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Abstract

One extinction hypothesis of the Columbian mammoth (*Mammuthus columbi*), called overkill, theorizes that early humans overhunted the animal. We employ two different approaches to test this hypothesis mathematically: analyze the stability of the equilibria of a 2D ordinary differential equations (ODE) system and develop a metapopulation differential equations model. The 2D ODE system is a modified predator-prey model that also includes migration. The metapopulation model is a spatial expansion of the first model on a rectangular grid. Using this metapopulation system, 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.

Keywords: mammoth, extinction, predator-prey model, metapopulation, population dynamics, differential equations, mathematical modeling, ecology

1 Introduction

The Columbian mammoth (*Mammuthus columbi*), a relative of modern day elephants (genera *Elephas* and *Loxodonta*), lived in North America during the Pleistocene, an era of time that spanned from approximately 1.8 million to 11,700 years ago. The Columbian mammoth went extinct at the end of the last ice age (in the Late Pleistocene) about 13,000 years ago. At this time, there was a mass extinction of megafauna on every continent except Africa and Southeast Asia [9, 10, 15]. In North America, 32 out of 41 large prey species went extinct during this event [1].

There are four dominant hypotheses as to why the megafaunal extinction took place: disease, climate change, a meteorite shower, and overkill. It is likely that a combination of these factors (whether in series or parallel) lead to the extinction [2, 17]. Our project focuses on overkill, a theory first proposed by Martin in 1973 [14]. Martin proposed that the migration of modern humans (*Homo sapiens*) from Asia into North America (over the Bering land bridge) around 13,500 years ago was the leading cause of megafaunal extinction. Despite the argument that the lack of kill-sites discovered in North America disproves this theory [12], it 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 of other species in the ecosystem [13].

We have chosen to study the Columbian mammoth specifically because its range was completely contained within North America and encompassed nearly all of the continental United States. In contrast, the woolly mammoth (*Mammuthus primigenius*), while found in North America, was also found outside it, predominantly in Siberia [15]. In this manner, we can treat the human migration into North America as an invasive species.

In 2001, Alroy conducted a stochastic difference equation simulation of the end-Pleistocene megafaunal extinction which incorporated the population dynamics of invading humans and 41 large mammalian herbivores. He found that, using some realistic combinations of parameter values, the model accurately predicted as many as 32 of the fates (extinction vs survival) of the prey species. In most instances, extinction of species occurred in multiple temporal waves, and interestingly, proboscideans (including Columbian mammoth) did not die off in the primary wave. Alroy concludes that anthropogenic extinction was unavoidable for many of the megafauna [1]. We hope to strengthen this conclusion through additional evidence from deterministic differential equation models.

Previous models of prehistoric scenarios have used differential equations to model the interaction and competition between early *Homo sapien* and Neanderthal (*Homo*

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neanderthalensis) populations and were able to conclude that even a competitive advantage as small as 1% would lead to the demise of the Neanderthal [11]. Mathematical research into population dynamics has resulted in the creation and analysis of models of invading species as well as conditions for extinction or assimilition [4]. Other work with models of interacting populations analyzed multi-stability and extinction of various forms of predator-prey systems of differential equations [5, 6].

In this paper, we attempt to determine if human overhunting alone could have caused the extinction of the Columbian mammoth. To do this, we use two different approaches to mathematically model human-mammoth interactions. First, we use an ordinary differential equations system to model the two populations interacting in a relatively small area, a single "patch." We analyze the stability of the single-patch model's equilibria to determine the long-term behavior of the system. Second, we expand the single-patch model into a metapopulation differential equations model to describe the two species interacting across a larger area.

This paper is organized as follows: In Section 2 we present and analyze the single-patch differential equation model. We expand the 2D system into a metapopulation model with migration between the patches in Section 3. Section 4 outlines our results. We conclude with a discussion in Section 5.

