Mathematical Modeling in Ecology:

What Killed the Mammoth?

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Abstract

One extinction theory of the Columbian mammoth (*Mammuthus columbi*), called overkill, hypothesizes that early humans overhunted the animal. We will employ three different approaches to test this theory mathematically: analyze the stability of the equilibria of a differential equations system, develop a differential equations model, and develop a discrete stochastic simulation. The system of ODEs is a modified predator-prey model that also includes immigration and emigration. The simulation is a stochastic temporospatial model based on a rectangular grid system designed to represent North America at the end of the last ice age. Using this simulation, we model the migration of humans into North America and the response in the mammoth population. These approaches show evidence that human-mammoth interaction would have affected the extinction of the Columbian mammoth during the late Pleistocene.

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1 Background

The Columbian mammoth (*Mammuthus columbi*), a relative of the modern day elephant, lived in North America during the Pleistocene, an era of time ~ 1.8 million to $\sim 11,700$ years ago. The Columbian mammoth went extinct at the end of the last ice age (in the Late Pleistocene) $\sim 13,000$ years ago. At this time, there was a mass extinction of megafauna in North America, as well as other parts of the globe including South America and Australia. In North America, 32 out of 41 prey species went extinct during this event [1].

There are four main theories to why this mass extinction took place: disease, climate change, a meteorite shower, and overkill. In reality, it is likely that a combination of these theories lead to extinction [2, 12] Our project will focus on overkill, a theory first proposed by Paul S. Martin in his 1973 paper for *Science*, The Discovery of America [10]. Martin proposed that the migration of *Homo sapiens* from Asia into North America $\sim 13,500$ years ago was the leading cause of megafaunal extinction. While some scientists argue that the lack of kill-sights in North America disproves this theory [7], the overkill theory has continued to remain a valid extinction theory. Some supporters of Martin's theory have even theorized that the extinction of mammoths and mastodons by humans was enough to affect the extinction other species in the ecosystem [8]

Previous models of prehistoric scenarios have used differential equations to model the interaction and competition between early *Homo sapien* and Neanderthal populations [6]. Mathematical research into population dynamics has resulted in the creation and analysis of models of invading species and under what conditions extinction or assimilition could occur [3] Other work with models of interacting populations has analyzed multistability and extinction of a various forms of the Lotka-Volterra predator-prey system of differential equations [4, 5].

In this project, we are trying to determine if human overhunting alone could have caused the extinction of the mammoth. To do this, we use three different approaches to model human-mammoth interactions. For model 1, we developed and ordinary differential equations system to model mammoth-human interactions. Using a nondimensionalization of this system, we analyzed the equilibria. In model 2, we used our ODE system to develop a metapopulation differential equations model to represent North America. Lastly, in model 3, we developed a discrete, stochastic simulation to model North America.

2   Parameter Sets

2.1   Parameter Information

$time = 1\ year$, $cell = 10\ mile^2$

Parameter	Units	Description	Value	Source
K	$\frac{humans}{cell}$	human carrying capacity	10	[10]
N	$\frac{mammoths}{cell}$	mammoth carrying capacity	250	[10]
y	$\frac{1}{time}$	human growth rate	$[\ln(1.001), \ln(1.034)]$	[10]
r	$\frac{1}{time}$	mammoth growth rate	$[\ln(1.04), \ln(1.05)]$	[13]
A	$\frac{mammoth}{cell}$	Allee constant	$[5, 8]$	[14]
a	$\frac{1}{time}$	human predation rate	$[1, 10]$	[10]
α	$\frac{mammoth}{cell \cdot human \cdot time}$	mammoth predation rate	$[10, 15]$	[10]
b	$\frac{mammoth}{cell}$	determines where predation saturates	$[1, 10]$	assumption
q	$\frac{1}{time}$	human migration rate	$[0.005, 0.05]$	assumption
z	$\frac{1}{time}$	mammoth migration rate	$[0.2, 0.5]$	assumption
W	$\frac{humans}{cell}$	human population size where mammoths migrate	$[5, 9]$	assumption
C	$\frac{mammoths}{cell}$	mammoth population size where humans migrate	$[3, 5]$	assumption

2.2   Latin Hypercube Parameter Space Sampling

We used a Latin Hypercube Parameter Space Sampling [11] (LHS) on our parameter ranges to find parameter value combinations with which to run the simulation. Our LHS worked by picked ten parameter sets from a predetermined range of values. It did this by creating a hypercube where each side represents a parameter. It then picked ten values for each parameter, effectively dividing the hypercube into a 10-dimensional grid. It then picked ten random combinations of these parameter values with only one requirement: once a parameter combination had been chosen, it could not be chosen again. The LHS gave us ten different parameter sets which we used to analyze our simulation. We performed this LHS using our parameter ranges, and found ten parameter sets (see Appendix Sec. 9.2).

