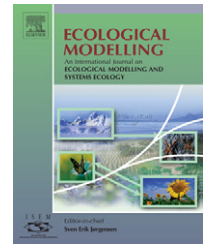


This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)

# The puzzle of North America's Late Pleistocene megafaunal extinction patterns: Test of new explanation yields unexpected results

Jeffrey V. Yule<sup>a,\*</sup>, Christopher X.J. Jensen<sup>b,c</sup>, Aby Joseph<sup>c</sup>, Jimmie Goode<sup>d</sup>

<sup>a</sup> School of Biological Sciences, P.O. Box 3179, Louisiana Tech University, Ruston, LA 71272, USA

<sup>b</sup> Department of Mathematics and Science, Pratt Institute, 200 Willoughby Avenue, Brooklyn, NY 11205, USA

<sup>c</sup> Department of Ecology and Evolution, SUNY Stony Brook, Stony Brook, NY 11794, USA

<sup>d</sup> Department of Mathematics, Louisiana Tech University, Ruston, LA 71272, USA

## ARTICLE INFO

### Article history:

Received 18 July 2008

Received in revised form

20 October 2008

Accepted 31 October 2008

Published on line 6 January 2009

### Keywords:

Pleistocene extinctions

Megafauna

Overkill

Allometric constraint

Functional response

Model assessment

Model design methodology

Parameterization

## ABSTRACT

Although Late Pleistocene extinctions disproportionately affected larger mammalian species, numerous smaller species were also lost. To date, no satisfactory explanation has been presented to account for this pattern. Beginning with the assumption that human predation caused the extinctions, we offer and test the first such explanatory hypothesis, which is predicated on considering more realistic functional response forms (i.e., those that allow for predator interference or prey sharing). We then test the hypothesis via a one-predator, six-prey ecological model that maintains transparency, minimalism of design, and maximal constraint of parameters. Results indicate that altering assumptions about one cornerstone of ecological modeling (i.e., functional response) fails to produce qualitative differences in survival–extinction outcomes—even in conjunction with a wide range of capture efficiency permutations. This unexpected finding suggests that no reasonable form of predation alone is capable of producing the survival–extinction pattern observed. We conclude that the matter of causation and the conclusions of previous Late Pleistocene extinction models remain far less certain than many have assumed.

© 2008 Elsevier B.V. All rights reserved.

## 1. Introduction

Late Pleistocene megafaunal extinctions occurred globally over a period of roughly 50,000 years, most severely affecting large ( $\geq 44$  kg body mass) mammals in Australia, Eurasia, and the Americas (Johnson, 2002; Barnosky et al., 2004; Koch and Barnosky, 2006). Polarized debate about the causes of the extinctions dates back to the nineteenth century, centering on anthropogenic effects (especially hunting) and climate (Grayson, 1984). Mathematical models have been

developed since the 1960s that seek to explain the extinctions (Budyko, 1967, 1974), but none have been entirely successful in explaining observed extinction patterns. Here, we assume that human hunting caused the extinctions and then go on to develop and test a mathematical conjecture about Late Pleistocene megafaunal extinctions that is more accurate in accounting for the general pattern of extinctions, more transparent, and simpler than the best-known recent model (Alroy, 2001). Our approach emphasizes the value of minimalist, transparent, open-access modeling efforts.

\* Corresponding author.

E-mail address: [jyule@latech.edu](mailto:jyule@latech.edu) (J.V. Yule).

0304-3800/\$ – see front matter © 2008 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2008.10.023

## 2. Refining Late Pleistocene extinction models

Alroy (2001) offers a computer simulation that purports to demonstrate that human hunting alone adequately explains Late Pleistocene megafaunal extinction patterns. Alroy's results have sometimes been interpreted (e.g., Koch, 2006) as lending strong support to the overkill hypothesis (i.e., that extinctions resulted from overhunting by humans) as first articulated by Martin (1967) and later refined and modeled by Mosimann and Martin (1975). Our research indicates that such an interpretation of the modeling evidence is premature and potentially incorrect. Alroy's (2001) model performs slightly better than a simplest case "model" that separates North American mammals into two groups based on mass – with a boundary between 118 kg and 223 kg – and assumes that all species above this threshold went extinct while all those below it survived (Fig. 1).

