

On the role of mobility and hunting effectiveness in a prey-predator model

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Abstract. We present a new, extended, predator-prey model for which we discuss the role of predators mobility and hunting effectiveness on the dynamics of the system. We show, via Monte Carlo simulations, that the maximum of predators' population density is a rather complex function of both – mobility and effectiveness of hunting. For a low mobility, larger effectiveness suits the predators better. When the mobility is large, the predators population is bigger if the predators are rather bad hunters. We have not observed temporal oscillations in the densities of both species.

1 Introduction

A lot of efforts have been expanded during recent years to explain complex cooperative behaviour among individuals. Important examples are provided by problems related to opinion formation [1], economical trading [2], the emergence of cooperation between selfish people [3], or competition among different species for survival [4,5].

In general population dynamics is described either via mean-field like or individual based models (IBM) [6,7]. IBM approach takes care of the fluctuations which, as it is well known, can play an important role in low dimensional systems [8] and may invalidate the predictions given by a mean-field approach. A large body of work concerns dynamical rules in which static agents evolve with some local rules in a synchronous (cellular automata like dynamics [9]) or asynchronous way (Monte-Carlo dynamics [10]). Many particular aspects of the population's dynamics can be investigated but the most interesting ones are the mechanisms presenting some generic characters which are present in different complex systems. It was noticed that in some circumstances the fact that the agents, or at least a part of them, could move on the lattice, may have important consequences on the dynamics of the system. It was demonstrated [11], in a somehow general context, that the combination of moving agents and game theoretical interactions gives rise to many self-organized behavioural patterns which can explain a variety of empirically observed social behaviours. Another example showing the importance of the mobility and efficiency of some agents is provided by the study of a spatial Prisoner's Dilemma game with two types of players (A and B) [12].

Thus the problem of competition between the mobility of the agents and their ability to interact in a more or less efficient way with the others appears to be a generic source of complex behaviour.

Prey-predators systems have been studied since many years, in the frame of evolutionary biology [13,14]. Beside the experimental investigations, there are many theoretical works aiming at modeling such systems. Since the pioneering works of Lotka and Volterra, many extensions have been proposed to model coexistence, destruction, invasion or adaptive changes of populations [15,16]. An abundant literature is also devoted to IBM modeling of such systems. However, very little has been done concerning the conjugated effects of the mobility and hunting effectiveness of the agents.

The role of the mobility alone of both prey and predators for patches models has been investigated by de Roos et al. (see [17] and references therein), both on the mean-field and IBM levels. They showed that when the predators were able to move, correlated oscillations in the prey and predator densities disappeared. Wolff [18] considered a model in which predators and prey can move and the predators die and reproduce with a probability depending on the time the predator had its last catch. Predators could either move intelligently, i.e. they move to a place with maximum number of prey, or they move randomly but only to nearest neighbour sites. Only in the first case oscillations in the densities of predators and prey have been observed. Moreover, the effects of over-hunting on the population survival has been investigated. Boccara et al. [19] and later in 2000 Monetti et al. [20], considered a predator-prey model in which the predators move, following some strategy, and catch the prey with a given probability. Predators can breed only after catching prey

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and they die with a given probability. The main problem studied was the conditions under which the system exhibits oscillations for the densities of the two species. Recently, Tobin et al. [21] studied the dynamic of patterns appearing in a mean-field like model of highly mobile predators attacking less mobile prey.

Thus, to the best of our knowledge, no systematic study of the effect of the competition between mobility and hunting effectiveness in prey-predators systems has been performed. The goal of this paper is to investigate this questions using a different model than the ones previously introduced. We shall use an IBM model and Monte Carlo simulations.

The paper is organized as follows. In Section 2 the model is defined and the conditions used for the numerical simulation spelled out. In Section 3, the results of the simulation are analyzed. Conclusions are drawn in the last section.