2 Single-Patch ODE Model

2.1 Model

We begin by modeling the human-mammoth interaction in a single sufficiently small area as a Rosenzweig-MacArthur predator-prey ordinary differential equation system [21]. Thus, the model is composed of two first-order ODEs, one describing the changes in the human population $H(t)$ and another describing the dynamics of the mammoth population $M(t)$.

The growth term for each population incorporates logistic growth [23] so that the populations are limited by carrying capacities (K_H and K_M respectively). We also employed a strong Allee effect [22, 24] for the mammoth birth term (with critical population size A). The strong Allee effect implies that for low population numbers ($M < A$), the population should decline. Allee effects can be attributed to many phenomena, perhaps most applicably is the idea that a greater population size would confer an increased protection from predators [8]. There has been evidence of an Allee effect in African elephants (*Loxodonta africana*) [20, 19] so we feel safe to assume one for the Columbian mammoth.

The predation term uses a Holling type III response so that, while hunting is a function of prey density, it also

accounts for the predators being generalists with alternative food supplies [7].

A migration term in each equation was included to reflect the movement of both species into and out of the patch. This migration term assumes that humans will immigrate into an area with a high population of mammoths (when $M > N_M$) and emigrate out of an area with a lower mammoth population (when $M < N_M$). Similarly, mammoths will emigrate out of an area with a large population of humans (when $H > N_H$) and immigrate into areas where there are few humans (when $H < N_H$).

Our model is given by the equations

$$\frac{dH}{dt} = r_H H \left(1 - \frac{H}{K_H}\right)$$
$$+ \frac{a_H M^2 H}{M^2 + b^2} + c_H H \left(\frac{M}{N_M} - 1\right), \quad (1a)$$

$$\frac{dM}{dt} = r_M M \left(1 - \frac{M}{K_M}\right)\left(\frac{M}{A} - 1\right)$$
$$- \frac{a_M M^2 H}{M^2 + b^2} + c_M M \left(1 - \frac{H}{N_H}\right). \quad (1b)$$

Each of the twelve model parameters and the assumed ranges of their values are given in Table 1. We obtained literature values for appropriate ranges for the first seven model parameters. Five parameters values required assumptions on their ranges. The predation saturation constant b was assumed to be between 1 and 10 mammoths, as a small human population is likely to be easily sustained for a long time by very few mammoths. The relative migration rates c_H and c_M were assumed to be generally on the same order of magnitude as birth rates for humans and an order of magnitude higher for mammoths. Finally, the external population sizes N_H and N_M had their assumed ranges chosen such that the mammoths would leave the patch when humans were at least halfway to their carrying capacity and humans would leave the patch when mammoths were at most below the Allee threshold A.

2.2 Analysis of Equilibria

We are interested in the stability of the equilibria of the model, which allows us to consider the long term behavior of the system. The single-patch model contains four equilibrium solutions (H^*, M^*): mutual extinction $(0,0)$, mammoth local extinction and human survival $\left(K_H\left(1 - \frac{c_H}{r_H}\right), 0\right)$, human extinction and mammoth survival $\left(0, \frac{1}{2}\left(A + K_M \pm \sqrt{A^2 - 2K_M A + K_M^2 + \frac{4K_M A c_M}{r_M}}\right)\right)$, and coexistence (expression omitted for brevity). Note that extinction in each of these cases, refers only locally for the patch in question.

Parameter	Units	Description	Value	Reference
K_H	humans	human carrying capacity	10	[14]
K_M	mammoths	mammoth carrying capacity	250	[14]
r_H	year^{-1}	human growth rate	$[\ln(1.001), \ln(1.034)]$	[14]
r_M	year^{-1}	mammoth growth rate	$[\ln(1.04), \ln(1.05)]$	[18]
A	mammoth	Allee effect critical population size	$[5, 8]$	[19]
a_H	year^{-1}	human predation rate	$[1, 10]$	[14]
a_M	$\frac{\text{mammoth}}{\text{human·year}}$	mammoth predation rate	$[10, 15]$	[14]
b	mammoth	predation saturation constant	$[1, 10]$	assumed
c_H	year^{-1}	human migration rate	$[0.005, 0.05]$	assumed
c_M	year^{-1}	mammoth migration rate	$[0.2, 0.5]$	assumed
N_H	humans	external human population size	$[5, 9]$	assumed
N_M	mammoths	external mammoth population size	$[3, 5]$	assumed

Table 1: A list of parameters and their values for patches representative of a 10-square-mile area used in Equations 1 and 6. Each of the entries in the "Value" column given in brackets is a range of viable values determined either from the literature or assumed ("Reference" column).

