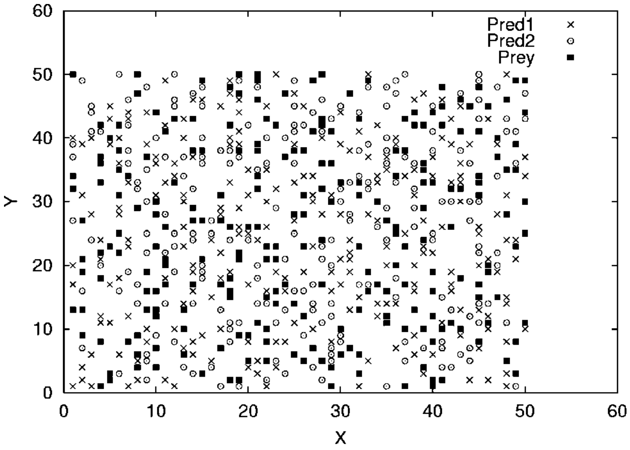

FIG. 6. Positions of the two most numerous types of predators' packs and prey herds after 10 000 MCS. $h=0.1$, $m=0.02$ (Pred1), 0.04 (Pred2).

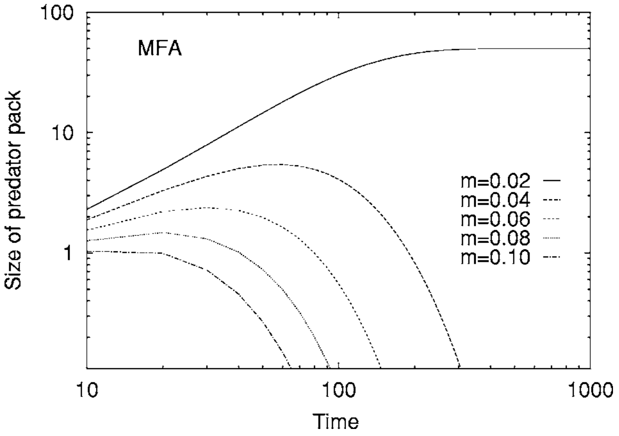

FIG. 7. Time dependence of the five types of predators as calculated from Eq. (6). $h=0.1$ for all predators.

$$n_i(t+1) = n_i(t) - n_i(t)m_i + \rho_i(t)/S \quad (i=1,\ldots,5), \tag{5}$$

which in the continuous time limit turns into a set of five coupled nonlinear differential equations

$$\frac{dn_i(t)}{dt} = -n_i(t)m_i + \frac{n_i(t)h_i}{S}. \tag{6}$$

It is not possible to give an analytical solution to this system of differential equations. However, they can be solved numerically using the Runge-Kutta method. In Fig. 7, the time dependence of the five groups of predators for the case of $h=0.1$ and $m=0.02$, 0.04,0.06, 0.08, and 0.10, respectively is given and could be compared with Fig. 1(a). In the long time limit, only one type of predator survives, the one with the smallest metabolic rate. In this particularly simple case the stationary state solution, $n_{s,1}$, of Eq. (6) for the surviving predators gives

$$n_{s,1} = (m_1)^{-1}, \tag{7}$$

which differs from Eq. (4) only by a prefactor.

Generally, more than one type of predators may survive and the stationary state conditions for $n_{s,i}=\lim_{t\to\infty} n_i(t) \neq 0$, read

$$\sum_{j=1}^{5} \sum_{\vec{R}\in V(\vec{r}_p)} n_j(\vec{R},t)h_j = \frac{h_i}{m_i}. \tag{8}$$

The simplest case is when only one of the $n_{s,j}$ is nonzero, this is the case investigated above. The more general case is when several $n_{s,j}$, $j=i_1,i_2,\ldots,i_M$ are not zero. Then one has

$$\frac{h_j}{m_j} = K, \quad j=i_1,i_2,\ldots,i_M, \tag{9}$$

where $K$ is a constant. It follows that Eq. (8) is of the form

$$\alpha_{i_1} n_{s,i_1} h_{i_1} + \alpha_{i_2} n_{s,i_2} h_{i_2} + \cdots + \alpha_{i_M} n_{s,i_M} h_{i_M} = K, \tag{10}$$

where $\alpha_{i_j} \in (0,1,2,3,4)$. As the right hand side is independent of the $h$'s, the solution should be of the form

$$n_{s,i_j} = \frac{K\beta_{i_j}}{\alpha_{i_j} h_{i_j}} = \frac{\beta_{i_j}}{\alpha_{i_j} m_{i_j}} \sim \frac{1}{m_{i_j}}, \tag{11}$$

where the coefficients $\beta_{i_j}$ are some constants. Thus power law behavior is also obtained in mean-field approximation but under some restrictive conditions. Note however that the prefactors are not the same in mean-field and Monte Carlo simulations due to the following reason. Since in the MFA by definition all packs of a given type of predators have the same size at a given time, there is no competition within the same group. In the Monte Carlo approach there are always other predators, as well as predators of the same type but in packs of a different size.

We have investigated also the extinction time as a function of $m$, and it turns out that again the most important is the ratio of the $m$'s of the competing predators. Predators with a given value of $m$ may live practically forever (provided it is not very high, like 0.1), if this is the lowest $m$ in the system, but they may be eliminated quite soon if this is one of the highest.