2 Model

We are considering a square lattice of dimensions $L \times L$. On the sites of the lattice two types of animals (agents) are put – predators (PD) and prey (PR). A site may contain only one animal or it may be empty. Predators eat prey, who feed on grass which is always available on all sites. The animals must move in order to breed and the progeny is put on empty sites only within a given distance from the parent. Prey disappear from the system when eaten by predators and predators may die if they do not catch a prey at least once during f time steps. Each predator is equipped with a “reserve”, filled after each kill with f portions. At each time step this reserve is reduced by one unit. Survival probability of a predator depends on the state of the reserve. The smaller is the reserve, the larger is the probability that the predator will be eliminated. Using Monte Carlo simulations we study the dynamics of such a system. The evolution rules are the following:

1. Within one Monte Carlo Step (MCS) a site j is chosen at random. If this site is occupied by a predator, we check its survival probability p_j according to the formula

$$p_j = 1 - \frac{r_j}{f}, \quad (1)$$

where r_j is the reserve of the predator j .

2. If the predator did not survive, we chose another site.
3. This procedure of choosing is repeated as many times (within 1 MCS) as there are animals at the beginning of that time step.
4. For the chosen animal (predator or prey) a site in the Moore neighborhood (8 nearest and next-nearest neighbouring sites) is randomly chosen. If the site is empty, the animal is moved there. If it contains an animal of the same type, nothing is done.
5. If the animal we choose is a predator and the new site contains a prey, the predator moves there, eats the prey and fills its reserve with f portions.

If the animal to move is a prey and the site contains a predator, the latter eats the former and the predator’s reserve is filled. The killing of a prey is realized with a probability k . If the killing does not take place, the move is not realized.

6. Both species produce offspring, but to do so it is necessary to move to an empty place. Predator moving with killing does not acquire the right for breeding. Moreover a predator must live at least f MCS to be considered adult fit for breeding. A prey as well as a predator may produce up to nb offspring, for which empty sites must be found in the Moore neighborhood of the parent. Each progeny is given just one try to find a vacant site. If a randomly chosen site is occupied, the progeny is not born. Hence, in very dense populations breeding could be rather rare. Each young predator receives its full reserve, allowing it to live without catching prey till its maturity.

In the present study we want to investigate the effect of the competition between mobility and hunting efficiency on the fate of the prey and predators populations.

In our model we allowed therefore predators to have different hunting efficiency (probability k) and we allow them to move up to n steps within one hunting event. This means that a predator may move up to n lattice sites after being once chosen. However, if during these steps it encounters a prey, its further moves are stopped, regardless if the hunt was successful or not.

The simulations were run on a lattice of linear size $L = 100$, with hard boundary conditions. Working with larger system sizes had no significant influence on the results. To take into account the stochasticity of the evolution rules, the results were averaged over 500 independent runs. Increasing this number did not affect the conclusions drawn from the 500 runs case. Initially the animals were put at random places in the lattice with equal concentrations 0.2. Changing it to 0.6 had no effect on the final results. The age of predators at time zero was put equal to 1, hence only after f MCS they could breed. In most of the cases, the maximum time of simulations was set at 2000 MCS.

The model has the following parameters: the lattice size L , the initial concentrations of predators and prey (taken to be equal to limit the number of free parameters), the maximum number of babies nb , also equal for the two species, the number n of steps a predator may make during one MCS, the hunt effectiveness k and the value of the reserve f .

To keep the number of independent parameters as low as possible, we have studied the role of the n and k on the dynamics of the system. Therefore we have fixed the values of the other parameters at $nb = 4$ and $f = 8$, since these were the minimal values for which the coexistence between PD and PR was possible over a wide range of the k and n .

