Predator-Prey Oscillations in a Cellular Automaton of Huffaker's Mite Experiment

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Abstract. Predator-prey interactions are commonly modeled using the Lotka-Volterra ordinary differential equations, producing intertwined predator and prey population oscillations. Scientists have attempted to reproduce these oscillations, such as Carl Huffaker and his 1958 experiment with mites and oranges. However, Huffaker was only able to produce sustained oscillations after adjusting his system's spatial factors. Particularly, increased space per orange and increased mite dispersal have a significant impact on achieving predator-prey oscillations. To address and confirm this result, we developed a cellular automaton model of Huffaker's mite experiment. We simplified his system to fit automata criteria, created rules to govern mite dynamics, tested model parameters relating to mite lifetime and fertility, and increased patches per orange and mite dispersal by wooden posts to determine the conditions for successful oscillations. The results of our simulations show that increasing prey dispersal and the number of patches available per orange is sufficient for producing lasting oscillations in our model. Secondarily, we concluded that a certain disparity between reproduction and lifetime parameters for the predators and prey is sufficient for oscillations as well. In conclusion, spatial complexity must be considered when attempting to achieve predator-prey oscillations experimentally.

1. Introduction. The theory of predator-prey dynamics began in the 1800s; before then, the changes of plant and animal populations were long known, but quantitative methods were rarely applied to study them [13]. With the move towards quantification in the 1800s, scientists began to recognize regular population changes with periods other than one year. At the same time, the Hudson Bay company was carefully tracking the number of lynx and hare pelts collected by North American fur traders. Their numbers eventually revealed dramatic periodic oscillations in populations that could not be explained by the seasonality alone and cemented the lynx and hare interactions as a classic predator-prey example [5].

However, it was not until 1920 that Alfred Lotka proposed a system of two autonomous ordinary differential equations which model the dynamics of two spatially homogeneous interacting populations - predators and prey - and predict phase-shifted oscillations between them. Lotka developed this system of equations on purely theoretical grounds but was at least partly inspired by Herbert Spencer and the related work on infectious diseases [10]. Shortly after, observations of fish numbers in the Adriatic Sea led Vito Volterra to propose the same equations [14]. Since the development of the Lotka-Volterra equations, there have been many attempts to test their predictions. In 1934, Georgy Gause published *The Struggle for Existence*, a book detailing his experiments to understand the predator-prey interactions between various species of protozoa. He found that Lotka-Volterra oscillations occur only

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under specialized conditions and concluded that some populations do not even allow these oscillations due to biological adaptations [6].

Gause's results spurred even more experimentation on predator-prey interactions, including ecologist Carl Huffaker's experiment with fruit mites in the 1950's. In an attempt to observe predator-prey interactions aligning with the Lotka-Volterra model, Huffaker experimented with oranges, a prey species of mite feeding on the oranges, and a predator mite to eat the prey. In 1958, he published a case where three oscillations occurred in both populations, previously unseen in predator-prey laboratory investigations [8].

However, Huffaker was only able to achieve oscillations by introducing very specific spatial adjustments that are not considered in the Lotka-Volterra system. By expanding available space on each orange and facilitating prey mite dispersal, Huffaker provided sufficient conditions for the oscillations seen in Figure 1b. According to Huffaker, "by utilizing the large and more complex environment so as to make less likely the predators' contact with the prey at all positions at once, ... it was possible to produce three waves or oscillations in density of predators and prey. That these waves represent a direct and reciprocal predator-prey dependence is obvious" [8]. The increased complexity of this particular habitat raises the probability that the prey will survive the exploitation by the predator, which is essential to the continued survival of the predator [8]. Thus, spatial heterogeneities must be carefully chosen in order to result in continued prey survival and predator-prey oscillations, which do not occur as easily as the Lotka-Volterra model suggested. [1]

Huffaker's population oscillations pose an interesting modeling question: what conditions result in predator-prey oscillations versus the extinction of one or both populations? The goal of this study was to build a spatially explicit model based on Huffaker's successful universe in Figure 1b, reproduce Huffaker's results, and provide theoretical support for the sufficiency of a carefully adjusted spatial arrangement in creating predator-prey oscillations.

To account for the important consequences of spatial adjustments in Huffaker's mite experiment that are missing from the Lotka-Volterra model, we chose a cellular automaton as our model. A cellular automaton is a "collection of 'colored' cells on a grid of specified shape that evolves through a number of discrete time steps according to a set of rules," applied iteratively, "based on the states of neighboring cells" [15]. Cellular automata usefully represent a dynamical system's "complex emergent behavior," originating from simple cells and basic rules for their motion [15]. A widely applicable group of models, cellular automata have been used for pattern formation in computation and information processing, cognition studies, physics, geographical systems, epidemiology, and biology [2].

In particular, we are motivated by Wa-Tor, a cellular automaton for a fictional predator-prey ecosystem on a toroidal, water-covered planet inhabited by fish and sharks [4]. The algorithm specifies several rules for motion and reproduction of fish and sharks based on the current state of each "patch" in the automaton [11]. Wa-Tor produces oscillations in both the fish and shark populations, leading us to modify it in hopes of generating similar oscillations