In part, Alroy (2001) assesses his model by comparing its outcomes to those of this simple one-line method. Delineating such an extinction boundary on the basis of mass correctly predicts 30 of 41 (73%) of actual survival–extinction outcomes, while Alroy's mechanistic model correctly predicts 32 of 41 (78%) of outcomes (Alroy, 2001). Alroy's simulation brings a welcome element of ecological interactivity to Late Pleistocene extinction modeling, particularly in regard to its linkage

between predator hunting success and predator reproduction. However, because the model simultaneously incorporates multiple complicating factors and is not an open access resource, it remains unclear how the simulation achieves this slight improvement over a simplest case approach. Part of the improvement might result from assumptions about the initial abundances of rarer species with limited geographic ranges (i.e., the pronghorns *Stockoceros conklingi* and *Stockoceros onusrosagris*) (J. Alroy, personal communication, 2006). Critiques of common modeling approaches (e.g., Ginzburg and Jensen, 2004) suggest that part of the improvement might also result from over parameterization (i.e., "fitting" a model to a particular data set by adding numerous unconstrained parameters). Such a suggestion is partially borne out by the depiction of the numerous parameter combinations that were run in achieving a best match to historical data (Alroy, 2001).

Many different models can explain a given situation (e.g., Brook and Bowman, 2004; Ginzburg and Jensen, 2004), but the consequences of this fact have been overlooked in the recent debate about Late Pleistocene extinctions. In the absence of transparency and simplicity, competing models have very limited means of distinguishing themselves. Given enough freedom to add parameters or assume particular values for critical parameters, a competent modeler can achieve a desired result, whether that is general extinction or survival of megafauna facing human hunting pressure. But a simple model that performs well from the outset is generally a more significant achievement than a highly

Species	Mass (kg)	Outcome	Species	Mass (kg)	Outcome
<i>Capromeryx minor</i>	21	E	<i>Bison bison</i>	422	S
<i>Pecari tajacu</i>	30	S	<i>Equus complicatus</i>	439	E
<i>Oreamnos harringtoni</i>	45	E	<i>Alces alces</i>	457	S
<i>Platygonus compressus</i>	53	E	<i>Cervacles scotti</i>	486	E
<i>Stockoceros conklingi</i>	53	E	<i>Euceratherium collinum</i>	499	E
<i>Stockoceros onusrosagris</i>	54	E	<i>Cervus elaphus</i>	500	S
<i>Rangifer tarandus</i>	61	S	<i>Bison priscus</i>	523	E
<i>Tetrameryx shuleri</i>	61	E	<i>Equus niobrarensis</i>	533	E
<i>Antilocapra americana</i>	68	S	<i>Equus scotti</i>	555	E
<i>Mylohyus fossilis</i>	74	E	<i>Equus occidentalis</i>	574	E
<i>Oreamnos americanus</i>	91	S	<i>Nothrotheriops shastensis</i>	614	E
<i>Ovis canadensis</i>	91	S	<i>Glyptotherium floridanum</i>	666	E
<i>Odocoileus virginianus</i>	107	S	<i>Bootherium bombifrons</i>	753	E
<i>Odocoileus hemionus</i>	118	S	<i>Camelops hesternus</i>	995	E
<i>Navahoceros fricki</i>	223	E	<i>Megalonyx jeffersonii</i>	1320	E
<i>Hemiauchenia macrocephala</i>	238	E	<i>Paramylodon harlani</i>	1990	E
<i>Paleolama mirifica</i>	245	E	<i>Mammuthus primigenius</i>	3174	E
<i>Ovibos moschatus</i>	286	S	<i>Mammut americanum</i>	3298	E
<i>Equus conversidens</i>	306	E	<i>Mammuthus columbi</i>	5827	E
<i>Holmesina septentrionalis</i>	312	E			
<i>Tapirus veroensis</i>	324	E			
<i>Equus francisi</i>	368	E			
			<b>Surviving (Extant)</b>	=	<b>S</b>
			<b>Extinct</b>	=	<b>E</b>

Fig. 1 – Simple one-line method of predicting Late Pleistocene mammalian extinctions in North America. Alroy (2001) achieves two additional correct outcome matches than this simplest-case method but does so at the expense of considerable complexity and lost transparency. Data and method from Alroy (2001).

parameterized model that reaches some desired goal after considerable trial and error in fitting to data (Ginzburg and Jensen, 2004).