To determine the stability of these equilibria, we linearize the system and find the eigenvalues of the resulting Jacobian matrix $J(H, M)$. For an equilibrium (H^*, M^*) to be stable, the real part of all of the eigenvalues of $J(H^*, M^*)$ must be negative [3].

The mutual extinction equilibrium has associated Jacobian matrix $J(0,0)$, which has eigenvalues

$$\lambda_1 = c_M - r_M \quad \text{and} \quad \lambda_2 = r_H - c_H. \tag{2}$$

Thus, the equilibrium is only stable when $r_M > c_M$ and $r_H < c_H$. This is interpreted as requiring the mammoths to reproduce faster than they migrate and humans would have to migrate faster than they reproduce. The mutual extinction equilibrium is likely to be unstable, since mammoths function much like their modern day cousin, the African elephant, who can travel up to 12 miles a day during migration, but only give birth once every 4-5 years. In contrast, paleolithic humans did not migrate nearly as quickly as 12 miles a day through pre-Holocene North America [14].

The mammoth extinction, human survival equilibrium has associated Jacobian matrix $J\left(K_H\left(1 - \frac{c_H}{r_H}\right), 0\right)$, which has eigenvalues

$$\lambda_1 = c_H - r_H \text{ and } \lambda_2 = c_M\left(1 - \frac{K_H}{N_H} + \frac{K_H c_H}{N_H r_H}\right) - r_M. \tag{3}$$

This implies the equilibrium is only stable when

$$r_H > c_H \tag{4}$$

and

$$1 + \frac{K_H c_H}{N_H r_H} < \frac{K_H}{N_H} + \frac{r_M}{c_M}. \tag{5}$$

This is interpreted as when humans are reproducing faster than they are migrating. This would not only fulfill the condition in Equation 4, but would also allow (assuming r_M is not significantly smaller than c_M) the condition in Equation 5 to be true as well. This equilibrium could potentially be stable for realistic parameter values.

Simple stability conditions for the remaining two equilibria would be difficult to obtain so the stability of these equilibria was assessed quantitatively only. We used a Latin Hypercube Parameter Space Sampling [16] (LHS) on the parameter ranges given in Table 1, and found ten parameter sets (see Table 2) that were used to determine the stability of each equilibrium. In each of the ten parameter sets, the mutual extinction, human extinction and mammoth survival, and coexistence equilibria were all unstable. However, the mammoth extinction and human survival equilibrium was stable for parameter set 8. Thus, for initial conditions conditions within the equilibrium's basin of attraction, mammoths would be destined to go extinct in the patch.

3   Metapopulation ODE Model

Although our ODE system may be used to model population dynamics of local populations of humans and mammoths interacting, the model is not adequate for representing populations on a continental scale. One problem that arises from the use of a single area to represent the entirety of the Columbian mammoth's range is the model uses the mass-action assumption. Under this assumption, any two individuals within the system have an equal probability of interacting with each other. For example, a human hunter in Oregon could kill a mammoth in Florida. Due to the size of the continent and the limited movement capabilities of humans and mammoths, it is clearly unrealistic that individuals could have interacted over such

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

Table 2: Ten different parameter sets created from a Latin Hypercube Sampling of the parameter ranges given in Table 1. These parameter sets were used to analyze the stability of the equilibria for the single-patch model. Additionally, they were the ten sets of parameters used for Monte Carlo simulations of the metapopulation model. For the metapopulation model, however, the last four columns were not used, since migration is defined differently, as described in Section 3.

great distances. To more accurately capture how early humans first migrated into North America from Asia, we need to adapt our previous model. We do this with a metapopulation model.