The following characteristics of the system have been recorded: concentration of predators (c_{PD}), concentration of prey (c_{PR}), average number of successful hunts (normalized by the number of predators and moves), average

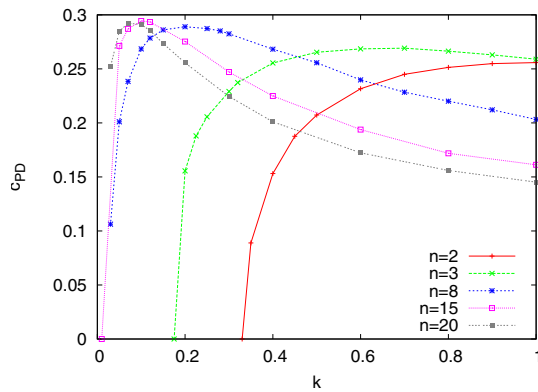


Fig. 1. (Color online) Density of the predator's population c_{PD} versus hunting effectiveness k for several values of the predators' mobility n .

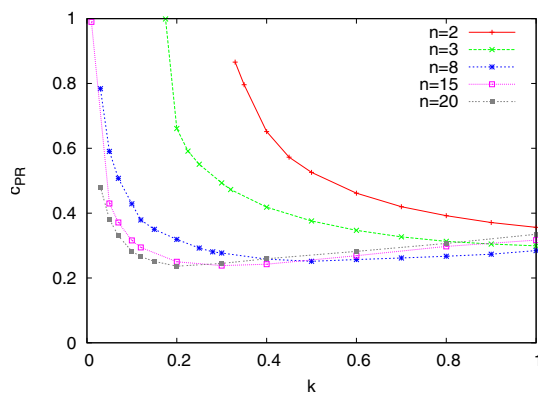


Fig. 2. (Color online) Density of the prey's population c_{PR} versus hunting effectiveness k for several values of the predators' mobility n .

number of steps a predator has made and the average number of offspring for predators (b_{PD}) and for prey (b_{PR}).

3 Results

Rather unexpectedly, the welfare of the predators' population, measured as its density, is not always increasing with increasing hunting effectiveness (see Fig. 1). When the predators could move just one step, they can survive only if they are perfect hunters, i.e. $k = 1$. When they can make two steps ($n = 2$), their maximum density is still at $k = 1$, but they can survive even when the hunting efficiency drops to $k = 0.35$. With increasing mobility we observe in Figure 1 that the maximum of the predators density moves to lower values of k , while the density at $k = 1$ goes down. The maximum becomes very pronounced for large n , but stabilizes itself at $k = 0.1$ for all $n > 10$. For $k < 0.05$ the predators' population could not survive, regardless of its mobility.

The dependence of the prey welfare (their density) on the predators hunting effectiveness is shown in Figure 2. It also has some unexpected features. When the mobility of predators is small ($n = 2, 3$) the density of prey

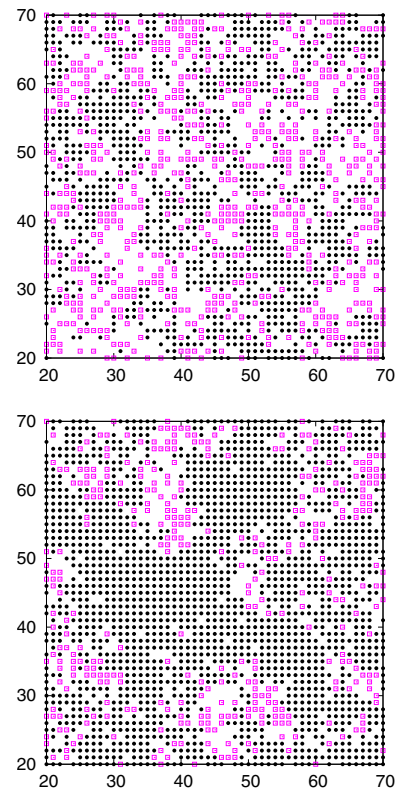


Fig. 3. (Color online) Positions of predators (open squares) and prey (full circles) at the end of simulations (2000 MCS) for the case of low mobility of the predators, $n = 2$ and perfect hunting effectiveness, $k = 1$ (upper panel) and lower effectiveness $k = 0.35$ (lower panel). For the sake of clarity, only a low-up part of the system is shown.

increases, as should be expected, with decreasing hunting success of the predators. When the mobility increases further ($n > 5$), the minimum shifts to lower values of the hunting efficiency, stabilizing itself at $k = 0.3$. Since at large mobility the maximum of the predators' density corresponds to $k = 0.1$, it is clear that there is no simple relation between the extrema of the predators and prey populations. The reason for this kind of behaviour could be deduced from the study of spatial correlations. Hence, we give some snapshots representing spatial configurations (see Fig. 3).