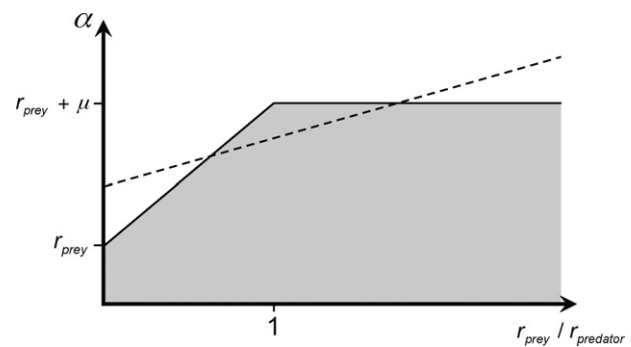
### 3. Berezovskaya–Karev–Arditi (BKA) space and the two-line method

Common sense suggests that larger species would be at greater risk of extinction, because greater mass correlates with numerous traits that increase extinction risk (e.g., decreased maximal rate of population increase,  $r_{\max}$ , increased home range size, reduced population size) (e.g., Peters, 1983; Johnson, 2002). Amongst the heaviest species (i.e.,  $\geq 500$  kg), both Alroy's simulation and the single-line method perform very well. Granted, there are exceptions, but those are to be expected; mass correlates with many ecologically relevant traits but not with all of them.

Both the single-line method and the Alroy simulation perform poorly in predicting survival–extinction outcomes among smaller species (i.e., those weighing  $\leq 55$  kg). Although common sense suggests that smaller species should be at reduced risk of extinction, a cluster of extinctions occurred amongst these species. Intriguingly, however, ratio-dependent functional response assumptions predict increased risk of extinction at higher and lower prey masses with reduced extinction risk at intermediate masses, thus laying the groundwork for a promising alternative modeling approach.

Berezovskaya et al.'s (2001) elucidation of ratio-dependent parameter space in single-predator, single-prey systems provides the intuition for envisioning the more complex parameter space of multi-prey systems. While the actual dynamics of systems involving three or more species might differ from those predicted by Berezovskaya–Karev–Arditi (BKA) space, the math necessary to visualize that parameter space does not exist. As a practical matter, then, we must begin our inquiry by relying on the math we have and the intuition it reveals. We have rescaled the original BKA parameter space so that the x-axis represents the ratio of prey  $r_{\max}$  to predator  $r_{\max}$ ; the y-axis remains unchanged in defining  $\alpha$ , the capture efficiency of human hunters in dealing with prey (Fig. 2 and Appendix A).

Within the gray parameter space, predator and prey coexist, while extinctions occur within the white parameter space. Because  $r_{\max}$  is inversely correlated with body mass, heavier species occur to the left of the x-axis and lighter species occur to the right. At the point labeled “1,”  $r_{\max}$  values for predator and prey are identical. The dotted line represents the simplest possible version of the assumed relationship between capture efficiency and  $r_{\max}$ /mass, i.e., smaller prey species are assumed to be relatively easier to capture than megafaunal species. (If the converse is assumed, megafaunal extinction is an inevitable outcome that need not be modeled.) Although represented as a straight line, the line may not be. Presumably for human hunters the line must both start at and eventually return to zero: humans are not known to prey selectively on mice-, vole-, and shrew-sized species, because the caloric costs of such hunting exceed the benefits. Two implicit assumptions of our analysis are that all prey species considered are within the size range hunted by humans and that



**Fig. 2 – Berezovskaya–Karev–Arditi Ratio-dependent parameter space and its predicted extinction/coexistence zones, where  $\alpha$  is the predator's capture efficiency of the prey species,  $r_{\text{prey}}$  is the prey species' maximal rate of population increase;  $\mu$  is the predator's death rate in the absence of prey; and  $r_{\text{predator}}$  is the predator species' maximal rate of population increase. Areas in yellow represent parameter space permitting coexistence between predator and prey; areas in white represent ecologically unstable parameter space within which extinction will occur. The dotted line indicates that when moving from left to right along a gradient of increasing capture efficiency and prey-to-predator maximal rate of population increase, two extinction-prone regions bracket a region of coexistence.**

prey mass correlates with susceptibility to capture by human hunters.

