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Article in *Computing in Science and Engineering* · February 2004

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## A SHORT GUIDE TO PREDATOR–PREY LATTICE MODELS

By Andrzej Pekalski

**T**HE MOTIVATION FOR WRITING THIS MINI REVIEW IS THAT MANY APPROACHES TO PREDATOR–PREY (PP) SYSTEMS HAVE BEEN DISCOVERED, OVERLOOKED, AND THEN REDISCOVERED AGAIN YEARS LATER. BRIEFLY DESCRIBING SOME OF THE PAPERS

that physicists have written about the subject over the last 20 years thus seems advisable. In broad terms, a predator–prey model describes the dynamics of two kinds of entities—specifically, one kind could be destroyed on contact with the other.

This review contains no detailed formulas, model descriptions, or techniques; rather, it presents the authors' assumptions, main results, and conclusions. Some unclear points still exist, despite the time elapsed from the first papers, so this review might inspire you to open research in new directions.

### Going Back to the Roots

PP system research starts with Alfred Lotka<sup>1</sup> and Vito Volterra<sup>2</sup> in the 1920s. Volterra proposed a model to describe the mutual interaction of different types of fish living in the Adriatic Sea and to explain oscillations in the number of fish caught there. Lotka arrived at similar equations—via reacting chemical ingredients—that also showed oscillatory behavior. We now know the equations as the *Lotka–Volterra* (LV) equations:

$$\frac{dN}{dt} = N(a - bP),$$

$$\frac{dP}{dt} = P(cN - e), \quad (1)$$

where  $a$ ,  $b$ ,  $c$ , and  $e$  are constants characterizing the populations of prey  $N$  and predators  $P$ . The LV equations are the simplest for describing the time evolution of two interacting populations. Predation reduces the prey population by the factor  $bNP$ , proportional to the number of predators and prey. Predators die at the rate  $eP$ , independent of the number of prey, but the predator population's growth is proportional to the number of individuals in both populations.

The LV equations have some obvious drawbacks. First, they say that in the absence of predators, the prey population will grow in an unlimited Malthusian way. This is unrealistic; there should be an upper limit to the number of prey that can live in a given habitat, which is also called the system's *carrying capacity*.

Furthermore, from the biological viewpoint, it isn't realistic to assume that animal breeding and feeding is continuous: there are breeding and hunting seasons, animals often use their own predation and evasion strategies, and so on. Using differential equations requires averaged quantities (such as density or death and birth rates). In physical terms, it means using mean-field-type approaches, which can mask certain effects or even be misleading.

Generally speaking, we can model biological systems via two approaches. In the first, we attempt to use mathematical equations or a computer program to describe a given biological situation with as much detail as possible. In many cases, this could require many parameters, but the model will be tailored strictly to the problem in question. Ecologists often use this kind of approach; their model parameters easily can reach 100.<sup>3</sup>

Physicists usually go with a different approach. They try to use only a few parameters and construct a general model with which they can discover the basic mechanisms responsible for the studied phenomenon. The literature describing the PP model in the spirit of Lotka's pioneering work, especially in ecological and biological

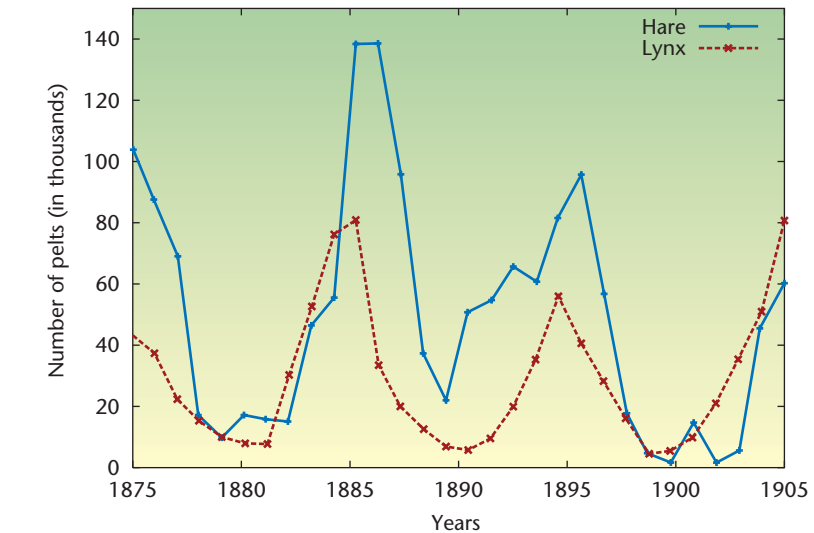
**P**rospective authors, particularly outside the Computer Simulations department editor's field, are encouraged to send him proposals for future contributions. Please contact Dietrich Stauffer, stauffer@thp.uni-koeln.de.

papers, is enormous—the Scirus search engine alone produces more than 20,000 entries. In this article, however, I'll restrict myself to papers written by physicists that deal with lattice models.

