

COMPETITION BETWEEN STOCHASTICITY AND DETERMINISM IN A LOTKA-VOLTERRA PREY-PREDATOR 2D LATTICE MODEL

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Certificate

This is to certify that Parivesh Priye has honestly carried out the tasks that were entrusted to him. This project was carried out at IISER Pune, under my supervision and the results obtained in due course are from his own original model.

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Abstract

We investigate the differences in prey-predator dynamics arising in a stochastic lattice model as a result of determinism (in the form of strategies for prey and predator with an aim to optimize the respective fitness) and stochasticity (in which the movement of the two entities is governed by highest random hopping weights assigned to neighboring cells). By means of Monte Carlo procedure, we simulate the model defined on a regular square lattice and discern the phase transition from an active state (where both species coexist) to an absorbing state (where one or both of the species are extinct). We find out that in a system with dominant predation, introducing intelligence in prey confers an additional advantage in terms of fitness which leads to their greater presence across sites on the lattice as compared to the predators who occupy fewer sites. Also, as we keep on increasing the probability of a prey to adopt the strategy of hopping to the neighboring site with the minimum number of predators, we find that predators vanish quicker than the situations where preys adopt a more random approach in hopping to the sites.

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Chapter 1

Introduction

Lotka [1] and Volterra [2] developed one of the first theoretical approaches for studying predator-prey dynamic system independently. The model consists of one predator whose only diet is one prey. A constant growth rate and mortality rate is assumed for the prey and predator respectively.

The Lotka-Volterra system of ordinary differential equations:

$$\begin{aligned}x'_t &= ax_t - bx_t y_t \\y'_t &= cx_t y_t - dy_t\end{aligned}$$

with positive x_0, y_0 and positive a, b, c, d describes a behavior of a predator-prey system in terms of prey and predator "densities" x_t and y_t . Here, a is the rate of increase of prey in the absence of predator, d is the rate of decrease of predator in the absence of prey while the rate of decrease in prey is proportional to number of predators bx_t and rate of increase in predator is proportional to number of prey $cx_t y_t$. Since the population numbers are integral, the above model has an underlying assumption that the numbers of both populations are large and densities are obtained upon normalization of population numbers by a large parameter, say P . Setting the time derivatives to zero yields three stationary states (a_s, b_s) :

1. the absorbing state with total population extinction which is linearly unstable for $\sigma > 0$.
2. predator extinction and prey explosion $(0, \infty)$ which for $c > 0$ is also linearly unstable (an absorbing state for the predators).
3. species coexistence $(a_s = \frac{a}{b}, b_s = \frac{d}{c})$

The fixed point is marginally stable as the eigen values of the Jacobian stability matrix are purely imaginary $i\sqrt{ad}$.

The model is inadequate as it fails to answer questions of extinction of populations, as the extinction never happens in the deterministic mean field model for any x_t, y_t in the phase plane. The solutions of the model are closed orbits in phase space which means that the nonlinear population oscillations are regular and periodic with amplitudes and frequencies contingent on the initial values $x(0)$ and $y(0)$. The model is also mathematically imprecise against spatial variations, stochasticity which casts a serious question on its biological relevance [3].

1.1 So, what was done to remove these inadequacies?

There have been modifications in the original Lotka Volterra model that have incorporated factors like intra-species competition, harvesting etc. that have a bearing on the dynamics. However, Lotka-Volterra model and its modifications fail to consider the reality that an individual is in general affected more by its local species density, and less by global density of species [4]. The models neglect spatial heterogeneities such as the uneven distribution of populations and resources, predation rates etc. in a given landscape. Experiments by Huffaker (1958) using mite populations have demonstrated that the population dynamics are significantly affected by spatial distribution of species and resources, and the prey and predator mobility. The lattice model was used by Satuvolvsky and Tome([4]) to investigate prey predator dynamics(one prey and one predator with no harvesting). The study exhibited oscillatory behavior of population densities of the prey and predator at both local and global levels.