We create an $n \times n$ square grid system with n^2 patches (each with area of 10 mile^2) to represent (at least a portion of) North America. For patch (i,j) each other patch $(i \pm 1, j \pm 1)$ within the grid is considered adjacent, so any one patch may have as many as eight neighbor patches. In this system, each patch contains a local population of humans and mammoths that are governed by the same dynamics as in Section 2 with the exception of the migration process.

In order to account for the movement of the species across the continent, we adjust the immigration/emigration term in both equations of our ODE system. Through the process of immigration, the populations of one patch can interact with the its neighbor patches. With a grid in place and an initial population of humans in patch $(1,1)$, the northwest corner of the grid, we can use this metapopulation model to emulate the spread of humans across the continent and see its affects on the mammoth population in North America.

The ODE metapopulation model for patch (i,j) is given by

$$\frac{dH_{i,j}}{dt} = r_H H_{i,j}\left(1 - \frac{H_{i,j}}{K_H}\right)$$
$$+ \frac{a_H M_{i,j}^2 H_{i,j}}{M_{i,j}^2 + b^2} + \sum_{g=-1}^{1}\sum_{h=-1}^{1} H_{i,j}^{\text{mig}} \quad (6a)$$

$$\frac{dM_{i,j}}{dt} = r_M M_{i,j}\left(1 - \frac{M_{i,j}}{K_M}\right)\left(\frac{M_{i,j}}{A} - 1\right)$$
$$- \frac{a_M M_{i,j}^2 H_{i,j}}{M_{i,j}^2 + b^2} + \sum_{g=-1}^{1}\sum_{h=-1}^{1} M_{i,j}^{\text{mig}} \quad (6b)$$

where the terms for migration between neighboring patches, H^{mig} and M^{mig}, are defined according to the rules:

if $M_{i,j} > M_{i+g,j+h}$, then

$$H_{i,j}^{\text{mig}} = c_{i+g,j+h \to i,j} H_{i+g,j+h} \frac{M_{i,j}}{K_M}; \quad (7a)$$

if $M_{i+g,j+h} > M_{i,j}$, then

$$H_{i,j}^{\text{mig}} = -c_{i,j \to i+g,j+h} H_{i,j} \frac{M_{i+g,j+h}}{K_M}; \quad (7b)$$

if $H_{i,j} < H_{i+g,j+h}$, then

$$M_{i,j}^{\text{mig}} = c_{i+g,j+h \to i,j} M_{i+g,j+h} \frac{H_{i,j}}{K_H}; \quad (7c)$$

if $H_{i,j} > H_{i+g,j+h}$, then

$$M_{i,j}^{\text{mig}} = -c_{i,j \to i+g,j+h} M_{i,j} \frac{H_{i+g,j+h}}{K_H}. \quad (7d)$$

Thus, the number of immigrating individuals is based on the populations of the neighboring patches and the number of emigrating individuals is based on the population of patch (i,j). As shown in Equation 7a, if the mammoth population in patch (i,j) is larger than that of a neighboring patch, then humans from that patch will migrate into patch (i,j). Otherwise, Equation 7b shows when the mammoth population in patch (i,j) is below that of a neighboring patch, then humans migrate out

of patch (i, j) into that neighboring patch. Similarly, as shown in Equation 7c, if the human population in patch (i, j) is below that of a neighboring patch, then the mammoths from that patch will migrate into patch (i, j). Otherwise, Equation 7d shows if the human population in patch (i, j) is larger than that of a neighboring patch, then mammoths migrate out of patch (i, j) into that neighboring patch. Note that migration is a zero-sum process, i.e.

$$\sum_{i=1}^{n}\sum_{j=1}^{n} H_{i,j}^{\mathrm{mig}} = 0 \quad \text{and} \quad \sum_{i=1}^{n}\sum_{j=1}^{n} M_{i,j}^{\mathrm{mig}} = 0. \qquad (8)$$