The LV equations show periodic oscillations in predator and prey population time dependencies. This is understandable biologically because if the predator population grows, it eats more prey, which decreases the prey population. Not all these predators will find enough food, though, so more of them will die of hunger. Having fewer predators lets the prey population rebuild, which in turn means more food for predators, which increases the number of predators, and so on. The now-famous plot of temporal dependence of the number of hare and lynx pelts the Hudson Bay Company sold at the end of the 19th century backs up this kind of reasoning (see Figure 1).<sup>4</sup>

Quite recently, two papers described the problem of PP density oscillations and studied the temporal shifts in their peaks.<sup>5,6</sup> They found that rapid evolution can influence the peaks' respective positions and lead to closed loops in the phase diagram. The LV equations produce such oscillations; on a phase diagram, PP density planes have the form of closed trajectories (or limit cycles) because a PP model based on LV equations is a conservative system. Even though Equation 1 is not structurally stable, there is no oscillation damping, which means a small parameter change causes a change in the phase plane's orbit.

The main problem in the LV equations—the uncontrolled growth of prey in the absence of predators—is most often avoided by adding the Verhulst factor.<sup>4</sup> Then, the LV equations have the form



**Figure 1. Temporal-dependence plots. The oscillations in the number of pelts the Hudson Bay Company sold of predators (lynx) and prey (hare) in the years 1875 to 1905.<sup>4</sup>**

$$\begin{aligned} \frac{dN}{dt} &= Na \left( 1 - \frac{N}{K} \right) - bNP, \\ \frac{dP}{dt} &= P(cN - e), \end{aligned} \quad (2)$$

where  $K$  is the system's carrying capacity. This takes care of the unbounded growth, but it generally destroys the existing limit cycles, which leads asymptotically to a constant solution. We also could add other terms to Equation 1, change the continuous hunting by predators, modify the area over which predators hunt, and so on.

A model using modified LV equations has no constant of motion and, apart from closed cycles, also shows trajectories that decay to zero over time, meaning the system advances to an absorbing state with one or both species extinct. Which scenario will be realized depends on the choice of  $a$ ,  $b$ ,  $c$ , and  $e$  parameters. However, if we consider another microscopic approach, such as one with Monte Carlo simulations, the fluctuations are present because of the technique's stochastic nature and could, in time, damp the oscillations.

Physicists' papers dealing with PP models fall into two broad categories.

In one, the authors try to explain why periodic oscillations are present in systems with fluctuations; in the second, they search for conditions when predators and prey coexist and study the phase transitions.

## Oscillations

Wilfried F. Wolff studied oscillations in PP systems in an unjustly forgotten paper back in the 1980s.<sup>7</sup> He constructed a model in which predators hunted only when hungry, and both types of animals could move randomly, escape (prey), or hunt (predators). This model, unlike most others, permits multiple occupancy of a given cell.

Wolff studied oscillations in the two populations' densities as a function of the system's carrying capacity by using LV equations and Monte Carlo simulations. He showed that undamped oscillations appear in the changed LV equations only if the carrying capacity is large enough; otherwise, there is just a fixed point. Small systems have relatively few prey, which also can be distributed spatially in a nonhomogeneous way, hence practically no correlations exist between prey and predator densities. Wolff distinguishes in this respect two regimes:  $K$ -limited (small  $K$ ) and predator-controlled (large  $K$ ).

Nino Boccara, O. Roblin, and Morgan Roger<sup>8</sup> published a paper a few years later in which they considered an automata network of predators. This network has a certain pursuit region within which predators can locate prey; simultaneously, prey has an escape zone inside which it can detect predators. Predators can catch prey only within the predation zone and even then only with a certain probability. After a catch, the predator gives birth to one offspring and can die with a given probability. If no predators are near a prey, the prey gives birth to an offspring. The authors compared solutions obtained via cellular automata

### ***Predators die if they're in a cell without prey.***

with mean-field ones, which sometimes (when animal mobility is large) gave a qualitatively correct description of the densities' temporal dependence. Unlike Wolff, the authors did not observe oscillations for large lattices; they attributed time dependencies' oscillatory character to the habitat's finite size. That said, Wolff considered much smaller lattices, so a large system in this case ( $200 \times 200$ ) still is smaller than the one Boccara and his colleagues studied ( $512 \times 512$ ).