3 Model 1: ODE System

3.1 System of Equations

We began with a simple, Lotka-Volterra predator-prey system [17]. The Lotka-Volterra model has both a birth term and a predation term:

$$\frac{dH}{dt} = -cH + dHM \tag{1}$$

$$\frac{dM}{dt} = aM - bMH \tag{2}$$

To reflect human growth more realistically, we used a logistic growth model [16] for the birth term. This model allows the population to only grow up to some specified carrying capacity K, after which it will cease to grow. For the same reason, we employed an Allee effect [15, 18] for the mammoth birth term so that the population cannot grow past some carrying capacity N, but if the population falls below a specific value A, it cannot recover and will eventually die out:

$$\frac{dH}{dt} = yH\left(1 - \frac{H}{K}\right) + dHM \tag{3}$$

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{N}\right)\left(\frac{M}{A} - 1\right) - bMH \tag{4}$$

Next, we modified the predation term using a Holling type II response [9]. This allows the hunting rate to be a function of the prey density, essential to a realistic simulation:

$$\frac{dH}{dt} = yH\left(1 - \frac{H}{K}\right) + \frac{aM^2H}{M^2 + b^2} \tag{5}$$

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{N}\right)\left(\frac{M}{A} - 1\right) - \frac{\alpha M^2H}{M^2 + b^2} \tag{6}$$

Finally, we added a migration term to reflect the movement of mammoths through North America and humans migration into the area. This migration term assumes that humans will immigrate into an area with a high population of mammoth ($M > C$) and emigrate out of an area when ($M < C$) and that mammoths will emigrate out of an area with a large population of humans, ($H > W$), and immigrate into areas where

$(H < W)$:

$$\frac{dH}{dt} = yH\left(1 - \frac{H}{K}\right) + \frac{aM^2H}{M^2 + b^2} + qH\left(\frac{M}{C} - 1\right) \tag{7}$$

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{N}\right)\left(\frac{M}{A} - 1\right) - \frac{\alpha M^2 H}{M^2 + b^2} + zM\left(1 - \frac{H}{W}\right) \tag{8}$$

We partially nondimensionalized this model by removing all units but $\frac{1}{time}$ to help reduce the number of parameters. To do this, we defined two new state variables, $\lambda = \frac{H}{K}$ and $\sigma = \frac{M}{N}$ then defined six new parameters to replace the dimensionalized model's twelve.

$$\frac{d\lambda}{dt} = y\lambda(1 - \lambda) + \frac{a\lambda\sigma^2}{\sigma^2 + \epsilon^2} + q\lambda(\theta\sigma - 1) \tag{9}$$

$$\frac{d\sigma}{dt} = r\sigma(1 - \sigma)(\beta\sigma - 1) - \frac{\mu\lambda}{1 + (\frac{\epsilon}{\sigma})^2} + z\sigma(1 - \lambda\chi) \tag{10}$$

$$\theta = \frac{N}{C} \quad \epsilon = \frac{b}{N}$$
$$\chi = \frac{K}{W} \quad \beta = \frac{N}{A}$$
$$\epsilon = \frac{b}{N} \quad \mu = \frac{\alpha K}{N}$$

We used this nondimensionalized model to find the equilibria of the system and analyze them.

3.2   Qualitative Analysis of Equilibria

We were interested in the stability of the equilibria, which would allow us to look at long term behavior for the system.

We first used Maple ^{TM}to find the system's equilibria. We found four equilibria:

Mutual Extinction:

$H = 0$

$M = 0$

Mammoth Extinction and Human Survival:

$H = K\left(1 - \frac{q}{y}\right)$

$M = 0$

Human Extinction and Mammoth Survival:

$H = 0$

$M = \frac{1}{2}\left(A + N \pm \sqrt{A^2 - 2NA + N^2 + \frac{4NAz}{r}}\right)$

Coexistence:

see Appendix Sec. 9.1

To analyze the stability of these equilibria, we used MAPLE ^{TM} to compute the Jacobian for the system, then input each of the equilibrium points and found the eigenvalues.