The first interesting case, i.e. when the predators could survive with hunting efficiency lower than $k = 1$, is when we allow them to move two steps. For $k = 1$ we see in Figure 3 (upper panel) that both populations tend to form rather small clusters which together with voids are intermingled. The densities are similar ($c_{PD} \approx 0.25$, $c_{PR} \approx 0.35$, $c_{void} \approx 0.4$). Hence the predators could move, catch the prey and there is room for their progeny.

When however $k = 0.35$, the population of predators is in a much worse situation. It is yet not endangered, but it will be if their hunting efficiency drops below 0.33. As can be seen from Figure 3 (lower panel), prey occupy nearly all space, forming a huge cluster and leaving only a small part of the system to the predators. Since the

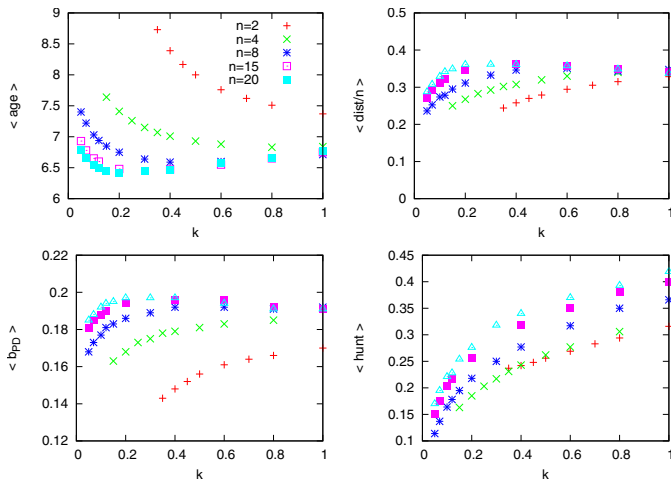


Fig. 4. (Color online) Characteristics of the predators versus hunting success. Clockwise: average age, average number of displacements (normalized by the maximum distance allowed, n), average number of progeny and average hunting success (normalized by the number of steps).

predators mobility is low, they cannot effectively penetrate the prey cluster. The predators have however enough space for putting their offspring and of course enough food, so they survive.

Although the prey are quite well off for $k = 0.35$, their birth rate is well below that for $k = 1$, and this is due to the compact clusters they form at low k and lower hunting efficiency of the predators. We have here a population of rather old prey, living quietly inside very big herds.

The situation looks quite different when the predators' mobility is large ($n = 15$). Now at $k = 1.0$ almost half of the territory is empty. Large mobility of predators and their high hunting efficiency lead to formation of very wide zones totally depleted of prey. Inside such zones many predators are doomed, since before they find a prey their reserves may well go down to zero. The surviving prey form rather large clusters, where the predators have no access, but there is also no room for the progeny. As the result, the reproduction rate of both species is quite low.

At $k = 0.1$, which corresponds to a maximum in the predators' population, spatial distribution is similar to the one for $n = 2$ and $k = 1.0$. There are rather small clusters of predators and prey, as well as of empty space. The densities are nearly equal and the prey birth rate is rather high. For $k = 0.1$ the average number of prey's progeny is much larger than predator's progeny, yet the densities are nearly equal, with a slight preference for the prey.

Situation in a stationary state at the end of simulations is well illustrated in Figure 4, showing more details about the predators' population – their average age, hunting effectiveness, number of offspring per MCS and the distance traveled (normalized by the maximum number of steps). All that as functions of k and for several values of n . It is evident that there is a saturation effect – the data for $n = 15$ and $n = 30$ are nearly identical.