The rates of migration are functions of the population sizes in the patches and their neighboring patches relative to the carrying capacities and of the coefficient parameters $c_{i,j \to k,l}$. These coefficient parameters are random variables, which are assigned a particular value for each realization of a simulation. The $c_{i,j \to k,l}$ are pulled from a continuous uniform distribution on the unit interval. These migration coefficients are defined to be symmetric, so $c_{i,j \to k,l} = c_{k,l \to i,j}$ and have a value of 0 for non-neighbor patches. The variability in these coefficients are how we account for terrain differences between two neighbor patches, which affect the speed or ease of migration between the patches. For example, the coefficient of migration could be much lower between patches representing a mountainous terrain than it would be in patches with a flat and even terrain.

4   Results

Our goal with the metapopulation model was to use the Monte Carlo method by running a number of realizations for each parameter set from the LHS (see Table 1) and determine the likelihood that mammoths went globally extinct.

The initial conditions used for the simulations were:

$$M_{i,j}(0) = 250 \qquad \forall\, i,j \qquad\qquad (9a)$$
$$H_{1,1}(0) = 10 \qquad\qquad\qquad\qquad (9b)$$
$$H_{i,j}(0) = 0 \qquad \forall\, (i,j) \neq (1,1). \qquad (9c)$$

That is, mammoths began at carrying capacity in every patch while humans began at carrying capacity in the northwest corner patch and at zero in all other patches.

Before examining a large grid where monitoring the population in each patch would be difficult, we first plotted the population dynamics from a four-patch (2×2) grid simulation. Figure 1 displays the results of that simulation. We see that in patch $(1,1)$ humans begin at carrying capacity and initially grow. The mammoths in patch $(1,1)$ are hunted and then leave the patch, causing the mammoth populations in the other three patches to initially increase. These populations quickly fall as

human populations in those patches increase and mammoths are hunted to extinction. Prior to extinction, there are small peaks in the mammoth populations as they try to evade the humans by moving to neighboring patches. As each patch's mammoth population approaches 0, human populations in each patch slowly decrease towards the carrying capacity.

Next, we ran the simulation on a 100-patch grid. Computational times prevented us from being able to increase the grid size beyond 100 and still produce a sufficient number of realizations. Instead of plotting both populations from each of the 100 patches, we created a time-lapse video to display humans spread through the grid and how the mammoth population responded. In the video stills in Figure 2, we observe a heat map representing population density in the patches. The humans start with only a small population in patch $(1,1)$, the northwest corner of the map, but quickly populate and spread across the grid, reaching a high population density in most patches. Mammoths start at a high population density throughout the grid, but as humans spread across the grid mammoths are killed and migrate away. Mammoths are eventually overtaken and hunted to extinction in most patches in this realization.

Finally, we ran a 100-patch simulation for 50 realizations for each of the parameter sets chosen by the LHS (in Table 2). Mammoths went globally extinct in every realization for every parameter set. We defined global extinction to be when no patch had local mammoth populations above the Allee threshold A.

Since extinction was guaranteed, we decided to track the time to global extinction for each realization and average across each parameter set. Figure 3 displays the mean extinction times for each parameter set. Next, we compared the average extinction times to the values of various model parameters. The parameter that was most correlated with mean extinction time was a_H, the gain humans obtain from predation. We fit a power function regression curve to the mean extinction times with a_H as the explanatory variable and obtained a coefficient of determination of $R^2 = 0.9967$, indicating that extinction time was heavily dependent upon a_H.