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[1]Today, we recognize that the Lotka-Volterra model is structurally unstable, and that small perturbations to the governing equations can change the asymptotic dynamics between damped oscillations, growing oscillations leading to extinction, or limit-cycle dynamics, each potentially depending on the initial conditions of the system [9].
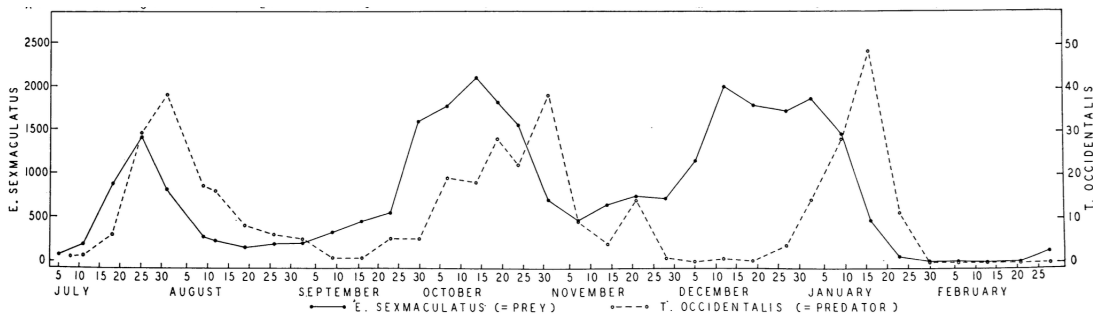
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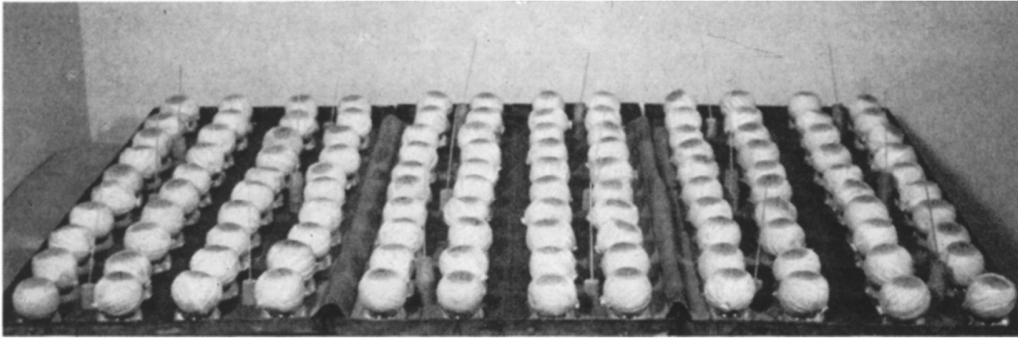
(b)

Figure 1: (a) *Arrangement of Huffaker's Universe Producing Oscillations* 120 oranges, each with 1/20 orange-area exposed, occupying all positions in a 3-tray universe with partial-barriers of petroleum jelly and wooden posts supplied - a 6-orange feeding area on a 120-orange dispersion with a complex maze of impediments. Trays are broadly joined by use of paper bridges [8]. (b) *Huffaker's Mite Populations' Oscillation Result* This graph demonstrates the oscillations in the predator and prey mite populations on which we base our cellular automaton [8].

73 in the context of Huffaker's experiment.

74   In the following simulation experiment, we developed and investigated a cellular autom-
75 aton of Huffaker's mite experiments. Guided by Huffaker's assumptions, procedures, and
76 results, we created rules that describe the predator-prey interactions within his experiments
77 in order to regenerate the population oscillations and extinctions. We then chose model-
78 ing assumptions that qualitatively recapitulate Huffaker's experiment. Via simulation of our
79 cellular automaton, we investigated the oscillations' sensitivity to the model's main spatial
80 parameters in order to establish parameter spaces where either extinction or oscillations can
81 be guaranteed. We also showed the importance of the disparity between the predator and prey
82 species' lifetime and reproductive parameters during the course of these investigations. Most
83 importantly, the results of our experiments parallel Huffaker's conclusion that the carefully
84 chosen spatial parameters are key factors in the existence of population oscillations.

85   **2. Methods.**

2.1. Huffaker's Universes. Huffaker's experimental procedure consisted of creating different "universes" (i.e., experiments) by arranging varying numbers of oranges and rubber balls that were connected by wires, had varied areas of surface exposed, and were replaced once the prey mites had exhausted all the nutrients. The outer rim of each 40-orange tray was coated in petroleum jelly to prevent the mites' movement outside the universe. With each unique universe, Huffaker made changes in system size and mite dispersal methods that he believed would progress toward continued population oscillations. Huffaker finally achieved three population oscillations after eight experiments; the successful universe consisted of 120 oranges, each with 1/20 of its area exposed, in three trays (see Figure 1a, which is Figure 5 from Huffaker's publication). For this universe, Huffaker increased the exposed area of the oranges from previous universes because "the need for an increase in... complexity had become obvious" [8]. Petroleum jelly partial-barriers were used to deter predator mite movement between oranges, and six wooden posts per tray were added to the successful universe. The prey mite species has the special ability to disperse over the petroleum jelly barriers using silken strands and air currents circulated by a fan in the room, so the wooden posts gave the prey the "equally important superior dispersal power" needed to combat the "superior dispersal power of the predator within local areas" [8]. A diagrammatic representation of Huffaker's successful universe design (henceforth, Grid Design 1) is show in Figure 2a.

2.2. Our Model. We developed our cellular automaton of Huffaker's successful universe to investigate the impact of spatial complexity on predator-prey dynamics. Generally, population simulation models over a discrete explicit space must choose whether or not to enforce an exclusion principle. If the model is non-exclusive, any number of individuals can occupy the same patch. Conversely, in an exclusive model, each patch is either empty or occupied by a single individual; while a cell is occupied, all other individuals are excluded from moving into that patch. Since exclusive models are the traditional choice for cellular automata, we decided to use this principle for our own model.