A plot of the dependence of the height of the $p_s$ as a function of $h$ produces a saturating curve, roughly corresponding to a hyperbolic tangent.

## IV. CONCLUSIONS

We have presented a simple, yet showing complex behavior, model of competing predators and everlasting prey. Predators are characterized by two tunable parameters, energy spent (called here *metabolic rate m*) and energy gains (*hunting ability h*). The problem of dynamics of a system depending on those two parameters attracted interest of biologists, mostly working in Reserve Parks [16,17], but so far not of the physicists. In constructing the model we have assumed, according to the biological data, that predators live in packs, and we have determined, via Monte Carlo simulations, how the distribution and the number of predators depend on those two parameters. We have found that the preferred size of the pack depends strongly on the ratio (and also value) of the $m$ parameters, but not on $h$. It should be stressed, however, that the role of the hunting ability is not negligible. It is true that the prey is always available (on occupied sites), but the distribution of the kill is made according to the hunting abilities of the participating predators. It is not therefore obvious that in the Monte-Carlo simulations the hunting ability would play a secondary role (see however the discussion concerning Fig. 2). In the MFA it is as important for the survival of the species as the second parameter, i.e., the metabolic rate.

Predators spending more energy, hence presumably having a larger body, will live in smaller packs, and will be less numerous than competing with the predators of a smaller body mass. This kind of situation is supported by field data [16], where similar figures showing distribution of pack sizes for the African wild dog has been presented.

We have shown that the preferred size of the pack scales with a simple power law. The system clearly self-organizes; starting from a random distribution of the pack sizes and governed by one simple equation, it arrives at an organized state where most of the predators live in well defined groups and the size of the group is characteristic for the predator. Scaling in the size distribution of animal groups have also been found, however not in the predator-prey systems, by Bonabeau *et al.* [20].

We have also shown the results obtained analytically, via mean-field approach. They exhibit a similar dependence, i.e., scaling, of the size of the packs on the metabolic rate. As could be expected, neglecting fluctuations in the MFA approach produces differences with respect to analogous simulation results. In the MFA, for the range of the $m$ and $h$ parameters we have considered in the Monte Carlo approach, we have arrived at the asymptotic situation in which only the predators with the lowest metabolic rate survived. If we impose the condition that more than one type of predators should survive, this implies that the ratios $h_i/m_i$ of each of the surviving species should be equal to the same constant $K$.

This constraint is not present for the lattice-based case, as shown by our Monte Carlo simulations, where more than one type of predators were living in the stationary state for different values of the ratio $h_i/m_i$. Clearly the results obtained from Monte Carlo are closer to biological data, hence they are more reliable than those obtained from the MFA.

Although our model is quite simple, it possesses rich solutions. It should be also noted that our model shows certain robustness since the dynamics depends rather weakly on particular values of either $m$ or $h$ (of course within certain limits). This seems to be correct, since one could not really expect to find the values of the parameters corresponding to a real life situation.

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[1] A. J. Lotka, Proc. Natl. Acad. Sci. U.S.A. **6**, 410 (1920).
[2] V. Volterra, *Leçons sur la Théorie Mathématique de la Lutte pour la Vie* (Gauthier-Villars, Paris, 1931).
[3] T. Antal and M. Droz, Phys. Rev. E **63**, 056119 (2001).
[4] M. Droz and A. Pękalski, Phys. Rev. E **63**, 051909 (2001).
[5] *Exploring Complexity: An Introduction*, edited by G. Nicolis and I. Prigogine (H. Freeman, New York, 1989).
[6] *Complexity: Life at the Edge of Chaos*, edited by Roger Lewin (Macmillan, New York, 1992).
[7] A. T. Bradshaw and L. L. Moseley, Physica A **261**, 107 (1998).
[8] R. Durrett and S. Levin, Theor Popul. Biol. **46**, 363 (1994).
[9] M. Droz, in *Modeling Cooperative Behavior in the Social Sciences*, edited by P. L. Garrido, J. Marro, and M. A. Munoz, AIP Conference Proceedings 779, p. 29 (2005).
[10] J. Maynard Smith and M. Slatkin, Ecology **54**, 384 (1973).
[11] W. F. Wolff, in *Ecodynamics, Contribution to Theoretical Biology* (Springer-Verlag, Berlin, 1988).
[12] N. Boccara, O. Roblin, and M. Roger, Phys. Rev. E **50**, 4531 (1994).
[13] R. Monetti, A. Rozenfeld, and E. Albano, Physica A **283**, 1 (2000).
[14] M. Droz and A. Pękalski, Physica A **298**, 545 (2001).
[15] M. F. He, Z. Wang, Q. Pan, and Y. Cai, Int. J. Mod. Phys. C **16**, 177 (2005).
[16] S. Crell, Anim. Behav. **54**, 1319 (1997).
[17] S. Crell and N. M. Crell, Conserv. Biol. **10**, 526 (1996).
[18] M. Shaffer, BioScience **31**, 131 (1981).
[19] T. Packer and T. M. Caro, Anim. Behav. **54**, 1317 (1997).
[20] E. Bonabeau, L. Dagorn, and P. Fréon, Proc. Natl. Acad. Sci. U.S.A. **96**, 4472 (1999).