5   Discussion

The qualitative analysis of the single patch ODE model revealed that all of the equilibria of the model were unstable for each of our LHS parameter sets except under parameter set 8. Parameter set 8 had the mammoth extinction and human survival equilibrium as stable. We believe the reason for this is primarily due to the values of c_H, c_M, and a_M. In parameter set 8, c_H is lower than in any other parameter set, c_M is the third highest, and
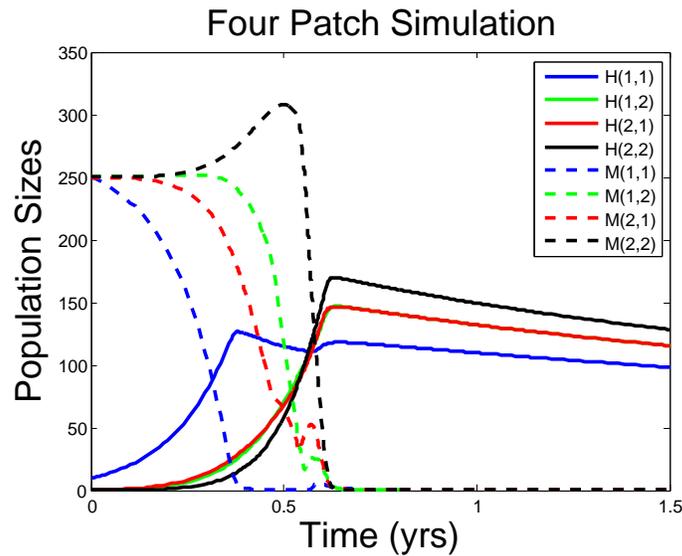
Figure 1: Graph of human and mammoth population sizes versus time (in years) in a four-patch simulation. The human populations are represented by solid curves and mammoth populations are represented by dashed curves while the curves for populations in patch $(1, 1)$ are blue, patch $(1, 2)$ are green, patch $(2, 1)$ are red, and patch $(2, 2)$ are black. Parameter set 1 from Table 2 was used.
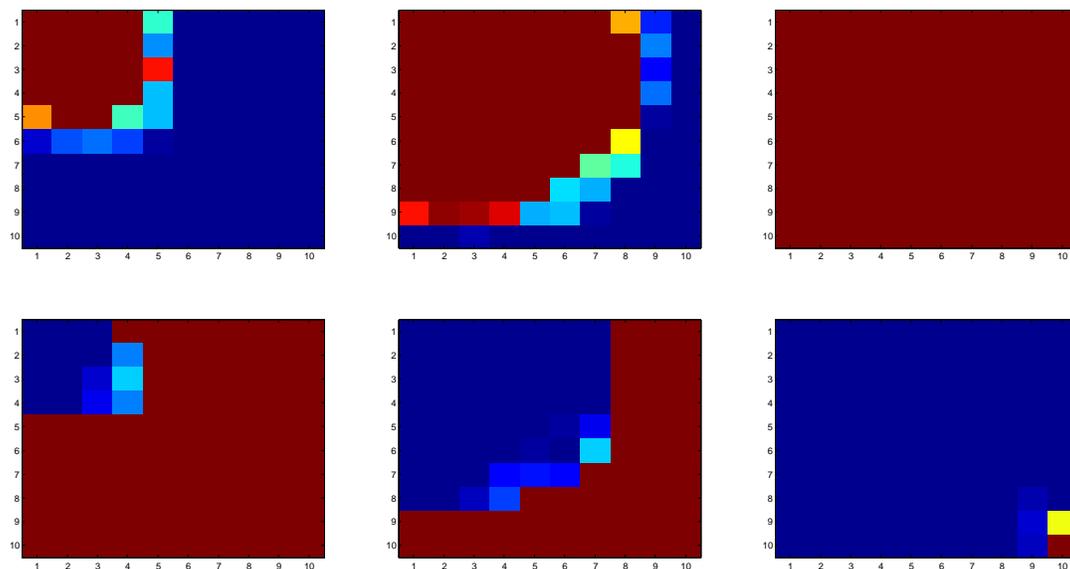

