Evaluating the "Prudent Predator" Effect with Spatial Movement: Let Us Be Prudent, Do Not Move

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Abstract

A model demonstrating the "prudent predator" effect is extended to include spatial movement. The effect disappears even when the movement policy is relatively conservative. Since the "prudent predator" effect was argued as an instance of group selection, the sensitivity of this effect to movement supports the claim that group selection is a weak force in evolution.

1 Introduction

Goodnight *et al.* present a spatial predator-prey model that demonstrates a "prudent predator" effect in [1]. They argue this is due in part to local extinctions of predators that over exploit the prey population, thereby endorsing group selection, which is still considered provocative [2] but some argue that the debate between single-level and multilevel selection ought to be dismissed [3]. This "prudent predator" effect is not captured by conventional models where space and local conditions are averaged and homogeneous.

This paper extends Goodnight *et al.*'s model to include spatial movement. The conjecture is that a sufficiently mobile population would not demonstrate the "prudent predator" effect. In some sense mobility ought to be expected to degenerate into the spatially averaged case where no "prudent predator" effect is found. If a population is mobile enough to reach anywhere in the space with equal probability, then one is directly approximating the spatially averaged case in its mechanics. The question is how much mobility is necessary to disrupt the "prudent predator" effect? Must mobility allow access to the whole space, just its local neighbors, or perhaps its neighbors at a distance r away?

Goodnight *et al.*'s original model does not include any mechanism for movement. It is sufficiently abstract that one could interpret each predator or prey as an immobile individual or a collection of neighboring populations whose interactions are spatially and therefore temporally limited. Extending the model with movement makes the interpretation of the predator or prey as mobile individuals more appealing and realistic for some cases. By extending this model, one can determine how sensitive Goodnight *et al.*'s claims are to spatial movement.

2 Method

Goodnight *et al.* use the terminology of host and parasites rather than prey and predator, which is an equivalent interpretation. This paper will adopt the same terminology and symbols for presenting the model that Goodnight *et al.* used to ease comparison.

2.1 Original Model

The model is a two dimensional probabilistic cellular automata with a lattice size of $L \times L$. Each cell may be in one of three states: empty 0, susceptible host S, or infected host I_τ. The state transitions are

$$\begin{aligned} P(0 \to S) &= 1-(1-g)^n && (1)\\ P(S \to I_\tau) &= 1-(1-\tau)^{m_\tau} && (2)\\ P(I_\tau \to 0) &= \nu && (3) \end{aligned}$$

where g is the host reproductive rate, n is the number of uninfected host neighbors, m_τ is the number of infected neighbors of transmissibility τ, and ν is the virulence of the parasite.

The transmissibility τ may be evolved rather than set as a parameter. This requires the following parameters: The initial transmissibility τ_0, the probability of mutation μ, and the mutation increment ϵ. When a pathogen I_τ reproduces, its offspring will have a transmissibility of $\tau \pm \epsilon$ with probability μ.

Evolving transmissibility requires a different formulation of the probability $P(S \to I_\tau)$ given in Equation 4 where $\pi_\tau = 1-(1-\tau)^{m_\tau}$.

$$\begin{aligned} &P(S \to I_\tau) = [1-\Pi_{\tau'}(1-\tau')^{m_{\tau'}}]\\ &\times \Big[\frac{\frac{\mu}{2}\pi_{\tau-\epsilon}+\frac{\mu}{2}\pi_{\tau+\epsilon}+(1-\mu)\pi_\tau}{\sum_{\tau''}(\frac{\mu}{2}\pi_{\tau''-\epsilon}+\frac{\mu}{2}\pi_{\tau''+\epsilon}+(1-\mu)\pi_{\tau''-\epsilon})}\Big] \quad (4) \end{aligned}$$

2.2 Experiment

Goodnight *et al.* let the transmissibility τ evolve and demonstrated that for the spatially distributed case, an evolutionary stable value for τ was found that did not cause the host population to go extinct. This was a fundamentally different result than the conventional spatially averaged analysis where larger values of τ always dominated smaller values, and τ was expected to approach a value of 1. Goodnight *et al.* argued this "prudent predator" effect was caused by group selection. This paper will replicate those results, but consider an additional parameter to add movement of the cells to determine how sensitive Goodnight *et al.*'s claims are.