Adam Lipowski studied temporal correlations between PP densities in a 1999 paper<sup>9</sup> by considering a simple microscopic model that uses Monte Carlo simulations. He showed that in a one-dimensional system, stochastic fluctuations destroy correlations between prey and predator densities, whereas in two- and three-dimensional systems, such correlations are present.

He concluded that periodic oscillations could be an intrinsic feature of some models; the reason for their appearance might be due to some sort of stochastic resonance.

In 2000, Roberto Monetti, Alejandro Rozenfeld, and Ezequiel Albano<sup>10</sup> considered a variant of Boccara's model by using Monte Carlo technique on a two-dimensional lattice. Each animal has a certain range of vision within which it can calculate the gradient of other species' density and react accordingly—escape or hunt. The model attributed the seemingly correlated oscillations in the two densities' temporal dependencies to the existence of a “percolating cluster” of prey. The model also grouped predators into small colonies scattered over the lattice. In a sense, it agrees with Wolff's model, which found that for small systems, prey form isolated clusters and that oscillations are absent.

Tibor Antal and Michel Droz<sup>11</sup> studied a simpler model, without additional conditions for animal behavior. Like Wolff, they allowed for multiple single-cell occupancy. Each cell can be in one of three states: empty, prey, or prey and predators. Transition rates from an empty state to prey and from prey to prey and predator are the model's only two parameters. Predators die if they're in a cell without prey. In the coexisting state, the authors found two regimes: those with and without spatial and temporal density oscillations. Whether the system is in the first or second state depends on the parameters' values. The authors supported Boccara's claim that the oscillations in global quantities die out when the system size increases.

Kamil Trojan and I used a Monte Carlo model to consider the problem of periodic temporal oscillations in densities.<sup>12</sup> In our model, prey has a chance to

hide from predators on some of the two-dimensional square lattice sites. Simulations showed high correlation between the oscillations—even if the system's size was rather small ( $50 \times 50$ )—if the cover sites' concentration was low, but this vanished if the concentration grew.

One word of caution when comparing conditions for the appearance of correlated oscillations in densities: nobody has established the role of the LV model's various modifications. It might help to build and investigate a model that incorporates most of the “realistic” assumptions and then check how switching them on and off changes the oscillations.

### **Stability and Coexistence**

Conditions for the coexistence of predators and prey are quite important from a practical viewpoint because they let us estimate the conditions necessary for preserving a status quo. They're also interesting from a physicist's viewpoint because PP systems generally exist in three states (phases)—one coexisting and two absorbing ones—for empty and prey only.

PP system stability could come from many sources, such as species migration, predators self-limiting their hunts, seasonal hunting due to the different predation skills of the younger versus more mature predators, and so on. John Maynard Smith and Montgomery Slatkin considered the last stabilizing factor in this list.<sup>13</sup> In their model, if a prey species is born in one season (summer) and survives the next (winter), it breeds the following summer. Predators also breed in summer but must eat to survive winter. Prey also can find shelter from predators. The authors showed that for some parameter values, the prey population (in the absence of predators) could fluctuate in time; for other values, it remains stable. The coexisting state is more

likely if the prey is nonoscillatory. Prey numbers in the coexisting state also should not drop below the number of prey in the absence of predators. The predators' different hunting skills increase the chance of coexistence, whereas the existence of shelter does not. Maynard Smith and Slatkin used differential equations in their analysis.

Wolff considered two different strategies: a predator could choose a site with the maximum number of prey, and prey could escape in the opposite direction. Four possible strategies thus exist: random movement of both species, hunting plus random, random plus escape, and hunting plus escape. Each action (hunting or movement) is realized with a certain probability. According to Wolff, escape offers prey certain advantages but only when confronted with predators' hunting strategies. However, hunting is always more efficient, regardless of the strategy the prey adopts. The combination of hunting plus random leads to a very fast extinction of prey and, consequently, predators. Wolff also considered a special case in which just 2 percent of predators are hunters and 2 percent of prey uses the escape strategy; the others move randomly. After a short time, hunters dominate the predator population, but after a longer time, the escape prey prevails.