Mutual Extinction	**Mammoth Extinction**
$\lambda_1 = -r + z$	$\lambda_1 = -y + q$
$\lambda_2 = y - q$	$\lambda_2 = z(1 - \chi + \frac{\chi q}{y}) - r$
Human Extinction	**Coexistence**
Too complicated to include in paper	Too complicated to include in paper

An equilibrium will only be stable when $\lambda_1 < \lambda_2 < 0$. For mutual extinction, this will only happen when $r > z$ and $q > y$. In biological terms, this would mean that mammoths would need to reproduce faster than they migrate, but humans would have to migrate faster than they reproduce. This is biologically illogical when we consider the fact that mammoths function much like their modern day cousin, the elephant, who can travel up to 12 miles a day, but only give birth once every 4-5 years. In contrast, paleolithic humans did not move nearly that quickly through pre-Holocene North America.

Mammoth extinction will be stable when $y > q$ and $1 + \frac{\chi q}{y} < \chi + \frac{r}{z}$. Biologically speaking, this would be when humans are reproducing faster than they are migrating. This would not only fulfill the first condition, but would also allow (assuming r is not significantly smaller than z) the second condition to be true as well.

Equilibrium 3 and equilibrium 4 are too complicated to find the stability conditions for, so we will use quantitative methods to analyze these equilibria under a specific parameter set.

3.3   Quantitative Analysis of Equilibria

To quantitatively analyze the first two equilibria (mutual extinction and mammoth extinction) for any parameter set, we could simply check whether the parameter set fulfills the equilibrium's stability conditions (listed previously).

We cannot derive stability conditions for the last two equilibria, so we had to rely on testing each equilibrium using all ten of our parameter sets from the LHS. For all sets, both equilibria were unstable.

3.4   Phase Plane

Using a parameter set from our LHS where mammoth extinction is a stable equilibrium, we found the phase plane for the system.
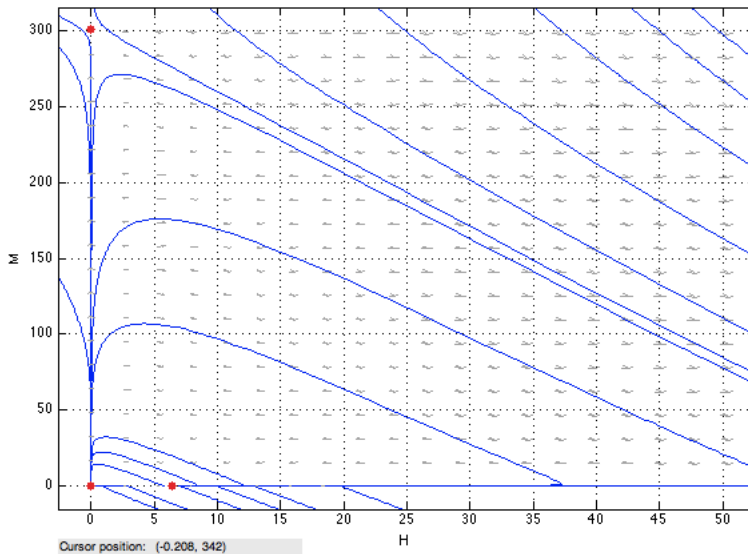

Figure 1: Phase plane of human population size versus mammoth population size with equilibria marked by red dots.

There are three equilibria marked in the phase plane with red dots. We see that they are mutual extinction, mammoth extinction and human extinction. For this parameter set, mutual extinction occurs when both populations are at 0, human extinction occurs when humans are at 0 and mammoths are around 300, (this is impossible because the mammoth population's carrying capacity is $N = 250$) and mammoth extinction occurs when mammoths are at 0 and humans are around 6. Thus, we see that mammoth extinction is the only equilibria that is viable for this parameter set.

We can also see that the mammoth population initially grows when the human population is small, but as human population approaches carrying capacity, we see mammoth population fall drastically.

4   Model 2: Metapopulation Differential Equations Simulation

4.1   Concept

Although our ODE system is efficient at modeling population dynamics caused by the interaction of a single human population with a mammoth population, these equations alone are not adequate at modeling popula-

tions on a continental scale. One problem that arises from the use of a single area to represent North America is that the model would use the Mass-Action assumption. This would mean that any two individuals within the system have an equla probability of interacting with each other. Under the Mass-Action assumption, a human hunter in Alaska could kill a mammoth in Florida. Due to the size of the continent and the limited range of movement of human and mammoth populations, it is unrealistic that individuals interacted over such great distances. Additionally, one of the main goals of our research was to model the spread of humans as they first migrated into North America from Asia. If we confined our model to one area, we would be unable to show this. Thus, we needed to develop another model.