Constructing an exclusive cellular automaton for Grid Design 1 necessitated creating rules to explain not just spatial movement but also the predator-prey interactions on each orange. To recapitulate the three neighboring trays, we constructed a 12×10 board (Grid Design 2), where we divided the top of each orange into 4 square patches (see Figure 2b). Thus, the full arrangement of patches was 24×20. The patches on each orange are important for aligning the experiment with the standard cellular automaton format, which allows our model to be spatially explicit on each orange. The first spatial complexity we incorporated was increasing space by adding more patches per orange that the mites can occupy, which then increases the area that is used to avoid predators.

To continue translating Huffaker's experiment to a cellular automaton, the petroleum jelly borders were encoded as reflecting boundary conditions around the trays. We neglected the petroleum jelly partial-barriers and the space between oranges, so moving between oranges and trays was just as easy as moving between neighboring patches. We based our initial conditions on Huffaker's but introduced 120 prey (1 per orange) and 27 predators placed randomly throughout the grid at the same time instead of using the 5-day time delay of Huffaker.

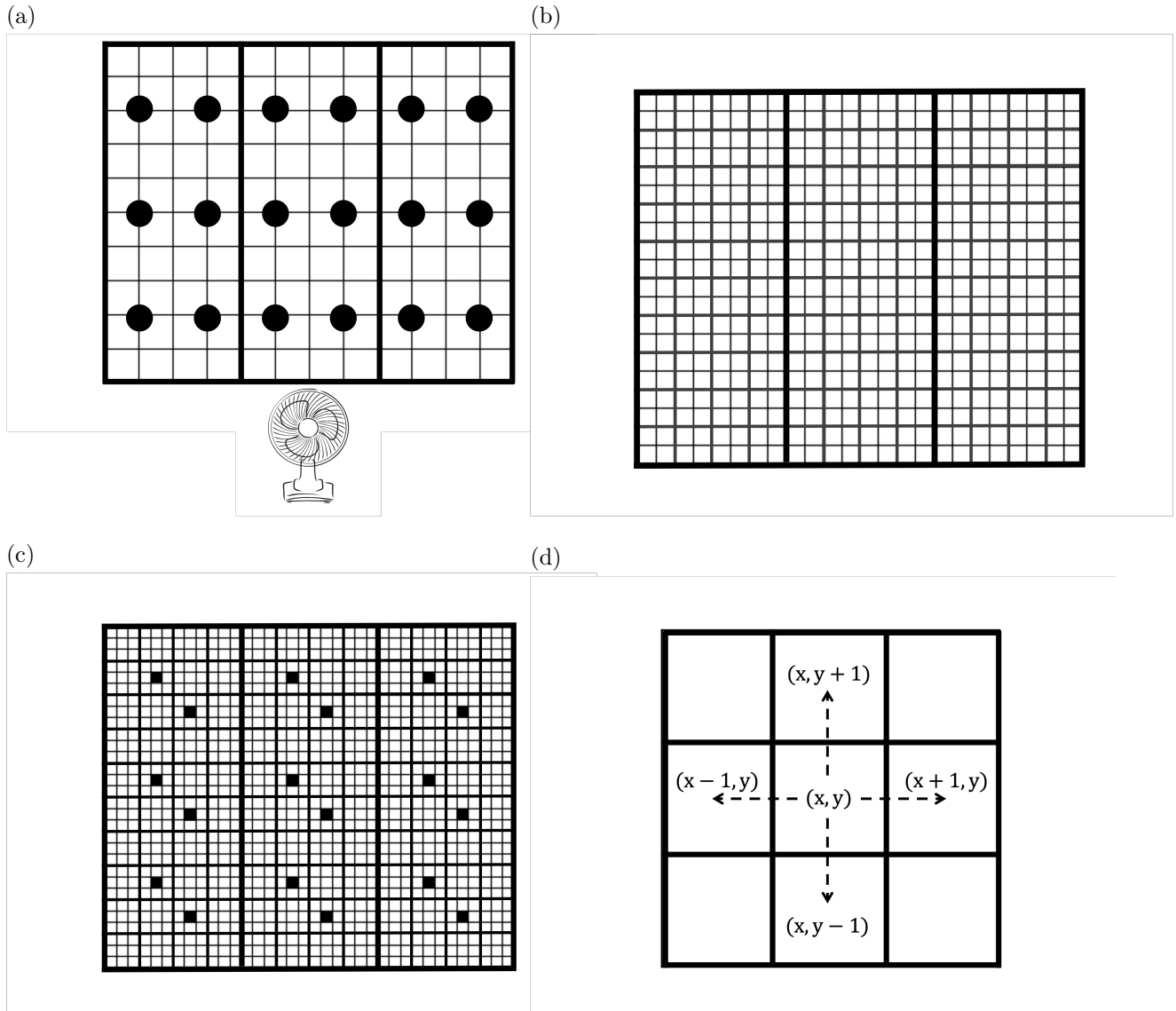The next step in defining our model was to determine the rules for both the predator

(a)

(b)

(c)

(d)

Figure 2: (a) *Grid Design 1.* This design was used to pictorially understand Huffaker's experiment, allowing the formulation of the automata rules. Each grid square represents one orange with multiple prey and predators on it. The thicker black lines are the divisions between trays with reflecting boundaries, and the black dots model the wooden posts, placed evenly throughout the universe. The fan represents the air currents present in the experiment to allow the prey mites to disperse using the wooden posts. Huffaker's successful universe also utilized petroleum jelly partial-barriers, which are not depicted here. (b) *Grid Design 2.* This grid incorporates the simplifications and assumptions listed above, with 4 patches per orange (24x20). It represents the control case of our model. (c) *Grid Design 3 and 4.* Grid Design 3 encapsulates the expansion from 4 patches per orange to 9 (each orange is a 3x3 grid now, 36x30 total grid). Grid Design 4 adds the black wooden posts. (d) *Mite Movement.* Using Von Neumann neighborhoods, mites are only able to move to a patch north, south, east, or west of their current position.

and prey populations that govern the cellular automaton's dynamics, which required some simplifications from Figure 2a. First, we defined discrete units of time called as timesteps. In one timestep, mites can move one patch, fertility can increase one point, and a predator can eat one prey (see the rules below). Next, in the updated model, we assumed the prey mites always have a food source at their location since oranges were replaced when depleted by the prey [8]. Therefore, we did not model the state of each orange.