The adaptation of BKA space we present provides an empirical basis for expecting that Late Pleistocene prey species of intermediate mass would have been more likely to persist, while those of greater and lesser mass would have faced an increased extinction risk. The relation between body mass and  $r_{\max}$  in BKA space suggests a refinement to the single-line method of predicting extinctions based on body mass: using two lines rather than one to subdivide the prey species list and predicting extinctions both above the higher and below the lower mass thresholds (Fig. 3).

The specific parameter values for  $\alpha$  remain unknown. As yet, we have no reliable method of ascertaining the capture efficiencies of vanished Paleoindian or aboriginal societies. Nor has a specific allometric relationship been defined that would allow modelers to estimate capture efficiency based on the mass of prey species. The current project explores reasonable ranges of these two unknown parameters. While the lack of empirically constrained parameter values precludes specificity, the relationship we identify offers a simple, reasonable empirical prediction of general anticipated extinction patterns. That is, although modelers lack  $\alpha$  values and so cannot predict in advance exactly where the boundaries between extinction and coexistence occur, we have a more accurate method of predicting the overall extinction–persistence pattern and have gone some way toward explaining its ecological underpinning. Under the prevailing circumstances of parametric uncertainty, this simple prediction recommends itself for at least two reasons. First, it follows from a fully transparent model that is amenable to scrutiny or modification. Second, the model does not rely on over-fitting or claim greater



Species	Mass (kg)	Outcome	Species	Mass (kg)	Outcome
<i>Capromeryx minor</i>	21	E	<i>Bison bison</i>	422	S
<i>Pecari tajacu</i>	30	S	<i>Equus complicatus</i>	439	E
<i>Oreamnos harringtoni</i>	45	E	<i>Alces alces</i>	457	S
<i>Platygonus compressus</i>	53	E	<i>Cervacles scotti</i>	486	E
<i>Stockoceros conklingi</i>	53	E	<i>Euceratherium collinum</i>	499	E
<i>Stockoceros onusrosagris</i>	54	E	<i>Cervus elaphus</i>	500	S
<i>Rangifer tarandus</i>	61	S	<i>Bison priscus</i>	523	E
<i>Tetrameryx shuleri</i>	61	E	<i>Equus niobrarensis</i>	533	E
<i>Antilocapra americana</i>	68	S	<i>Equus scotti</i>	555	E
<i>Mylohyus fossilis</i>	74	E	<i>Equus occidentalis</i>	574	E
<i>Oreamnos americanus</i>	91	S	<i>Nothrotheriops shastensis</i>	614	E
<i>Ovis canadensis</i>	91	S	<i>Glyptotherium floridanum</i>	666	E
<i>Odocoileus virginianus</i>	107	S	<i>Bootherium bombifrons</i>	753	E
<i>Odocoileus hemionus</i>	118	S	<i>Camelops hesternus</i>	995	E
<i>Navahoceros fricki</i>	223	E	<i>Megalonyx jeffersonii</i>	1320	E
<i>Hemiauchenia macrocephala</i>	238	E	<i>Paramylodon harlani</i>	1990	E
<i>Paleolama mirifica</i>	245	E	<i>Mammuthus primigenius</i>	3174	E
<i>Ovibos moschatus</i>	286	S	<i>Mammut americanum</i>	3298	E
<i>Equus conversidens</i>	306	E	<i>Mammuthus columbi</i>	5827	E
<i>Holmesina septentrionalis</i>	312	E			
<i>Tapirus veroensis</i>	324	E	<b>Surviving (Extant)</b>	=	<b>S</b>
<i>Equus francisi</i>	368	E	<b>Extinct</b>	=	<b>E</b>

**Fig. 3 – Two-line method of predicting Late Pleistocene mammalian extinctions.** This simplified, intuitive approach achieves two more correct outcome matches than [Alroy's \(2001\)](#) opaque and much more complex method. Data from [Alroy \(2001\)](#).

precision than prevailing parameteric uncertainty can justify. It is a simpler modeling tool but one that has the potential to work.