Rozenfeld and Albano<sup>14</sup> and later Monetti and his colleagues<sup>10</sup> took Boccar's model and used it with lattice-gas formalism. Predators and prey have a certain (equal) vision range within which they could respectively catch prey or evade predators. The authors constructed a two-parameter phase diagram in the plane that they could change—specifically, they could change a predator's probabilities of catching prey and giving birth to one offspring. They found two phases: coexisting and absorbing (prey only). The

phase transition is of the second order and belongs to the directed percolation universality class.

Qamar Khan and Rameshwar Jaju studied a different PP system stability problem.<sup>15</sup> Using differential equations, they studied a system with two kinds of prey and one type of predator. Their basic assumption was that large groups of prey could defend themselves well, so predators hunted for isolated animals or small herds only. Their main result was that if the concentration of the prey were high enough, the predators had no chance to feed and could become extinct.

Via Monte Carlo simulations and mean-field type calculations, Rouzbeh Gerami and Reza Ejtehadi<sup>16</sup> studied a system with randomly moving herbivores (predators) and immobile plants (prey). A predator reproduces with a given rate and dies if it does not eat during a certain time. The model allows multiple occupancy of a site such as during the birthing process, when the progeny is put in the same site as the parent and receives half of its food reserve. The authors obtained a trivial (absorbing) fixed point and some stationary fixed points in the phase space of average prey and predator densities. In these stationary states, predators and prey are distributed in separated clusters.

Antal and Droz restudied their model—in particular, the line of phase transitions between the coexisting and absorbing phases.<sup>17</sup> For some parameter values, the transitions are to a single absorbing state, so they belong to the directed percolation universality class. For other values, a different line of phase transitions links to an infinite number of absorbing states; critical exponents' classical values characterize this transition. The bicritical point where the two lines meet belongs to another, new, universality class.

Droz and I<sup>18</sup> considered a lattice model in which many of the previously described models' features are present, plus some new ones. To survive, both species must eat; to breed, an animal must move and find a partner in the neighborhood. The pair produces more than one offspring, unless there is no place in the parents' Moore neighborhood. (The Moore neighborhood on a square lattice consists of

*Escape offers prey  
certain advantages  
but only when  
confronted with  
predators' hunting  
strategies.*

eight sites, which are a site's nearest or next nearest neighbors.) A certain percentage of lattice sites act as a cover for prey, but prey can't eat or breed on such sites. We found three asymptotic states: coexisting, prey only, and empty. The probability of arriving at a given state depends on the initial animal densities, the amount of cover, and the way this cover is arranged (a close-packed cluster or scattered over the lattice).

In a follow-up paper,<sup>19</sup> we studied the effects of the animals adopting different strategies. The general model was the same—both species must eat, with the prey eating the grass that grows on all lattice sites except those with cover. We compared four strategies: predators moving randomly, prey moving away from a predator, preda-



tors moving in the direction of randomly moving prey, and both species moving randomly. The chance of coexistence depends not only on the initial densities of animals and cover, but also on the strategies the species adopt. No one universal strategy is good for all initial conditions, though. Our main conclusions were that predators are more vulnerable to strategy choice; their attempts to find food (*hunting* in Wolff's terminology) quite often leads to the extinction of both species. When the initial concentration of predators is low, strategy choice is not important, but in extreme conditions, the prey's strategy might be crucial for coexistence. Our conclusions agree with Wolff's findings and known biological data.<sup>20</sup>

Quite recently, a paper incorporated many features of the previously discussed PP models along with some new ones.<sup>21</sup> Using a cellular automata approach, the authors investigated a system with three types of entities—predators (wolves), prey (sheep), and grass, on which the sheep feed. They described the animals using the Penna aging model and examined the conditions for reaching a coexisting, absorbing, or empty state. Because of its complexity, the model contains many parameters and was studied in a limited subspace.

We can look at the PP system from a completely different viewpoint—for example, as an ensemble of interacting particles in a reaction–diffusion process. Haim Taitelbaum and his colleagues<sup>22</sup> studied the spatiotemporal properties of a system with one static or mobile trap (a predator) and many random walkers (prey). Whenever prey moves into a predator-occupied site, it vanishes from the system (is “eaten” by the predator); the predator lives forever. There is, of course, no oscillation in the densities or problems with species coexistence. The authors determined the trapping rate,

distribution of prey around the trap, and the segregation on the Sinai model, which shows how far we can go from the original fish-catch models.

In this short introduction, I concentrated on lattice versions of PP models. An excellent but rather out-of-date introduction to continuum versions of the LV equations appears elsewhere.<sup>23</sup> At least two questions remain open or not completely understood: What are the reasons for the observed oscillations in two species' time-dependence concentrations? What are the most important parameters that influence the species' dynamics and coexistence?

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