Motivated by the Wa-Tor fish and shark dynamics model [4], we defined the following movement, life, and reproduction processes. Movement neighborhoods follow von Neumann neighborhood rules (see Figure 2d); mites are only able to move to an adjacent patch north, south, east, or west of their original position. The prey mites move between patches according to a random walk, meaning that at each time step, each mite selects an empty adjacent patch with uniform probability to which it moves. If no empty patch is adjacent to the mite, it does not move. When a predator moves at each timestep, it moves according to a biased random walk, prioritizing all adjacent prey patches as movement targets. If no prey patches are adjacent, then the predator moves to a random empty adjacent patch. If all adjacent patches are occupied by predators, then the predator stays in place.

To track survival, our model assigns a certain number of life points, L_predator, to each predator mite. Predator mites gain life points by eating prey and lose a fixed number of life points, L_predator_loss, each timestep that they go without eating. If a predator mite reaches 0 life points, it dies. Since prey mites have an unlimited food source and only die by predation, we do not track their life points.

To simulate reproduction, each mite has a fertility counter starting at 0 points. A mite gains one fertility point for each timestep it is alive. Once the fertility counter for the prey or predator reaches the fertility threshold (either F_prey or F_predator, respectively), then if there is an empty adjacent patch, the mite can reproduce, spawning another mite on that empty adjacent patch. If no empty patch is available, the mite waits to reproduce until an empty patch becomes available. The fertility thresholds for prey and predator mites are different; by making predators reproduce less often, the prey hopefully have more of a chance to survive.

Finally, we worked without the wooden posts at first to simulate extinction and ensure the model's capability. The second spatial complexity considered by Huffaker that our model incorporates is the wooden posts, which give the prey mites more opportunities to escape predators by dispersing across the grid. Listed below are the rules governing the automata model.

Table 1: **Model Variables**

Variable	Description	Units
F_prey	Prey fertility threshold	Fertility points
F_predator	Predator fertility threshold	Fertility points
L_predator	Predator initial life points	Life points
L_predator_loss	Predator life point loss rate	Life points per timestep

Predators:

1. Predators initially have L_predator life points, and they gain 1 life point by eating

a patch of prey.

2. When a predator moves at each timestep, they prioritize any random adjacent prey patch. If no prey squares are adjacent, then the predator moves to a random empty adjacent patch. If all adjacent patches are occupied by predators, then the predator stays in place.

3. When a predator moves to a prey patch, it becomes a predator patch.

4. If a predator goes one timestep without eating, `L_predator_loss` life points are subtracted.

5. If a predator reaches or exceeds the fertility threshold of `F_predator` fertility points, and only if there is an empty adjacent patch, the predator can reproduce, another predator patch is added adjacent to the current patch, and its fertility level is reset to zero.

6. If the predator falls to zero life points, it dies, and the patch it was on becomes empty.

Prey:

1. Prey die by predation only.

2. If a prey mite survives long enough to reach or exceed the fertility threshold of `F_prey` fertility points, and there is an adjacent empty patch, then it reproduces, a new prey is added to an adjacent empty patch, and its fertility is reset to zero.

3. When the prey move, they move to any random adjacent patch at each timestep. We implemented the rules and assumptions of the simplified model described in the rules above in Python, modifying publicly available Wa-Tor code [11]. Each run's initial conditions consist of one prey mite on each orange (120 total) and 27 predators placed randomly throughout the grid; therefore, each model run is randomized and unique while reproduction remains synchronized. Implementing reflecting boundary conditions is essential to the verisimilitude of our results – simulated mites may not leave the grid.

2.3. Enhanced Dispersal. In section 3, we first describe simulation situations that yield extinction; Huffaker initially only recovered mutual extinction of both mite species. To achieve oscillations, Huffaker had to carefully adjust the system by increasing the number of oranges, changing the exposed area of each orange, and adding wooden posts from which prey mites can jump. These adjustments allowed the prey to disperse across the universe and escape predators that would otherwise drive them extinct. To test the impact of these adjustments on our model, we replicated Huffaker's process: we increased space by modifying the system grid from 4 patches per orange to 9 patches per orange (Grid Design 3), corresponding to increasing the exposed area of each orange; and we increased the dispersal ability of the prey mites by adding wooden posts (Grid Design 4). We simulated each wooden post occupying a patch on an orange (see Figure 2c) by implementing the following changes in our update rules for prey.

4. Prey can move to either a random adjacent patch or a wooden post at each timestep. If they choose the wooden post, then the prey "jump" to another other wooden post selected uniformly at random.

5. Posts are placed at positions (4, 7), (4, 16), (4, 25), (7, 4), (7, 13), (7, 22), (16, 7), (16, 16), (16, 25), (19, 4), (19, 13), (19, 22), (28, 7), (28, 16), (28, 25), (31, 4), (31, 13), and (31, 22) on the grid. Position (0, 0) is located in the southwest corner of the grid.

To view the implementation of the rules and grids for our cellular automaton, please see our simulation code included in the supplemental material.