#### 4. Methods

To test our hypothesis, we explored the parameter space dynamics of a multi-prey system. We developed a one-predator, six-prey deterministic numerical simulation model relying on ordinary differential equations. The prey growth component generalizes as:

$$\frac{dN_i}{dt} = r_{\max_i} N_i \left( 1 - \frac{N_i}{K_i} \right) - f(\cdot)_i P, \quad (1)$$

where  $i = 1, 2, \dots, 6$  with  $i$  representing the  $i$ th prey species,  $N$  is the population size,  $K$  is the carrying capacity,  $f(\cdot)_i$  represents the functional response form for the predator's capture of the  $i$ th prey species, and  $P$  is the predator density.

To determine whether functional response choices incorporating predator interference or prey sharing would provide a better match to observed extinction patterns, we tested the model under three different functional response assumptions: the Holling Disc Equation ("Type II" Prey Dependence, which does not include predator interference), Beddington–DeAngelis (a simple derivative of the Holling Disc Equation incorporating a predator interference parameter,  $i$ , which provides a measure of the time spent interacting

with other predators), and Ratio Dependence (which assumes complete sharing of prey among predators, an assumption consistent with a technologically sophisticated, cooperatively foraging omnivore exploiting available prey) (see [Table 1](#) for a summary comparison of how the current model compares to other major published Late Pleistocene extinction models).

Holling Disc/Type II functional response is represented by the expression:

$$f(N)_i = \frac{a_i N_i}{1 + \sum_{i=1}^6 a_i h_i N_i}, \quad (2)$$

where  $a$  is the predator capture efficiency and  $h$  is the handling time (i.e., the time between a predator capturing one prey item and the next). The Beddington–DeAngelis elaboration of Holling Type II is represented by the expression:

$$f(N, P)_i = \frac{a_i N_i}{1 + \sum_{i=1}^6 a_i h_i N_i + i P}, \quad (3)$$

The final functional response form, Ratio Dependence, is represented by the expression:

$$f\left(\frac{N}{P}\right)_i = \frac{\alpha_i (N_i/P)}{1 + \sum_{i=1}^6 \alpha_i (N_i/P)}, \quad (4)$$

where  $\alpha$  is the predator capture efficiency.

**Table 1 – Summary comparison of major Late Pleistocene extinction models.**

Model	Number of prey species modelled	Form of model	Dynamic interaction in predator–prey demographics?	Functional response form	Full and transparent presentation of model
Budyko (1967, 1974)	1	Differential equation	No	Unrelated to prey density	Yes
Mosimann and Martin (1975)	1	Difference equation	No	Unrelated to prey density	No
Whittington and Dyke (1984)	1	Difference equation	No	Unrelated to prey density	No
Belovsky (1987, 1988)	2 (hunted food, gathered food)	Difference equation	Yes	Special case	Yes
Winterhalder et al. (1988)	1 or 2	Difference equation	Yes	Special case	No
Winterhalder and Lu (1997)	Up to 4	Difference equation	Yes	Special case	No
Choquenot and Bowman (1998)	1	N/A	No	Holling II	No
Alroy (2001)	42	Difference equation	Yes	Unique form	No
Brook and Bowman (2002)	1	Difference equation	No	Holling III	No
Brook and Bowman (2004)	1	Difference equation	No	Holling III	No
Yule et al. (2009)	6	Differential equation	Yes	Holling II, Beddington–DeAngelis, and Ratio Dependence	Yes

**Table 2 – Prey Species Included in Models.**

Species	Mass (kg)	Status
<i>Capromeryx minor</i> (Diminutive pronghorn)	21	Extinct
<i>Pecari tajacu</i> (Collared peccary)	30	Surviving
<i>Odocoileus hemionus</i> (Mule deer)	118	Surviving
<i>Equus conversidens</i> (Mexican horse)	306	Extinct
<i>Megalonyx jeffersonii</i> (Jefferson's ground sloth)	1320	Extinct
<i>Mammuthus columbi</i> (Columbian mammoth)	5827	Extinct