2.3 Movement

One additional parameter is added to control probabilistic movement $\rho \in [0,1]$. Each timestep an empty cell 0 has a probability ρ of swapping with one of its neighbors, either a susceptible host S or an infected host I_τ. Restricting consideration to the von Neumann neighborhood, the probabilities given in Equation 5 and Figure 1 describe the movement probability.

$$P(c_0 \to c_i) = \begin{cases} 1-\rho & i=0 \\ \frac{\rho}{4} & \text{otherwise} \end{cases} \quad (5)$$

The original model is then a degenerate case of the extended model and can be recovered by letting no movement take place with $\rho = 0$.

The algorithm used for movement updates the cells asynchronously and restrains each cell to one movement, or swap, per timestep. This conserves the types of cells in the population and restrains the movement of a cell to the von Neumann neighborhood per timestep, and it prevents unwanted biases that depend on order in

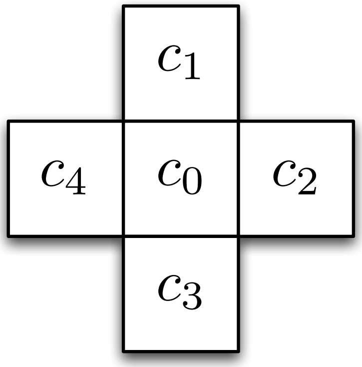

Figure 1: von Neumann neighborhood labeled from c_0 to c_5

which the cells are updated. Even with maximum movement probability $\rho = 1$, cells will only be able to move in their neighborhood on the condition that empty cells are neighbors that have not already moved this timestep.

2.4 1D Model Considered

A one dimensional probabilistic cellular automata was investigated as a potential simplification of Goodnight *et al.*'s model. The parameter r defined how many cells to the left or right were considered neighbors. Finding parameters that produced a stable interaction of hosts and parasistes was non-trivial. Many parameters resulted in simulations where all parasites went extinct or all hosts and parasites went extinct. However, some insight can be derived for why a one dimensional model is not sufficient to capture the dynamics this paper is interested in.

Figure 2 shows a time series of the simulation, with the top row representing the initial state, and the bottom row representing the final state.

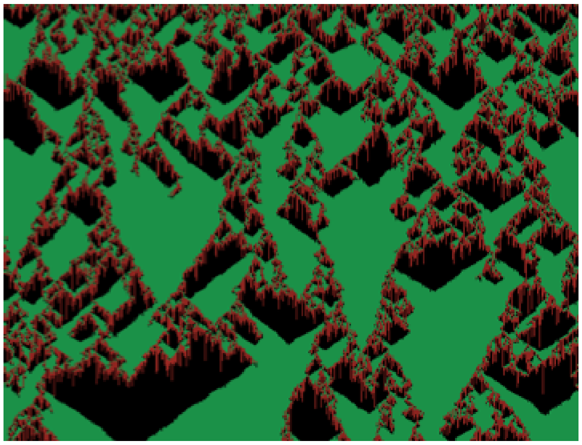

Figure 2: Time series for a one dimensional probabilistic cellular automata. Green represents the susceptible hosts S, red represents the infected hosts I_τ, and black represents the empty cells 0. The first row represents the state at time t_0, the second row t_1, and so on. Parameters: $r = 2$, $\nu = 0.188$, $g = 0.5$, $\tau_0 = 0.265$, $\mu = 0.15$, $\epsilon = 0.05$, and $L = 515$.

The figure shows a recurrent theme seen in many of the stable simulations in one or two dimensions: a population of hosts is bounded by a set of parasites. The parasites eat away the hosts over time, forming a green wedge of hosts lined by red parasites on the wedge's boundary. Unless a host has escaped through the boundary of parasites, the whole group of hosts is eventually eaten.

In a one dimensional cellular automata, The size of the boundary for a contiguous group of n hosts is 2, completely independent of the group size. In a two dimensional cellular automata, the size of the boundary for a group of n hosts can vary a great deal but is always greater than 2. Assuming the group was arranged as a square, the boundary size would be $4\sqrt{n}$. The important difference is, the boundary size is not independent of n as is the case in the one dimensional model.

In the two dimensional simulation shown in Figure 5, one can see parasites on the boundaries of hosts, but because the boundaries are larger, the boundaries are not always covered with parasites, and there is more opportunity for the hosts to escape and reproduce before being preyed on by parasites again. The difference in boundary sizes is thought to be the reason that a one dimensional simulation does not show evolutionarily stable host and parasite interactions.