2.4. Parameter Space and Simulation Approach. To determine the parameter values for our model, we had to experiment to identify a combination of L_predator, F_prey, and F_predator that robustly permitted oscillations. We first used the baseline values from the published Wa-Tor model [11] for these parameters in our very first test runs, noticing the importance of the difference in magnitudes. Then, to be more complete in our sample of the parameter space, we tested every possible combination of 1 and 10 (chosen due to their simplicity and differing orders of magnitude), with 3 positions in order for L_predator, F_prey, and F_predator and with -1 predator life point loss per timestep if not eating prey.

Using this approach resulted in 8 combinations of 1 and 10 for testing the following three experiments that evaluate whether the model variables together with the increased patches per orange and wooden posts create immediate extinction, oscillation with extinction, or continued oscillations. First, Experiment 1 uses Grid Design 2 with 4 patches per orange as our control; we expected runs to result in extinction. Then we increased the number of patches per orange to 9 (Grid Design 3) and ran Experiment 2 to test for oscillations. Then we added the wooden posts (Grid Design 4) for Experiment 3 to add further complexity the system. Therefore, we tested a total of 24 cases with 100 simulations per test case, resulting in analysis of about 2400 plots individually by sight. To evaluate the results of these tests, we compared each simulation's plot with Huffaker's three-oscillation graph; a successful run for our model is defined as one that produces at least 3 population peaks (like Huffaker's successful result), which counts as an oscillation. See the parameter space results table (in the supplemental material), where oscillations are recorded according to which population went extinct first or not at all. We counted how many simulations with oscillations occur out of these 100 simulations to quantify how likely oscillations are in each situation. Each simulation terminates after 500 timesteps.

From these investigations, we determined that the combination of L_predator=1, F_prey=1, and F_predator=10 demonstrated more stable and likely oscillations that were the most similar to Huffaker's results. Therefore, we used this combination as the foundation of our parameter space and analyzed the results for this combination of parameter values, as detailed in section 3 below.

3. Results. In accordance with the parameter space described above, Table 2 shows the parameters for the first 3 experiments, where we carefully adjusted the spatial arrangement by increasing the amount of patches per orange and adding wooden posts for increased prey mite movement.

3.1. Experiment 1: 4 patches per orange. Likely predator and prey extinction. This experiment is represented by Grid Design 2, where each orange is divided into four patches (24x20 total grid) and the parameter values are as listed in Table 2. Experiment 1 is the model's control case, replicating the experiment where Huffaker failed to produce oscillations. There are fewer patches per orange on the grid and no wooden posts. Potentially due to the lack of space, the probability of both populations going extinct without oscillating was an overwhelming 89/100. As seen in Figure 4a, the populations often go extinct very quickly.

Table 2: Experiment Parameters

Variable	Experiment 1 (Grid Design 2)	Experiment 2 (Grid Design 3)	Experiment 3 (Grid Design 4)	Experiment 4 (Grid Design 4)
F_prey	1	1	1	2
F_predator	10	10	10	20
L_predator	1	1	1	2
L_predator_loss	-1	-1	-1	-2

Only 9/100 simulations produced oscillations with extinction after at least 3 population peaks, and just 2/100 simulations produced continuous oscillations (see Figure 3a).

3.2. Experiment 2: 9 patches per orange. Likely but noisy oscillations. Experiment 2 uses Grid Design 3, where the amount of space in the grid is increased by dividing each orange into 9 patches instead of 4. This action increases the grid size to 36x30, giving the prey more spaces to evade the predators. The same parameters as Experiment 1, listed in Table 2, were employed. In this experiment, we found a significant increase in the occurrence of oscillating populations; only 25/100 of runs had both populations going extinct without oscillations, and 75/100 featured oscillations (64/100 oscillations without extinction, 11/100 oscillations with eventual extinction, shown in Figure 3b). However, despite their increased probability, the resulting oscillations appeared noisy and inconsistent – not like Huffaker's oscillations (see Figure 1b and Figure 4b).

3.3. Experiment 3: 9 patches per orange, wooden posts. Improved shape but oscillations likely end in extinction. Experiment 3's features include 9 patches per orange, the same parameters given in Table 2, and the addition of the wooden posts, which Huffaker used to increase the prey mites' dispersal ability. The posts' inclusion led to, once again, a significant increase in the probability of oscillations: a 51/100 chance (46/100 chance of oscillations eventually going extinct, and 5/100 chance of continued oscillations, shown in Figure 3c). Though the difference from the control is not as large, with this experiment it is still more likely to observe population oscillations than not. Pictured in Figure 4c, this experiment's results have varied oscillation stability and an increased probability of extinction for both species at the end, but they also have less noise and more pronounced oscillations than Experiment 2. We hypothesized that using a multiple of the parameter ratio would help stabilize the oscillations and eliminate the end extinction.