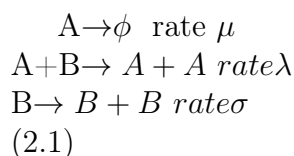
1.1.1 Motivation behind our study

We adopt the stochastic approach to take into account the localization of an individual of a species and its local interactions by invoking the 2D lattice Model. The dynamics is governed by stochastic rules representing processes like death and proliferation and the rules are formulated at an individual level. Models of ecosystems which use this approach are amenable to numerical computations. [5] introduced quenched randomness into the lattice to take into account the varying rates of predation, birth of prey and death of predator in the real habitat and found that this variability enhances fitness and led to formation of patches of habitation. Also in the real biological systems, the entities(preay and predator) are intelligent beings i.e. their movements within a habitat is dictated by measures that would maximize the chance of their survival. For predator, this would mean that they would seek portions of the landscape that abound in prey and preys would like to avoid the patches of habitat that are relatively abundant in predators. In our model, we incorporated a combination of these intelligent moves and completely random moves (for the prey)in the prey-predator model and tried to deduce the biological implications of the ensuing dynamics. As supported by the results of our simulation, we found that intelligence alone cannot result in coexistence as it did lead to extinction of species. Some stochasticity is necessary to bring about coexistence.

Chapter 2

Our Model

We consider a two-species system of diffusing particles or population numbers subject to following dynamics:



The predators die spontaneously at rate $\mu > 0$, whereas the prey 'B' proliferate with rate $\sigma > 0$. a_t and b_t respectively denote the predator/prey population densities.

2.1 Model Description

The lattice model has four components:

- A Lattice, which is a finite set of discrete points called sites, which are filled by both preys and predators and represents their location.
- A finite set of states: For simulating the diffusing and interacting points on a lattice, in the report, a site can acquire one of these states:
 1. (0): the site is empty. This site is regarded as containing a resource that is the nutrient for the prey species B.
 2. (1): the representative particle is a prey (B)
 3. (2): the representative particle is a predator (A)
- The neighborhood definition: a rule that defines the location of sites that influence the state of a particular site.
- Transition Rules: Rules that determine how the state of a given site would evolve. In our model, these rules are either stochastic or driven by game-theoretic strategies.

In this report, the lattice is two-dimensional. The predator/prey densities evolve in discrete time steps governed by a set of rules that are local, stochastic or deterministic(in case a strategy is adopted).

2.1.1 Neighborhood definition

The neighborhood of a particular site is defined as the four squares at distance of one unit from site (except the diagonal squares). This means, a chosen particle can hop to one of the four sites located : up, down, left or right.

2.1.2 Model Assumptions

- All variables are defined in the domain of the non negative real numbers.
- All three reactions as well as the nearest-neighboring hopping are to be interpreted as stochastic processes.
- Species interactions are local.
- Prey birth takes place only when the local carrying capacity (in our model, it is equal to 100).
- In the absence of predation, growth rate of prey is logistic.

Chapter 3

Monte Carlo Simulations

3.1 Data Structure

In the model, we have unrestricted site occupation. Basically, to simulate diffusion and interacting particles on the lattice, one requires four operations which get repeated in different combinations :

1. Particle Selection: A lattice occupant is selected with a probability which is proportional to the density of a species in a given site. This implies that if a site has more preys than predators, a prey is more likely to be chosen.
2. Number Determination: This operation determines the number of particles of any given species on a given site at a given instant. This demands fast execution and hence one has to take care while ordering particles in the data structure.
3. Add: a new particle is inserted into a lattice.
4. Remove: This operation 'destroys' a particle from the lattice.

Thus a particle movement is nothing but a sequential Remove and Add.

In the code, we maintain matrices for both species A (predator) and B (prey). According to the dynamics, after each Monte Carlo time step, the entries of the matrices are updated. Any entry (say A_{MN}) of the matrix can be used to locate the site and the value gives the number of the entities occupying the site. We interact with the head of each site-local list or an occupant that is directly chosen through random selection.

3.1.1 Monte Carlo Procedure

For each iteration of the simulation, a lattice occupant is chosen (according to the probability as described in the above subsection) and it hops to a nearest-neighbor site. Subsequently, it might undergo an on-site reaction. After each such iteration, we increase the time step by $1/(N(t))$, where $N(t)$ is the total number of particles at that instant.