In order to solve both of these problems, we created an $n \times n$ rectangular grid system with n^2 cells (each with area of 10 mile^2) to represent North America. In this system, each cell contains both a human and mammoth population that can interact with each other. In order to account for the movement and migration of populations across the continent, we incorporated an immigration/emigration term into both equations of our ODE system. Through the process of immigration, the populations of one cell can interact with the cells adjacent to it, known as its neighbor cells. With a grid in place and an initial population of humans in cell (1,1), we can use our new model to observe the spread of humans across the continent and see its affects on the mammoth population in North America.

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4.2   Equations and Immigration/Emigration Terms

We used a modified version of our original ODE system for this simulation, with the general model for any cell (i,j):

$$\frac{dH_{i,j}}{dt} \quad = \quad yH_{i,j}\left(\frac{1-H_{i,j}}{N}\right) + \frac{aM_{i,j}^2 H_{i,j}}{M_{i,j}^2 + b^2} + H_{neigh} \tag{11}$$

$$\frac{dM_{i,j}}{dt} \quad = \quad rM_{i,j}\left(1 - \frac{M_{i,j}}{N}\right)\left(\frac{M_{i,j}}{A} - 1\right) - \frac{\alpha M_{i,j}^2 H_{i,j}}{M_{i,j}^2 + b^2} + M_{neigh} \tag{12}$$

The birth and predation terms are unchanged from our first model, but the immigration terms (H_{neigh} and M_{neigh}) have been modified to account for the migration of populations between neighboring cells.

$$\text{If } M_{i,j} > C, \text{then } H_{neigh} = \left(\sum_{g=-1}^{1} \sum_{h=-1}^{1} q_{i+g,j+h \to i,j} H_{i+g,j+h} \right) \left(\frac{M_{i,j}}{C} - 1 \right) \tag{13}$$

$$\text{If } M_{i,j} < C, \text{then } H_{neigh} = \left(\sum_{g=-1}^{1} \sum_{h=-1}^{1} q_{i,j \to i+g,j+h} H_{i,j} \right) \left(\frac{M_{i,j}}{C} - 1 \right) \tag{14}$$

$$\text{If } H_{i,j} < W, \text{then } M_{neigh} = \left(\sum_{g=-1}^{1} \sum_{h=-1}^{1} z_{i+g,j+h \to i,j} M_{i+g,j+h} \right) \left(1 - \frac{H_{i,j}}{W} \right) \tag{15}$$

$$\text{If } H_{i,j} > W, \text{then } M_{neigh} = \left(\sum_{g=-1}^{1} \sum_{h=-1}^{1} z_{i,j \to i+g,j+h} M_{i,j} \right) \left(1 - \frac{H_{i,j}}{W} \right) \tag{16}$$

With these new migration terms, we can now show how model how human migration is impacted by the size of the mammoth populations in each cell, and how the mammoth migrations are affected by the the size of the human populations in each cell. As shown in equation (13), if the mammoth population in cell (i,j) is larger than a certain threshold, then humans from neighboring cells will migrate into cell (i,j). Equation (14) models the situation in which the mammoth population in cell(i,j) is below the threshold, and humans migrate out of cell (i,j) and into its neighboring cells. The migrations of the mammoth populations can be modeled in a similar fashion. As shown in equation (15), when the human population in cell (i,j) is below a given threshold, the mammoths in the neighboring cells will migrate into cell (i,j). Equation (16) models the situation in which the human population in cell (i,j) is larger than the given threshold, and mammoths emigrate into its neighboring cells. Thus, the number of immigrating individuals is based on the populations of the neighboring cells and the number of emigrating individuals is based on the population of cell (i,j).

The coefficients of migration between two neighbor cells (q for humans and z for mammoths) are randomly determined at the beginning of every run of our simulation; the same value is used regardless of the direction that the populations are migrating between the two cells) and non-neighbor cells have a value of 0. Thus, $q_{i+g,j+h \to i,j} = q_{i,j \to i+g,j+h}$ and $z_{i+g,j+h \to i,j} = z_{i,j \to i+g,j+h}$. These values (ranging from 0 to 1) represent the frequency of migrating individuals that account for variations in terrain between two neighbor cells. For example, the coefficient of immigration would be much lower in cells representing a mountainous terrain than it would be in cells in a flat and even terrain because individuals could travel much easier on the flat terrain. The human coefficient of migration between two cells (q) is $\frac{1}{25}$ the value of z for the same two cells. This is because humans travel at a slower rate than mammoths can.