3.4. Experiment 4: 9 patches per orange, wooden posts. Best oscillation shape, stability, and continuation. As just mentioned, this experiment tested whether a multiple of the parameter ratio would stabilize the oscillations. We decided to double the parameters given in the previous experiments as seen in Table 2 in hopes of refining the oscillations to look more like Huffaker's. This experiment resulted in an 85/100 probability of observing oscillations – 65/100 continuous oscillations and 20/100 oscillation with eventual extinction (see Figure 3d). Therefore, the chance of immediate extinction was drastically reduced to only 15/100. By adjusting the parameters, the oscillation quality was observed to significantly improve. The oscillations are more consistent and pronounced, less noisy, and more likely
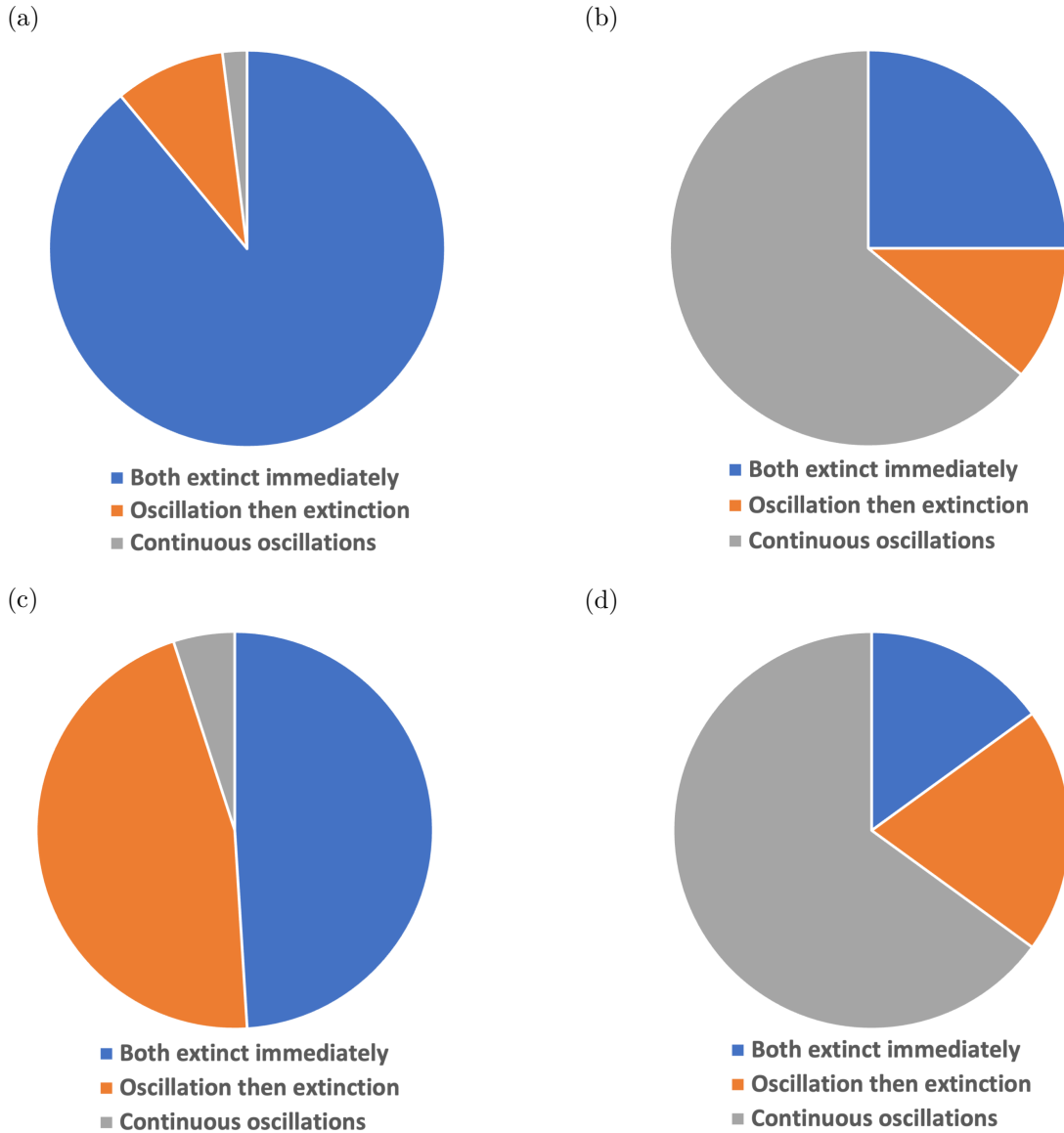
(a)

(b)

(c)

(d)

Figure 3: Proportion of simulations resulting in both populations extinct immediately (blue), oscillation then extinction (orange), and continuous oscillations (gray) for (a) *Experiment 1 Results*, (b) *Experiment 2 Results*, (c) *Experiment 3 Results*, (d) *Experiment 4 Results*.

to not end in extinction (see Figure 4d). In conclusion, this combination of parameters and spatial aspects was our best attempt at simulating Huffaker's experiment and results.