Here, we outline the steps for the unconstrained, stochastic Monte Carlo simulation of the Lotka-Volterra Model on the lattice

1. Select a lattice occupant from a random site. If the random site is empty, keep selecting a random site until you hit a non-empty site from where one lattice occupant can be chosen to hop to a neighboring cell with probability 1.
2. This step is where you can incorporate strategies for hopping for the entities. In a naive world (where no one adopts strategies), a particle can hop to one of the four neighboring cells. For simulating a scenario where one can have intelligent particles, one has to determine the odds of migration to each of the neighboring cell and let the particle hop to the one that enhances the fitness of the hopping species the most.
3. If the occupant is a B particle (Prey), generate a random number p_1 that lies between $[0, 1)$; if $p_1 < \sigma$, add another new B particle to the current site. This step is the prey proliferation, $B \rightarrow B + B$. Also, if the number of preys in the cell is already ≥ 100 , the hopped prey can not reproduce in that cell.
4. If the occupant is an A particle(predator)
 - If there are any B particles(preys) on this site: for each B generate a random number p_2 between 0 and 1. If $p_2 < \lambda$, remove that prey and add one predator in its place. This is the predation interaction, $A + B \rightarrow A + A$. To make the model biologically more plausible, we have also introduced quenched randomness in λ in the sites. This simply means that we have a matrix for λ assignment to the sites. The values come from a gaussian distribution having a mean and variance (which can be changed in the code).
 - generate a random number p_3 in $[0, 1)$ and if $p_3 < \mu$, A is removed i.e. we have predator death, $A \rightarrow \phi$.

In our simulations, none of the possible events are mutually exclusive. This means that we can have simultaneous diffusion and on-site reactions. We initialize the matrices of A and B (We have mostly populated with an integer between 0 and 5 or between 0 and 10).

3.2 Boundary Conditions

We invoke periodic boundary conditions for random hopping as well as the hopping according to a strategy.

Chapter 4

Results

First, we set to verify the results that were obtained in [6]. Then, we go on to investigate the effect of introducing a mix of intelligent moves and random moves by preys and only random moves by predators and try to study the competition between stochasticity and determinism.

4.1 Verification of known results and their interpretation

We took a 256×256 square lattice and run it with rate parameters ($\mu = .5, \sigma = .2$) and plotted $a(t), b(t)$ as functions of time t .

We found (as in [6]) that early time regimes are marked by significant oscillations, as shown in figure 4.1(a). As time progresses, amplitude of these initial oscillations decreases considerably although they sustain for a long time. When the predation rate was increased to 1 as compared to 0.5, amplitudes of the oscillations were suppressed as evident in figure 4.1(c). This means that that as we increase the reaction rates, interactions are rendered more local. As predation rates have seen a considerable increase (two-fold), we expect that the prey density would see a rapid decline, followed by the predators. We investigated the model with suites of values of the parameters but was unable to detect a coexistence regime that is governed by a stable fixed point (which is approached without any population oscillations). For high reaction rates, however, these oscillations become remarkably damped. As seen from figure 4.1(b), the long time regime is governed by stochastic fluctuations about the attractive fixed point at the center of the graph.

4.1.1 Introducing intelligence in preys

As seen from the above dynamics from the figure 4.1 (a) and (c), the system under study is predator-dominant as across time, predator density (number of predators per site) is more than prey density. This prompted us to introduce intelligence in the prey species to check if this would confer them with distinct advantage over the predators who were to hop randomly without any strategy in place. We expected