4.3 Grid Design

To represent North America, we designed a rectangular, $n \times n$ grid with 10 mile^2 cells. Each cell can interact with its eight adjacent neighbor cells.

1,1	1,2	1,3	1,4
2,1	2,2	2,3	2,4
2,2	3,2	3,3	3,4
2,3	4,2	4,3	4,4

Figure 2: Sample grid used to represent North America

4.4 Simulation Results

We ran a variety of simulations in an attempt to fully understand the behavior of the model. Our initial conditions for the simulations were:

$$M_{i,j}(0) \quad = \quad 30 \quad \forall \quad i,j \tag{17}$$

$$H_{1,1}(0) \quad = \quad 5 \tag{18}$$

$$H_{i,j}(0) \quad = \quad 0 \quad \forall \quad (i,j) \neq (1,1) \tag{19}$$

First, we ran a simulation for a four-cell grid and looked at the graph of the population sizes versus time:
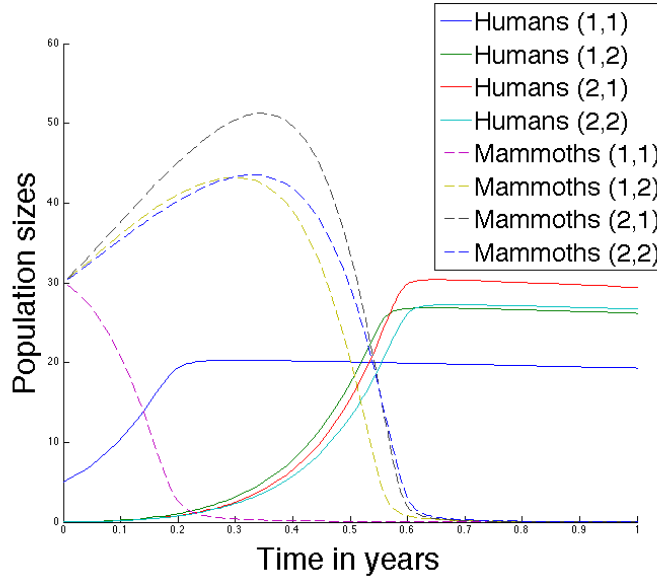
Figure 3: Graph of human and mammoth population sizes versus time (in years) here human population is represented by a blue solid line for cell $(1, 1)$, a green solid line for cell $(1, 2)$, a red solid line for cell $(2, 1)$, and an aqua solid line for cell $(2, 2)$. Mammoth population is represented by a purple dashed line for cell $(1, 1)$, a yellow dashed line for cell $(1, 2)$, a gray dashed line for cell $(2, 1)$, and a blue dashed line for cell $(2, 2)$.

We see that in cell $(1, 1)$ humans start at a population of 5 and grow to some constant population size. The mammoths in cell $(1, 1)$ leave the cell almost immediately, sending the mammoth populations in all other cells up almost immediately. These populations quickly fall though as human populations in those cells grow and mammoths are hunted to extinction. As all mammoth populations reach 0, human populations in cells $(1, 2)$, $(2, 1)$, and $(2, 2)$ stabilize to some constant population size.