4. Discussion. The model's experiments have one main conclusion: a carefully adjusted spatial arrangement and the disparity between the predator and prey species' lifetime and reproductive parameters are together sufficient to produce population oscillations for this
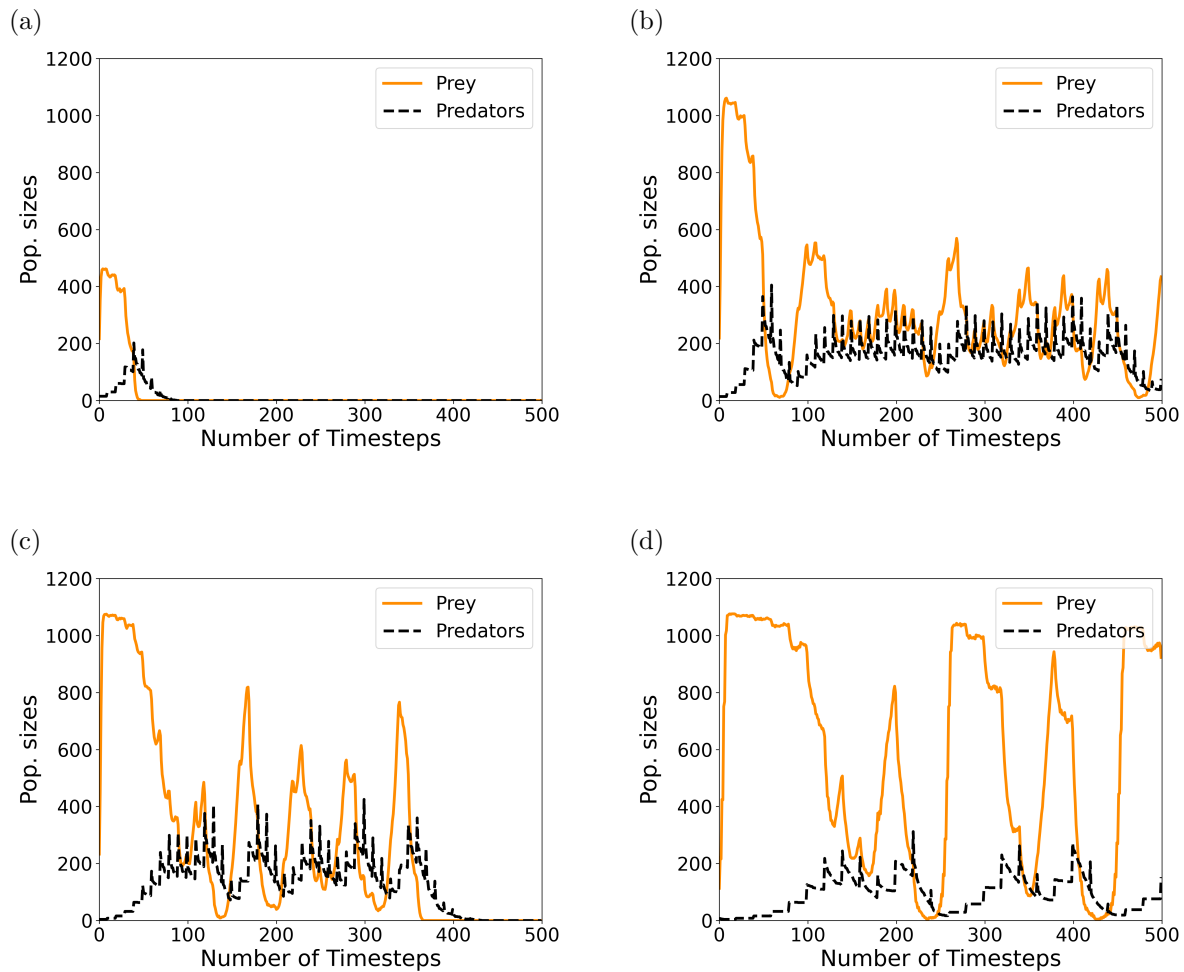
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Figure 4: Sample of Simulation Outcomes. (a) *Experiment 1 Result.* The most common outcome of Experiment 1 is immediate extinction after one population peak. (b) *Experiment 2 Result.* The oscillations occurred more often and continued longer, but they seem noisy compared to Huffaker's result in Figure 1b. (c) *Experiment 3 Result.* This experiment's results show clearer oscillation amplitude, but they are still varied and typically end in extinction for both. (d) *Experiment 4 Result.* The oscillations have improved consistency and shape, and they are the most similar to Huffaker's out of all four experiments.

system.

Though predator-prey oscillations are theoretically easy to produce, they are very difficult to achieve experimentally. Huffaker had to revise his experimental system several times to produce oscillations in a very complicated, particular environment. Likewise, oscillations were not easy to replicate in our model either. A grid representing one space per orange or four spaces per orange was not enough to have even a 50% chance of oscillations, since the prey mites could not escape the predators long enough to survive, leading to the predator species'

starvation. Increasing the number of patches per orange to 9 (36x30 grid) and introducing the wooden posts both increased the probability of oscillations to over 50%. This expansion of space on each orange gave the prey a higher probability of evading the predators and surviving longer, since there were more spaces per orange that were more likely to be unoccupied by predators. The prey's extended survival in turn allowed the predators to survive since their food source still existed, creating the cyclical oscillation pattern. Also, the addition of the wooden posts to the grid contributed to the increased probability of oscillations. By jumping to a wooden post from which prey could move to an adjacent orange or any other wooden post on the grid, the wooden posts provided another opportunity for prey to escape the predators and increase their probability of survival. Huffaker also concluded that spatial strategies that give the prey a higher chance of survival are more likely to lead to oscillations. Thus, our model's results support Huffaker's conclusion that carefully adjusting space to provide prey more ways to survive the predators' hunt is key when striving for predator-prey oscillations and align with Huffaker's experiment which concludes the same.

A concurrent conclusion from our model is the importance of disparity between the predator and prey species' lifetime and reproductive parameters. In combination with increasing the patches per orange and prey mite dispersal via the wooden posts, identifying the difference (by order of magnitude of 10) between the predator and prey parameters was sufficient to producing oscillations. The parameter values given in Experiment 4 resulted in the most consistent oscillations that were also the most similar to Huffaker's results in shape and occurrence. Perhaps this disparity in parameter values can be explained by the size and food difference between the predator and prey mite species. The prey mites are much smaller with an inexhaustible food source and so require less reproductive resources, meaning a smaller value of F_prey); meanwhile, the predators require more resources to reproduce and have to feed on the mites to gain them so F_predator should have a higher value. As for why this disparity allows oscillations, making the predator fertility threshold higher means they reproduce more slowly, giving the prey mites more time to recover and increasing their chance of survival and further population oscillations. For future cellular automata modeling of predator-prey dynamics, this parameter disparity conclusion could be important to reproducing population oscillations.

Thus, by varying our system's spatial, dispersal, lifetime, and fertility parameters to favor the survival of the prey, our model produced oscillations that reproduce Huffaker's results and mimic the oscillations of the Lotka-Volterra model. Therefore, we hypothesize that the careful increase in spatial complexity and other specific adjustments to ensure prey survival are sufficient to produce predator-prey oscillations. However, the adjustments and parameters will of course depend on the biological system and the species of the interacting populations.