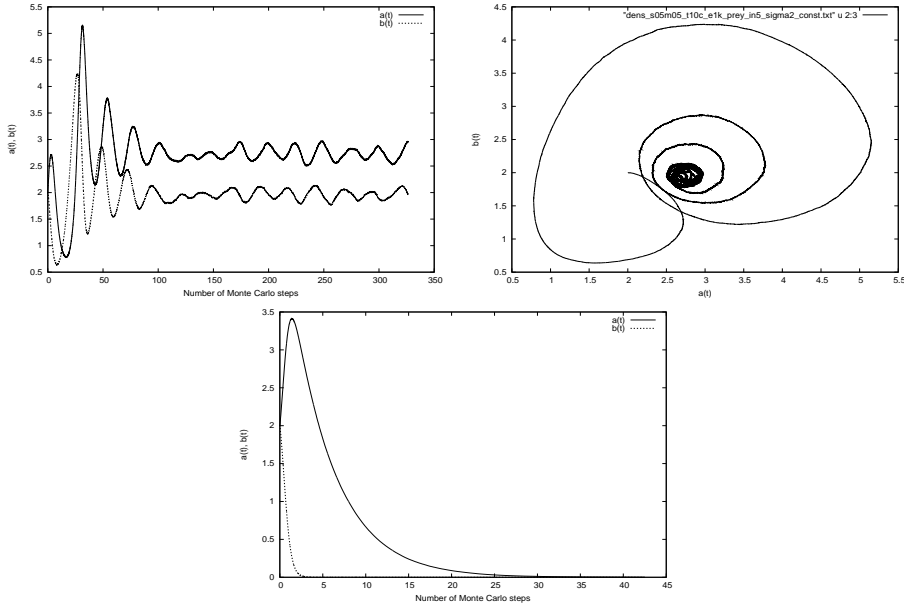


Figure 4.1: (a) Predator $a(t)$ and prey $b(t)$ densities versus time in a simulation run over 256×256 lattice, with random initial distribution, and rates $\mu = .5$, $\sigma = .2$, $\lambda = .5$ (b)Trajectory in the $a - b$ phase plane from the simulation data in (a),(c) Predator $a(t)$ and prey $b(t)$ densities versus time with all parameters same except λ which is 1.

this advantage to reflect in a dramatic increase in the prey density as compared to previous situations in 4.1. We present here, the results of our findings in the figure 4.2. The parameter, (p) , is the probability of adopting a strategy by prey. $1 - p$ would thus represent the probability of a prey performing a random hopping from a site to the neighboring ones.

We observe that as p increases, preys outcompete their counterparts faster. This can be attributed to the fact that since preys employ strategy (which is to hop to a site having the minimum number of predators) with a greater probability, they outnumber the predators (who hop randomly) at most of the sites. For random hopping of the predator, we generate four numbers between 0 and 1 and treat them as the probability of hopping to the four neighboring cell. The random number that takes the maximum value corresponds to the site where the predator is most likely to hop and undergo an on-site interaction subsequently. Since our code involves choosing a non-empty site for choosing a particle for hopping Sec. 3.1.1.

, we have witnessed a situation where the simulation stops after we hit an empty site more than $N \times 256 \times 256$ times (where N can be varied in the code). This happens as locally predators go extinct on many of the given sites. One can continue the reaction further by careful selection of non-empty site after this scenario. However, the dynamics up to this point clearly reflects the advantage that adopting a productive strategy renders on the preys. We also generated the matrix corresponding to the number of species per site (to be seen once the reactions had stopped as per our

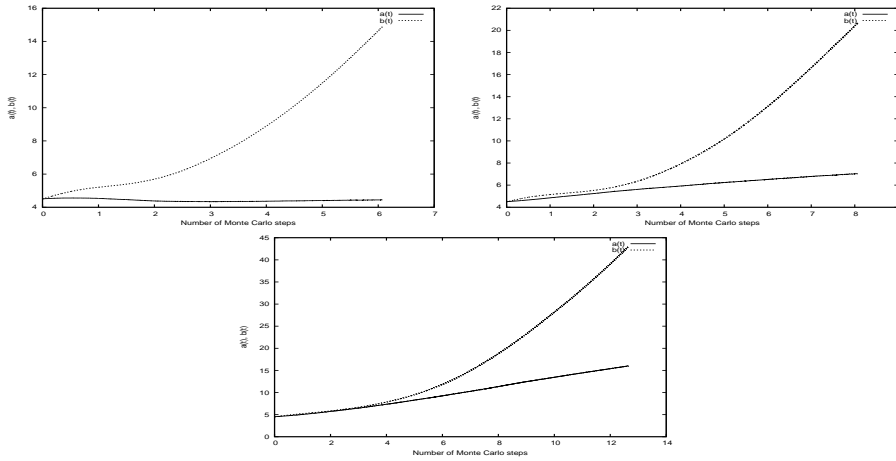


Figure 4.2: Predator $a(t)$ and prey $b(t)$ densities versus time in a simulation run over 256×256 lattice, with random initial distribution, and rates $\mu = .5$, $\sigma = .2$, $\lambda = .5$ and parameter $p=0.7, 0.5$ and 0.3 respectively

code)for these values of parameters: $\mu = 0.2, \sigma = 0.2, \lambda = 0.5, p = 0.5$.