We next ran the model for a 100 cell grid. Instead of plotting this as a graph, we created a video to show humans spread through North America and how the mammoth population responded. In the video stills, we observe a heat map representing population density on the continent.
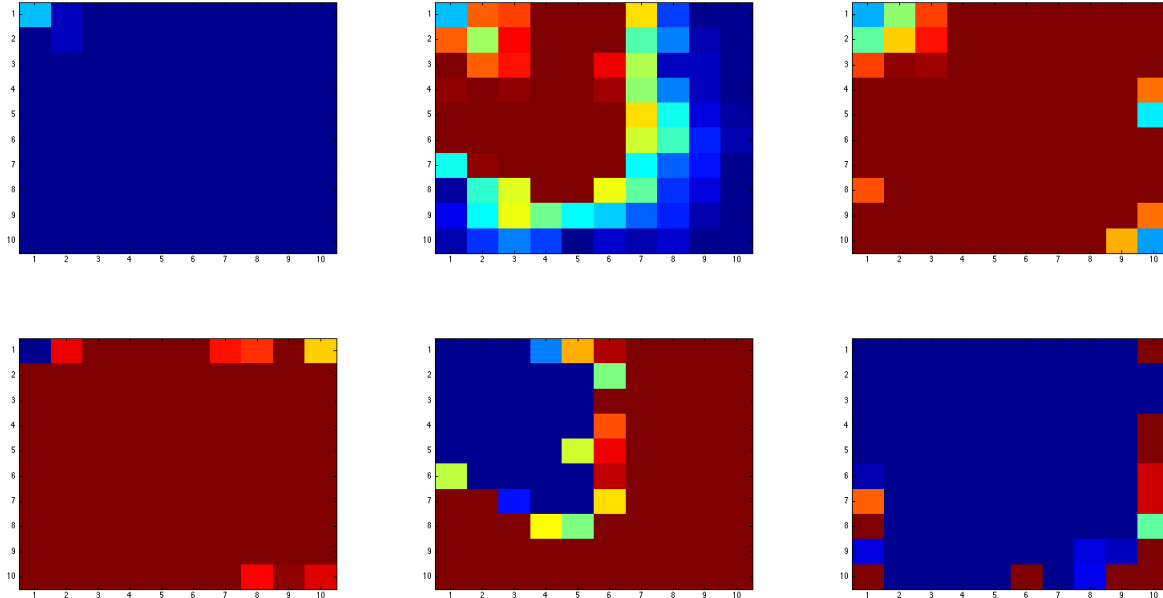
Figure 5: The top three boxes are heat maps of human population density over time where blue is low density and red is high density. The bottom three boxes are heat maps of mammoth population density over time.

We see that humans start with only a small population in cell $(1, 1)$, but quickly populate and spread across the grid, reaching a high population density in most cells.

Mammoth start at a high population density, and as humans spread across the grid mammoths migrate away, but are eventually overtaken and hunted to extinction in most cells.

Finally, we ran a 100 cell simulation for 100 realizations, using each of the parameter sets once. (In total, we ran 10 sets of 100 realizations each.)

Mammoths went extinct in 75% of the realizations for the first parameter set, 44% for the second, 2% for the third, and 0% for the remaining parameter sets.

While this model is more realistic than our first model, it still has two major limitations:

1. It does not model extreme cases

2. Because of the computational aspects of the simulation, running the model for a grid size over 100 cells is not realistic with respect to time

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5 Model 3: Discrete State Stochastic Simulation

5.1 Concept

Our third and final approach was to create a discrete state, stochastic simulation. We used a discrete state model because it allowed for a more realistic simulation. In our continuous model, we allowed things such as 0.573 mammoths or 7.6498 humans to occur. In our discrete model, human and mammoth population must be whole numbers. We used a stochastic model because it allowed for a randomness in the model that would allow us to simulate extreme cases.

5.2 How the Simulation Works

For this simulation, we used the same grid design as before. Each cell in this grid has a human population and a mammoth population. Every time the simulation runs it:

1. Calculate rates

   $\frac{dH_{birth}}{dt} = yH(1 - \frac{H}{K})$

2. Calculate probabilities

   $P(H_{birth}) = \frac{\frac{dH_{birth}}{dt}}{rate_{total}}$

3. Generate uniformly distributed random number u that "chooses" which event will happen

4. Rescale u and use it to choose what cell the event will happen in

5. Change population size(s) based on event

For this simulation we used a Poisson process, which means that the time between two consecutive events is a random number t with an exponential distribution. This means that there is a very high probability that t will be a short amount of time, and there is a very low probability that t will be a long amount of time, but there is still a chance.

5.3 Simulation Results

Because of coding difficulties, we have not expanded this simulation past a two cell grid. While this means that we cannot gather serious results from this model, it provides a perfect stepping stone to a future project on the subject. With that being said, we can see the results of the simulation for a two cell grid. (*See Appendix 9.4 for sample code.*)