Our model captured Huffaker's experiment with minor modifications that did not hinder us from successfully reproducing his results. The most significant modification is that our model does not include the space between oranges. However, we can speculate that this modification was not important in reproducing oscillations; perhaps since we give the prey more space on the oranges to escape, the predators typically stay on the oranges where the majority of the prey are anyways and thus are not affected by the space between oranges. We were not able to implement the petroleum jelly partial-barriers either, which may have slowed down both the prey and predators and perhaps contributed to why we have achieved some

continuous oscillations where Huffaker did not. We are also not entirely sure of the mites' reproduction processes, so we began by using Wa-Tor parameters and adapted them according to our model's capabilities – they may not exactly align with Huffaker's experiment. However, we achieved oscillations under the same conditions that Huffaker produced them, and we did not find oscillations under the conditions when Huffaker did not observe them either; we even found seemingly continuous oscillations. In addition, our model aligned with Huffaker's initial conditions and boundary conditions. Our model and experimental method also followed Huffaker's process of first finding extinction conditions then modifying the system to increase the patches per orange and prey mite dispersal through wooden posts to achieve oscillations. Therefore, our model accomplished our project's main goal of replicating Huffaker's results.

5. Conclusions. Our model supports the hypothesis that allowing the prey species more paths to evade predators can produce predator-prey oscillations. Without the sufficiently increased space on each orange and added wooden posts, both populations quickly go extinct in our model. Our concurrent hypothesis is that disparity in the fertility and life parameters between prey and predator are important to reproducing oscillations as well, because they provide another way to increase the chance of the mite's survival. In the future, our model could be used to investigate how the space and life parameters affect the amplitude and frequency of oscillations. Such follow-up investigations may include answering how increasing the factor of the parameter values given in Table 2 affects the shape of oscillations and how space affects the frequency and magnitude of the oscillation peaks. Future directions may also include exploring the probability of extinction, examining the time until extinction, and automating the classification of simulations as "oscillating" or not.

Our conclusions show the potential for more research exploring predator-prey interactions across space and discovering new perspectives on past predator-prey models. Since most previous mathematical predator-prey models do not account for spatial complexities, these models should be re-investigated to more thoroughly understand the coexistence of predator and prey species and the conditions needed for them to survive together. After all, the classical lynx and hare oscillation example from the 1800s is flawed: the populations were recorded across different regions of Canada, and sometimes the changes in lynx population preceded those of the hare [7]. The Lotka-Volterra model neglects the importance of spatial complexity in allowing population oscillations [3]. Our model and simulation results join Huffaker's experimental observations in calling for spatial considerations to be more widely applied to study predator-prey population dynamics.

REFERENCES

[1] N. Bacaer, *A Short History Of Mathematical Population Dynamics*, Springer, 2010, https://openlibrary.org//books/OL25982946M.

[2] F. Berto and J. Tagliabue, *Cellular Automata*, in The Stanford Encyclopedia of Philosophy, E. N. Zalta, ed., Metaphysics Research Lab, Stanford University, Spring 2022 ed., 2022.

[3] J. R. Chasnov, *The Lotka-Volterra Predator-Prey Model*, 2022, https://math.libretexts.org/Bookshelves/Applied_Mathematics/Mathematical_Biology_(Chasnov)/01%3A_Population_

381   Dynamics/1.04%3A_The_Lotka-Volterra_Predator-Prey_Model.

382 [4] A. K. DEWDNEY, *Sharks and Fish Wage an Ecological War on the Toroidal Planet Wa-Tor*, Scientific

383   American, (1984), pp. 14–22.

384 [5] C. ELTON AND M. NICHOLSON, *The Ten-Year Cycle in Numbers of the Lynx in Canada*, Journal of

385   Animal Ecology, 11 (1942), pp. 215–244, https://doi.org/10.2307/1358.

386 [6] G. F. GAUSE, *The Struggle for Existence*, The Williams & Wilkins company, 1934, https://asantos.webs.

387   ull.es/The%20Struggle%20for%20Existence.pdf.

388 [7] C. A. HALL, *An Assessment of Several of the Historically Most Influential Theoretical Models Used In*

389   *Ecology and of the Data Provided In Their Support*, Ecological Modeling, (1988), pp. 5–31.

390 [8] C. B. HUFFAKER, *Experimental Studies on Predation: Dispersion Factors and Predator-Prey Oscillations*,

391   Hilgardia, 27 (1958), pp. 343–383, https://doi.org/10.3733/hilg.v27n14p343.

392 [9] M. KOT, *Elements of Mathematical Ecology*, Cambridge University Press, 2001, https://openlibrary.org/

393   /books/OL7712565M.

394 [10] A. J. LOTKA, *Analytical Note on Certain Rhythmic Relations in Organic Systems*, Proceedings of the

395   National Academy of Sciences, 6 (1920), pp. 410–415, https://doi.org/10.1073/pnas.6.7.410.

396 [11] *Wa-Tor World*, 2017, https://scipython.com/blog/wa-tor-world/.

397 [12] A. RANSOME, *On epidemics: Studied by means of statistics of disease*, British Medical Journal, 2 (1868),

398   pp. 386–388, https://doi.org/10.1136/bmj.2.406.386.

399 [13] A. A. RUSNOCK, *Vital Accounts : quantifying health and population in eighteenth-century England and*

400   *France*, Cambridge University Press, 2002, https://openlibrary.org//books/OL7754833M.

401 [14] V. VOLTERRA, *Fluctuations in the abundance of a species considered mathematically*, Nature, 118 (1926),

402   pp. 558–560, https://doi.org/10.1038/118558a0.

403 [15] E. W. WEISSTEIN, *Cellular Automaton*, https://mathworld.wolfram.com/CellularAutomaton.html.