3 Results

The focus of this paper is on how movement might affect the evolutionarily stable transmissibility τ_{es}. Figure 3 shows statistics for the transmissibility over a long period of time for several values of movement probability ρ. The graph of $\rho = 0$ replicates the results found in [1] where the transmissibility τ converged to an evolutionarily stable value. However, as the movement probability ρ increases, the evolutionarily stable transmissibility approaches 1. This makes it indistinguishable from the spatially averaged analysis and demonstrates that a small perturbation, for the cells are only moving within their von Neumann neighborhood each timestep, is sufficient to destroy the "prudent predator" effect found in [1].

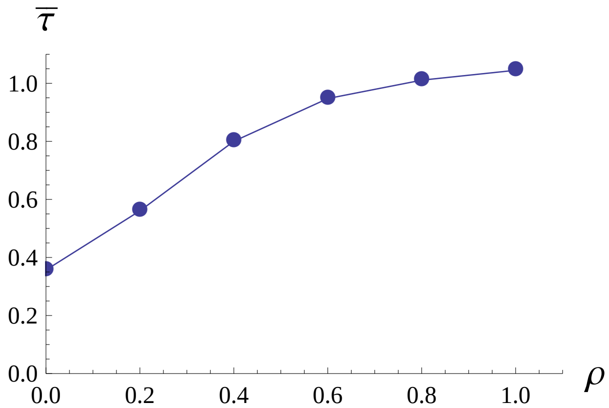

Figure 4: The mean transmissibility $\bar{\tau}$ versus the movement probability ρ. The greater the movement probability, the greater the mean transmissibility $\bar{\tau}$, which approximates the evolutionarily stable transmissibility τ_{es}. The $\bar{\tau}$ values taken from timestep 100,000 of each simulation. Movement probabilities of 0.6 and above seem to accord with the conclusions of the spacially averaged analysis.

Figure 4 shows the mean transmissibility $\bar{\tau}$ vs the movement probability ρ at timestep 100,000. The mean transmissibility $\bar{\tau}$ approximates the evolutionary stable transmissibility τ_{es}, and clearly shows that it is monotonically increasing as a function of ρ and the mean transmissibility $\bar{\tau}$ approaches 1 for a movement probability ρ of 0.6 or greater. So it does not take much movement to disrupt the "prudent predator" effect.

Figure 5 shows the state of the simulation after 100,000 timesteps. Note the greatly increased number of parasites that correlates with the increased transmissibility in Figure 3.

4 Conclusion

This paper replicated the "prudent predator" effect demonstrated in [1]. Goodnight *et al.* argues that the spatially averaged analysis and spatial simulations have fundamentally different results:

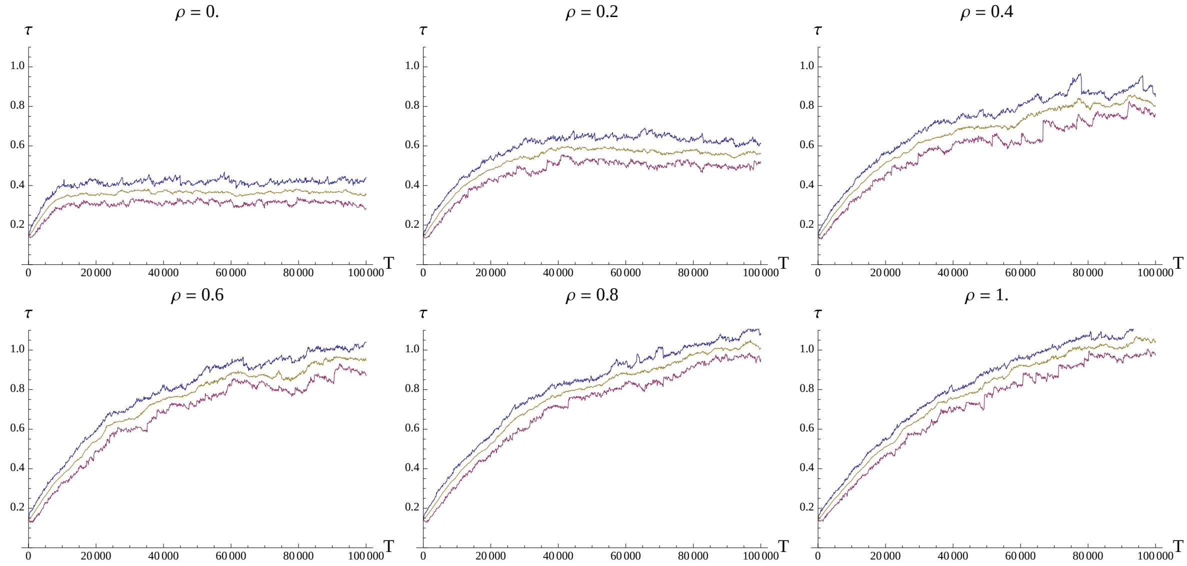

Figure 3: Minimum, maximum, and mean transmissibility shown over time for various values of movement probability ρ. The graph for $\rho = 0$ replicates the same stable transmissibility values as shown in [1]. These graphs show that even limited movement causes evolutionary stable τ_{es} value to change. The parameters used are $\tau_0 = 0.15, \nu = 0.2, g = 0.05, \mu = 0.15, \epsilon = 0.15$, and $L = 250$. These parameters will be used in subsequent figures unless otherwise noted. Simulated for 100,000 timesteps and sampled every 100 timesteps.

the spatial simulation demonstrates a “prudent predator” effect, while the spatially averaged analysis does not. This paper confirms the “prudent predator” effect but shows that the spatial simulation is very sensitive, and the relatively conservative addition of probabilistic movement is sufficient to disrupt the “prudent predator” effect.

One might conclude that since the “prudent predator” effect is not lost until the movement probability ρ is greater than 0.6, that this was to be expected since movement is essentially averaging the space within the spatial simulation. However, even with the movement probability ρ set to the maximum of 1, each cell can only move within its von Neumann neighborhood each timestep. In order for this movement algorithm to truly approach the spatially averaged case by means of “shuffling” its cells, the movement algorithm would need to be reapplied such that the cells could end up anywhere in the lattice. At minimum the movement algorithm would need to be applied $2L$ times to allow one cell to reach any other cell in the lattice to more closely approximate the spatially averaged case. ($2L$ being the manhattan distance between one cell and its farthest cell.)

To further show how conservative this movement algorithm is, consider that in a fully populated lattice with no empty cells, movement

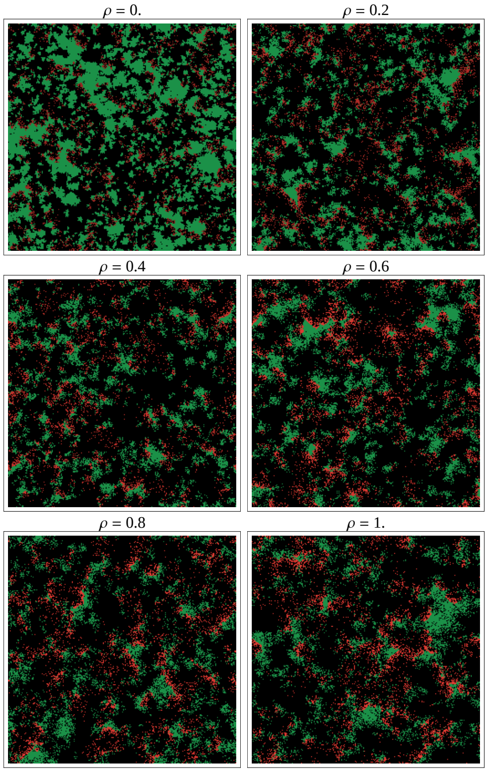

Figure 5: Plot of simulations for various values of movement probability ρ on timestep 100,000. Green represents susceptible hosts S. Red represents infected hosts I_τ. And black represents empty cells 0.

makes no difference because hosts and parasites do not move over one another. Only empty cells are candidates to move into. So even applying the movement algorithm $2L$ times would not shuffle its contents to match the spatially averaged assumptions. This shows that the conclusions of the spatially averaged analysis appear to be more robust than the spacial analysis.

Since Goodnight *et al.* argue that the “prudent predator” effect is an instance of group selection, the results presented in this paper seem to call into question the potency of group selection. Group selection may be a force in evolution, but this paper suggests that it is a weak one.

References

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