These are four realizations of the same parameter set and initial conditions. The variance in the graphs is due to the stochastic nature of the simulation alone:
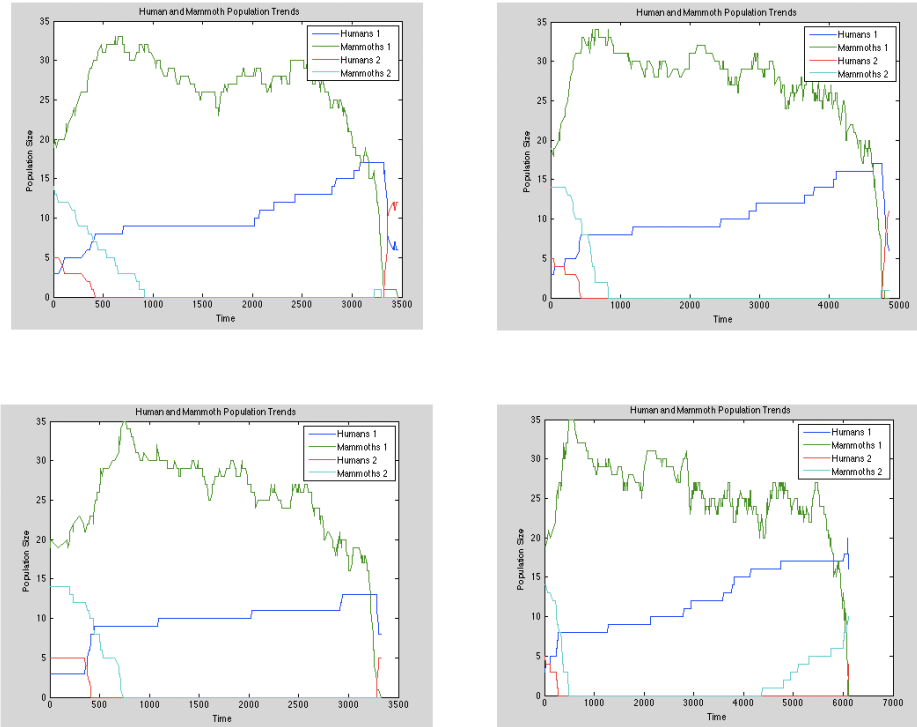

Figure 6: Four realizations of the two cell simulation using the same parameter set and initial conditions for all realizations (*see Appendix sec. 9.3*) here the x-axis is time (in years) and the y-axis is population size. Human population is represented by a dark blue line for cell 1 and a red line for cell 2, and mammoth population is represented by a green line for cell 1 and a light blue line for cell 2.

We can see that in the first three realizations (left to right, top to bottom) mammoths in both cell 1 and cell 2 die off. In two of these cells it takes about 3500 years, and in the other it takes almost 5000 years for mammoths to go completely extinct. In the fourth realization we see segregation, where mammoths and humans coexist in separate cells.

6 Results

6.1 Model 1

We see that mammoth extinction is only stable under certain parameter conditions. Because of this, we cannot draw a singular conclusion from this method. What this model did tell us though, was that for realistic parameter ranges, it is very unlikely that mutual extinction, human extinction, or coexistence will be stable, and there are parameter conditions under which mammoth extinction is a stable equilibrium.

6.2 Model 2

Initially, this model seems to give dire results for the overhunting hypothesis. We must consider not only the percentages extinct though, but why the populations are not going extinct as well as our extinction criteria.

When a mammoth population did not go extinct, we looked at the video and graphs for a single realization with that parameter set. We expected to see mammoth recolonizing in cells behind the human wave, but instead we saw these cells remain dead. Mammoths were not going extinct across the continent for the simple reason that humans were not spreading fully across the continent. We can see in figures 4 and 5 that even when mammoth populations did reach the extinction criteria, humans had not fully populated every cell in the grid at the simulations end, letting mammoth populations survive in a few cells. Increasing the number of timesteps the simulation takes before ending could possibly lead to a higher extinction rate of mammoths.

We must also realize that our extinction criteria are extremely conservative. Under less extreme criteria, we might see more mammoth extinction.

Another limitation of our model is size. A 100 cell grid only represents one one-hundredth of North America, but running one realization for a hundred cell grid takes more than $\frac{1}{2}$ minute. Running a 1,000,000 cell grid (the size of North America) would take more than 83 hours per realization.

6.3   Model 3

Because of the extremely limited size of this model, we cannot draw any serious conclusions yet. This model did make coexistence through segregation a viable outcome though. It would be interesting to see if this phenomenon is found in larger grids as well.

This model also suggests that even with randomness in the simulation, under realistic parameter conditions it is very likely that mammoths will go extinct at the hands of humans for a small area.

7 Discussion

At this point we must ask, did we answer our question?

First we look at Model 1, there are realistic parameter sets where mammoth extinction is a stable equilibrium. While this alone does not answer our question, it suggests that under certain conditions, humans alone could have caused the extinction of the Columbian mammoth.