Figure 2: Time captures of one realization of the metapopulation model using a 100-patch grid and parameter set 1 from Table 2. The top row of images is heat maps of human population density while the bottom row represents the mammoth population. Dark blue represents low population density while red is high density. The images (from left to right) were taken at $t = 1$, $t = 1.7$, and $t = 2.4$ years. Mammoths went globally extinct at $t = 2.5$ years for this realization.
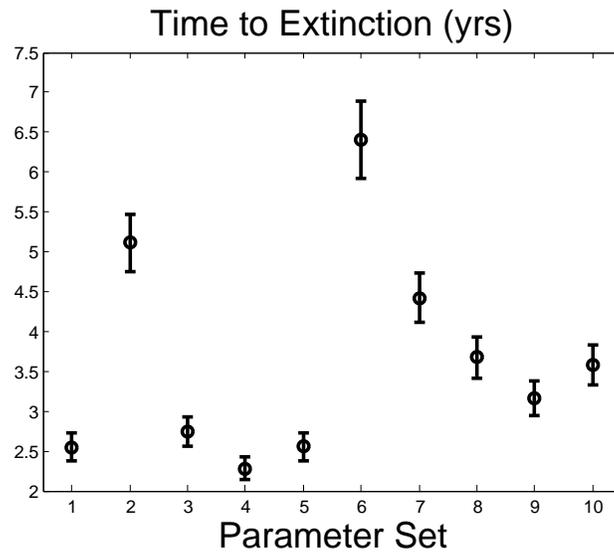
Figure 3: Graph of time (in years) until mammoths went globally extinct in a 100-patch simulation. The horizontal axis gives the parameter set. Each point is an average of 50 realizations with the error bars indicating $\pm$ two standard deviations.

a_M is the second highest. In such a scenario, Humans would not emigrate out of the patch quickly, mammoths would leave the patch quickly, and the high value of the predation coefficient for mammoths implies a dramatically negative effect from being hunted. These factors in concert are likely the cause for the model to result in mammoth extinction (for initial conditions within the basin of attraction).

Yet, it is expected that the single-patch ODE model would frequently result in mammoth persistence. Mammoths immigrate into the patch from an infinite mammoth reservoir of constant density N_M. When $c_M > r_M$, mammoths are able to rapidly migrate into the patch and there is guaranteed persistence of the mammoth population. However, there is no analogue of this in the metapopulation model, as each patch only communicates with its neighboring patches. This further enforces our decision to incorporate the spatial heterogeneity attained by using a metapopulation model.

For the metapopulation simulation, computational time was a constraint for us. We certainly recognize that a 100-patch grid representing 1,000 square miles is only about 0.0338% of the area of the range of the Columbian mammoth (which is approximately that of the contiguous United States). However, running one realization for a 100-patch grid on average took about 12.6 minutes on our machines. Running a 295,906-patch grid (the size of the contiguous United States) would take more than 25 days per realization, assuming the computational time

would scale linearly. This also does not even account for having to increase the length of time in the simulation so that humans could spread across a greater area. Nevertheless, because our simulation incorporates a variety of terrains by use of the random coefficients of migration, and since those had little effect on the outcome of the simulations, it is similarly unlikely that increasing the size of the grid to more closely match that of North America would change the outcome of the simulation.

The closed population mechanism of the metapopulation model helped guarantee that mammoths went globally extinct for all ten parameter sets. Extinction times ranged from 2.3 to 6.4 years for a 1,000-square-mile grid. Linearly scaling these extinction times up for an area approximately the size of the Columbian mammoth range gives 6,800 years to 19,000 years. These are about an order of magnitude too large when compared to the literature. However, it should be considered that our extinction criteria are extremely conservative. Under less extreme criteria, we should see much earlier global mammoth extinction times. Additionally, starting mammoths at carrying capacity in every patch was another conservative assumption. In reality, mammoth populations would be in flux due to natural predator-prey dynamics. Finally, linear scaling of the extinction times is another conservative assumption. Simulated extinction times for a grid of realistic size are likely to grow sublinearly from the smaller grid because the human wavefront expansion is more closely dependent on the diagonal distance of the

grid as opposed to its area.

The single-patch model had some realistic conditions that led to mammoth extinction and the metapopulation simulation resulted in conceivable extinction times. While our results do not indicate the overkill theory is undoubtedly holding the proverbial smoking gun, it is certainly plausible under our model assumptions that overkill could have been the sole reason for the demise of the Columbian mammoth.

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