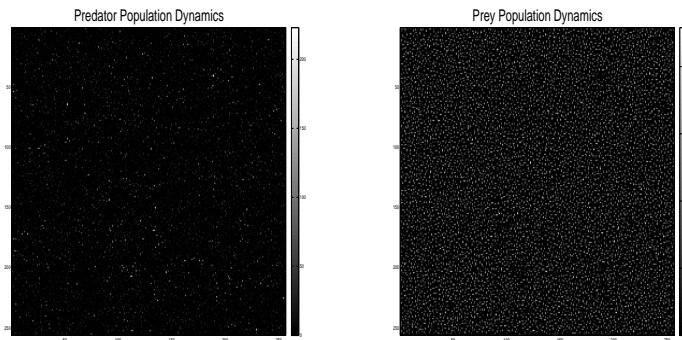


Figure 4.3: (a)predator occupation on the lattice (b) prey occupation on the lattice

Dark spots pertain to empty sites and as the color gets lighter, site occupancy rises. As can be seen from figure 4.3, one can see that most of the sites are marginally filled with predators as compared with those populated with preys.

4.1.2 Remarks about the code

The codes used to run Monte-Carlo simulations need to be very efficient because:

- As we increase the initial site occupancy of the sites, the number of Monte-Carlo steps that the simulation takes to run decreases. This is because number of such times steps scales as $1/N(t)$.

- One can toy with total number of iterations to increase the time span. However, this affects the time-efficiency of the code.
- The dynamics that we have obtained is for the first few Monte Carlo Steps. Essentially after this, predators are so rare that they are seldom picked up (by chance) to hop to neighboring sites and interact with other particles. Because it remains to be seen what happens after this stage in the dynamics, we posit that predators might get wiped out purely due to their death rate (They might not too as the equations are stochastic!). One can also observe coexistence with pronounced presence of preys and predators confined to certain sites (much like the present scenario).

Chapter 5

Discussion

Biological ecosystems present interesting diversities. Notably, competing species co-exist and keep employing effective strategies to further their own fitness. This means that a species has tactics of movement, food location etc. that tend to maximize their payoffs from their endeavors. Keeping this in mind, we modelled prey-predator Lotka-Volterra system stochastically, also incorporating game-theoretic movement techniques adopted by prey (as our system was dominated by predators essentially, we wanted to see if equipping preys with intelligence rendered them with some advantage over the predators). We found that most of the sites saw the extinction of predators except some of the sites that were occupied by them. On the other hand, preys occupied more number of sites in general as compared to the predators. We also wanted to investigate the competition between stochasticity and determinism. We did this by varying the probability of a prey adopting a strategy rather than hopping randomly to a neighboring cell. We found that when determinism was high in the system (in the form of intelligent moves by prey most of the time), predators got extinct locally quicker as compared to when stochasticity was higher. However, with intelligence present in the system, predators were eventually confined to few sites in the whole lattice and preys were relatively more abundant than them. As opposed to the original purely stochastic model with uniform predation rates, where predators are dominant (although preys coexist), we did manage to avert this upper-handedness by introducing intelligence in the preys.

5.0.3 Future Course

We are to test the effect of intelligence in a landscape with spatially varying predation rates. We expect that this model will be biologically more realistic and would shed light on important aspects of the system. One other interesting thing that one can look at is the effect of adaptive intelligence on the dynamics. Adaptive intelligence means that an entity can look around (i.e. analyze its neighboring cells) and its probability of adopting a strategy would be contingent on its need to do so. For e.g if a prey finds itself at a site surrounded by few predators, it may perhaps not employ intelligence as opposed to a situation where it has relatively more predators in its vicinity and it becomes prudent to exercise intelligence to survive.

References

- [1] A. J. Lotka, *J. Am. Chem. Soc.* 1595 (1920) 42.
- [2] V. Volterra, *Variazioni e fluttuazioni del numero d'individui in specie d' animali conviventi.*
- [3] D. Neal, *Introduction to Population Biology*, Cambridge University Press, 2004.
- [4] J. E. Satulovsky, T. Tome, *Stochastic lattice gas model for a predator-prey model*, *Phys. Rev. E* 49 (1994) 5073.
- [5] U. Dobramysl, U. C. Tauber, *Spatial variability enhances species fitness in stochastic prey-predator interactions*, *Phys. Rev. Lett.*
- [6] M. Washenberger, M. Mobilia, U. Tauber, *Influence of local carrying capacity restrictions on stochastic predator-prey models*, *J. Phys. Condens. Matter* 19.