Next, we can look at Model 2. Again, we see that for our simulation, there exists realistic parameter conditions under which mammoths go extinct. While our simulation is only represents a small portion of North America, this still suggests that even for extremely conservative extinction criteria, mammoths go extinct at the hands of humans. In addition, we see that mammoths go extinct under multiple, random migration conditions. Again, this alone does not answer our question, but it strongly suggests that humans alone had the capabilities to cause the extinction of an entire species.

Finally, we look to Model 3. While this model is realistically too small to draw many conclusions from, we can see that even when incorporating randomness into a model (to represent extreme cases), human overhunting is enough to cause mammoth extinction on a small scale under some parameter conditions.

Alone, none of these models provide a strong enough case to answer our question. Together though, we can say with some certainty that under the correct conditions, humans overhunting alone could have caused the extinction of the Columbian mammoth.

8 Future Directions

8.1 Model 1

To further analyze this model, a sensitivity analysis could be performed to determine which parameters the model is most sensitive to. Using this sensitivity analysis, parameter ranges could be refined even more.

8.2   Model 2

Further work could be done on this model by expanding the grid to a larger portion of North America, using a longer time span for the simulation so that humans have a chance to spread across the grid, and using more refined parameter ranges for our simulation. Additional sensitivity analysis could also be performed by running another LHS then using these parameter sets in the simulation.

8.3   Model 3

Since this is the most limited model, it has the most potential for future work. First, The simulation must be expanded past a two cell grid to more accurately represent North America. Sensitivity analysis using an LHS could be performed to look at how the model works over ranges of parameter space.

9 Appendix

9.1 Coexistence Equilibrium

(nondimensionalized)

$$r\beta\sigma^2 + \sigma(-r - r\beta) - z + r = 0$$

$$r\beta y\sigma^6 + \sigma^5(-ry - r\beta y + zq\chi\theta) + \sigma^4(ry + az\chi - zy + 2ry\beta\epsilon^2 + zy\chi + \mu q\theta - zq\chi) + \sigma^3(a\mu 2zq\chi\theta\epsilon^2 - q\mu +$$
$$\mu y - 2ry\beta\epsilon^2 - 2ry\epsilon^2) + \sigma^2(\mu q\theta\epsilon^2 - 2zq\chi\epsilon^2 - 2zy\epsilon^2 + az\chi\epsilon^2 + 2zy\chi\epsilon^2 + 2ry\epsilon^2 + ry\beta\epsilon^4) + \sigma(-\mu q\epsilon^2 + zq\chi\theta\epsilon^4 +$$
$$\mu y\epsilon^4 - ry\epsilon^4 - ry\beta\epsilon^4) - zq\chi\epsilon^4 + zy\chi\epsilon^4 + ry\epsilon^4 - zy\epsilon^4 = 0$$

9.2 Parameter Sets

Parameter Set	y	a	b	q	r	A	α	z	C	W
1	0.0237	8.0611	9.4623	0.0404	0.0395	5.5509	13.5954	0.2594	3.0496	7.2730
2	0.0101	2.4568	5.1982	0.0229	0.0471	7.8002	12.1257	0.2023	3.3543	5.8742
3	0.0294	7.1550	3.4307	0.0487	0.0404	5.6317	12.9399	0.3604	3.5872	6.2844
4	0.0030	9.3177	1.4927	0.0126	0.0439	6.0450	13.2375	0.4420	3.6465	5.0591
5	0.0072	8.3160	8.7196	0.0291	0.0481	7.4892	10.3371	0.4951	4.4658	8.7977
6	0.0182	1.5843	2.4764	0.0232	0.0416	7.0539	11.7268	0.3824	4.2570	8.3457
7	0.0127	3.0830	5.8975	0.0413	0.0457	7.1140	14.8006	0.2662	3.8716	7.4196
8	0.0205	4.3353	6.6317	0.0074	0.0468	6.6377	14.2925	0.4227	4.1162	6.8224
9	0.0321	5.9224	4.2181	0.0354	0.0423	6.2961	10.9096	0.3068	4.9218	5.7760
10	0.0152	4.7508	7.8136	0.0151	0.0448	5.2890	11.3723	0.3423	4.6368	7.8533

9.3 Model 3 Parameter Set

$$y = 0.014 \quad K = 50 \quad b = 2 \quad q = 0.1$$
$$C = 5 \quad\quad k = 0.1 \quad A = 6 \quad\quad N = 32$$
$$\alpha = .13 \quad\quad z = 0.1 \quad W = 15$$

Initial Conditions:

$$H(1,1) = 3 \quad M(1,1) = 19$$
$$H(1,2) = 5 \quad M(1,2) = 14$$

10 References

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