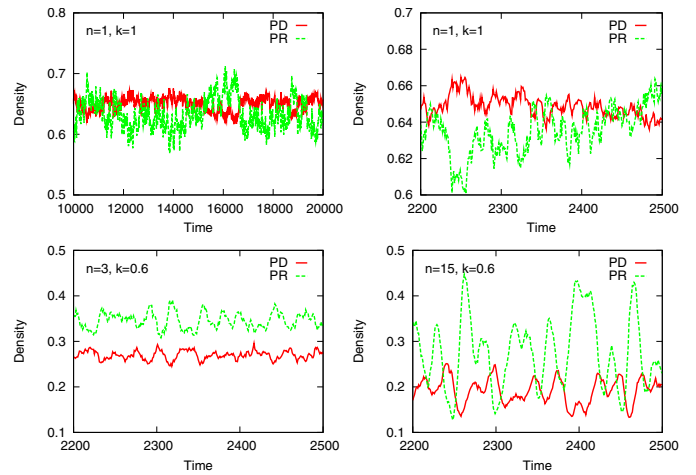


Fig. 5. (Color online) Time dependence of the predators (PD) and prey (PR) concentrations for very low ($n = 1$), intermediate ($n = 3$) and high ($n = 15$) mobility. Top right figure is a blow-up of a part of the top left one.

The data also show clearly that when the mobility is very high and the hunting effectiveness low, the population of predators have the largest birth rate, the average age is lowest and the average distance covered is also largest. Close to predators extinction, i.e. for $k < 0.05$, their birth rate drops dramatically, the population is getting older and do not move much. When the mobility of predators is small ($n = 2$) the dependence of all above characteristics on k has a more straightforward and monotonic character; hunting effectiveness goes down linearly, birth rate decreases faster than linearly and the average age is also growing. For intermediary mobility, i.e. $n = 8$, the pattern is between the low and high mobility, resembling however more that for high mobility.

In their paper de Roos et al. [17] observed that allowing for mobility of predators reduced greatly the oscillations in the densities of prey and predators observed in some models [22].

To check how the mobility and hunting effectiveness would influence the time dependence of the densities in our model, where both prey and predators are moving and moreover the mobility of predators could be regulated, we have performed long (2×10^4 MCS) simulations. There were no noticeable simple periodic oscillations (see Fig. 5). However the densities seemed to be correlated, as shown in the blow-up of the part of the long runs. In order to check for possible correlations, we have calculated the correlation coefficient r , [23] allowing for some time lag τ between the moments the data were taken:

$$r(\tau) = C^{-1} \begin{cases} \sum_{t=1}^{T-\tau} g_1(t, \tau) & \text{for } \tau \geq 0 \\ \sum_{t=1}^{T-|\tau|} g_2(t, \tau) & \text{for } \tau \leq 0, \end{cases} \quad (2)$$

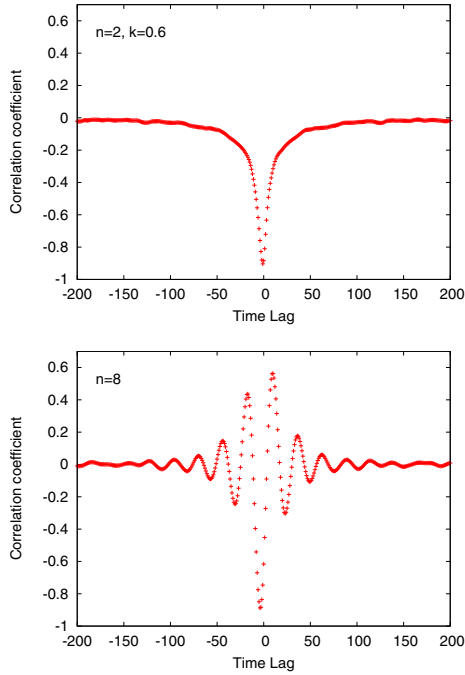


Fig. 6. (Color online) Correlation coefficient of prey and predator's densities for medium chasing efficiency ($k = 0.6$), $n = 2$ (upper panel), and $k = 0.6$, $n = 8$ (lower panel).

where

$$g_1(t, \tau) = (c_{PR}(t + \tau) - \langle c_{PR} \rangle_\tau) (c_{PD}(t) - \langle c_{PD} \rangle_0) \quad (3)$$

$$g_2(t, \tau) = (c_{PR}(t) - \langle c_{PR} \rangle_0) (c_{PD}(t + \tau) - \langle c_{PD} \rangle_\tau), \quad (4)$$

T is the time of simulations and

$$\langle c_x \rangle_\tau = \frac{1}{T - \tau} \sum_{t=\tau}^T c_x(t), \quad x = PR, PD \quad (5)$$

$$C = \sqrt{\frac{\sum_{t=1}^T (c_{PR}(t) - \langle c_{PR} \rangle_0)^2}{\sum_{t=1}^T (c_{PD}(t) - \langle c_{PD} \rangle_0)^2}}. \quad (6)$$

The results for $k = 0.6$ and for small ($n = 2$) and intermediate ($n = 8$) mobility, are shown in Figure 6. For $n = 2$, only anticorrelation effects ($r < 0$) are present, large for small time lags and decreasing to vanish for time lags larger than 50 MCS. The situation is similar for $n = 1$ where nearly perfect anticorrelations are observed at time lag zero. However, the characteristic decay time is larger than the one for $n = 2$ by two orders of magnitude, thus asking for very long simulation times (up to 10^6 MCS).

For $n > 3$, there are quite strong anticorrelations for small time lags, weaker correlations ($r > 0$) at larger time lag, then even weaker anticorrelations at greater time lag etc. The amplitudes are the strongest at zero time lag and decay with growing time lag.

This effect of diminishing correlations of the prey and predator densities in the case of mobile hunters is the result of changing the environment (neighbouring prey and

predators) during each chase event. Predators' probability of breeding, hence change of the density, depends on a new environment into which the predator moved. Therefore the local correlations between prey and predators are weakened. On the other hand since the mobility is reduced by the exclusion principle, the old neighbourhood has some influence, which reflects itself in the anticorrelations.

In our model both predators and prey move, if possible. Even for very low mobility ($n = 1$) we have not observed oscillations of the densities. We may say that mobility, by changing spatial patterns, is bringing the results closer to those which could be obtained via mean field. When the mobility is high, the lattice sites at the peak of the predators' concentration ($k = 0.1$) are nearly equally distributed among predators, prey and empty sites. When $n = 1$ and $k = 1.0$, over 60% of sites are occupied by prey, forming large clusters, and the rest is divided, again in roughly equal parts, between predators and voids.

4 Conclusions

We have presented and discussed a model of a predator – prey system in which both types of animals are moving and catching the prey is realized with a given probability. Predators' survival probability goes down with the time from the last catch and after a given period of unsuccessful hunt the predator is eliminated. We have shown that there is no simple dependence of the predators and prey densities on neither hunting efficiency nor on the mobility of the predators. When the predators are rather immobile, being a perfect hunter pays off. However if the predators move more and they are good hunters, they could kill many prey and then the predators population would be endangered from overhunting. Depending on the combination of mobility and hunting effectiveness, prey and predators organize themselves in different spatial patterns. High hunting effectiveness leads, in general, to formation of rather dense and large prey clusters, which only in this form could survive. When the effectiveness is low, the clusters are much smaller, meaning that even small groups of prey could survive, and the groups of predators, prey and void are intermixed. A population of perfect hunters could survive for any mobility, but predators capable of moving just to a nearest neighbouring site must be perfect hunters in order to exist. When the mobility increases, also poorer hunters have their chance. There are nevertheless some limitations. Increasing the mobility to values greater than $n = 15$ produces no changes in the results. Even for very large mobility a population of very poor hunters ($k < 0.01$) will be eliminated. The dynamics of the system can be understood in terms of temporal and spatial correlations between the interacting agents.

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