The change in density of human predators is described by the model's final equation:

$$\frac{dP}{dt} = \sum_{i=1}^6 e_i FR_i - 0.067P, \quad (5)$$

where  $e$  is the predator conversion rate of prey to offspring and 0.067 is the predator death rate in the absence of prey. Here, the predator growth rate is determined by the summation of prey offtake minus a death rate in the absence of prey, creating an explicit link between predator success and reproduction.

The six prey species we consider include both extant and extinct species (Table 2). They were selected both to provide a range of size classes and to include species that bracket historical survival–extinction outcomes that are difficult to explain solely on the basis of allometric relationships between body mass and  $r_{\max}$  (Fig. 1). The species are: *Capromeryx minor* (21 kg), *Pecari tajacu* (30 kg), *Odocoileus hemionus* (118 kg), *Equus conversidens* (306 kg), *Megalonyx jeffersonii* (1320 kg), and *Mammuthus columbi* (5827 kg).

We constrained all parameters using established allometric relationships when such relationships were known or by making explicit assumptions (Table 3). One key allometry remains undefined: the relationship between prey mass and predator efficiency in capturing prey. Our secondary goal in constructing the model was to explore the unknown allometry for capture efficiency, which involves two unconstrained parameters: the capture efficiency constant and capture efficiency allometric scaling power. While the two varieties of capture efficiency that occur in the functional response forms we explore are analogous in terms of their biological meaning, they have different units and so are not directly comparable. In the Holling II and Beddington–DeAngelis functional responses, capture efficiency is denoted by  $a$  and is measured in units of  $1/\text{time} \times \text{individual}$ . Under Ratio Dependence, capture efficiency is denoted by  $\alpha$  and is measured in units of  $1/\text{time}$ . Regardless of units, the postulated allometric relationship between prey body mass,  $m_i$ , and capture efficiency are analogous, depending on some capture efficiency power, PowerCE, for both functional response forms and one of two constants,  $C_a$  and  $C_\alpha$ , which differ between the two functional response forms, as follows:

$$a = C_a m_i^{\text{PowerCE}} \quad (6)$$

$$\alpha = C_\alpha m_i^{\text{PowerCE}} \quad (7)$$

Without assuming that  $C_a = C_\alpha$ , we explored various estimates of  $C_a$ ,  $C_\alpha$ , and PowerCE by testing a wide range of parameter

**Table 3 – Parameterizations—allometric constraints and assumptions.**

Parameter	Allometric power assumed	Source
$r_{\max}$ (maximal rate of population increase)	–0.36	Caughley and Krebs (1983)
$K$ (carrying capacity)	–0.75	Damuth (1987)
$e$ (conversion efficiency)	1	Assumption: all herbivore flesh has equal per kg nutritional value
$h$ (handling time)	1	Assumption: time to prepare and digest herbivore flesh is proportional to its mass
$a$ or $\alpha$ (capture efficiency)	Unknown	The parameter our model explores

combinations and evaluating the match between simulated and actual extinction outcomes.

Our approach involved no difficulties for the Holling Type II and Beddington–DeAngelis models, but one aspect of the ratio-dependent model requires clarification in regard to a potential complicating factor. The ratio-dependent functional response contains the rational expression:

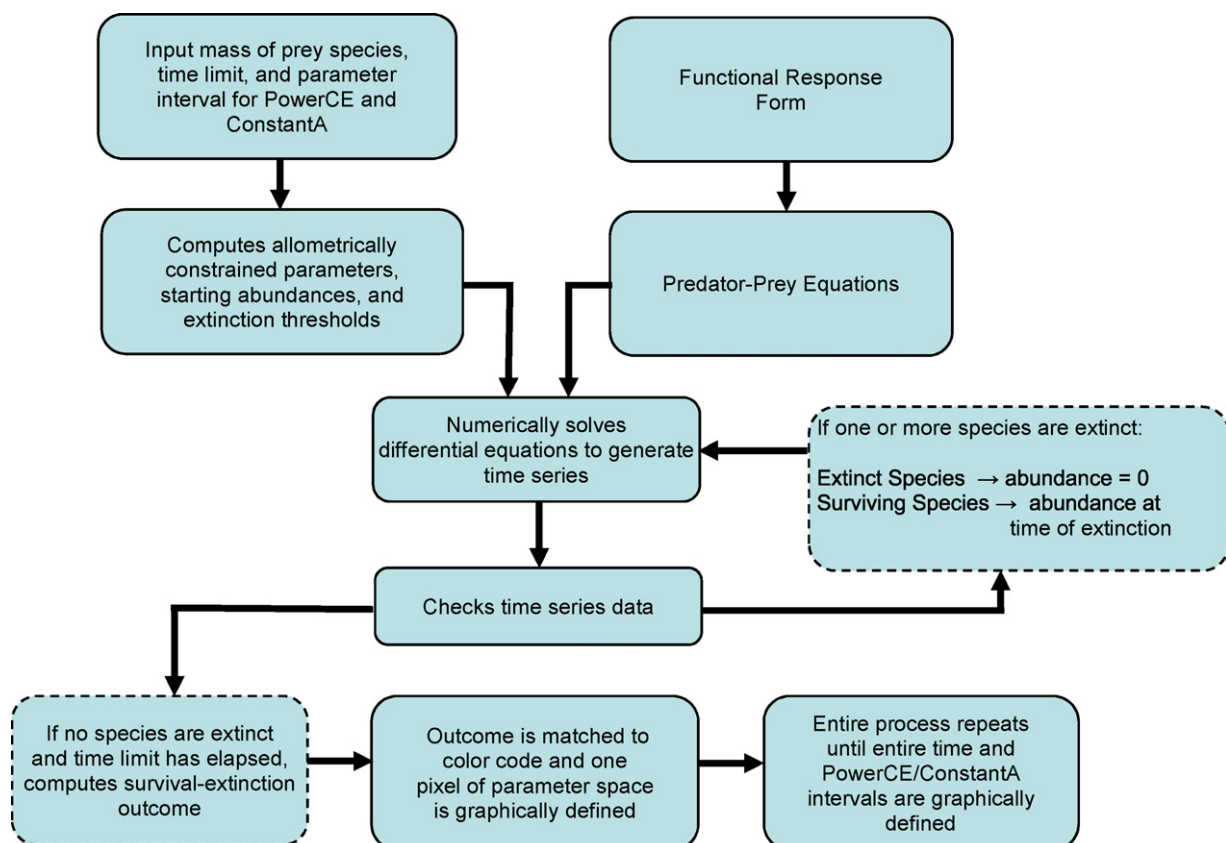
$$\frac{\alpha(N/P)}{1 + \alpha h(N/P)}$$

Because the predator density,  $P$ , reaches zero for a variety of parameterizations, the expression  $(N/P)$  becomes meaningless, causing the numerical simulation algorithm to produce error messages. We addressed this issue by designing the model to set functional response to zero when  $P$  equals zero.

Simulations were performed using a *Mathematica* notebook composed of three modules. The first module performs numerical simulations representing the interaction between human predators and six prey species. The model requires

nine input parameters that were held constant between all simulations: initial predator abundance (defined as a density of 0.1 per km<sup>2</sup>), predator extinction threshold (defined as a density of 0.01 per km<sup>2</sup>), the mass of the each of the six prey species, and the number of one-year time steps (500). The initial module computes remaining parameters (i.e., carrying capacity,  $r_{\max}$ , conversion efficiency, handling time) using established allometric relationships or stated assumptions (Table 3).

The output of this model is a set of six lists, each one representing a time series of abundances for the six prey species and the population of human predators. The second module analyzes these lists and looks for extinction events, which are defined as any prey population that decreases to 5% or less of its carrying capacity. (Human carrying capacity is not defined *a priori* but is instead determined by hunting success.) Once an extinction event is discovered, all other abundances are set to the abundance at the time of the extinction event.



**Fig. 4 – Model flow chart.**

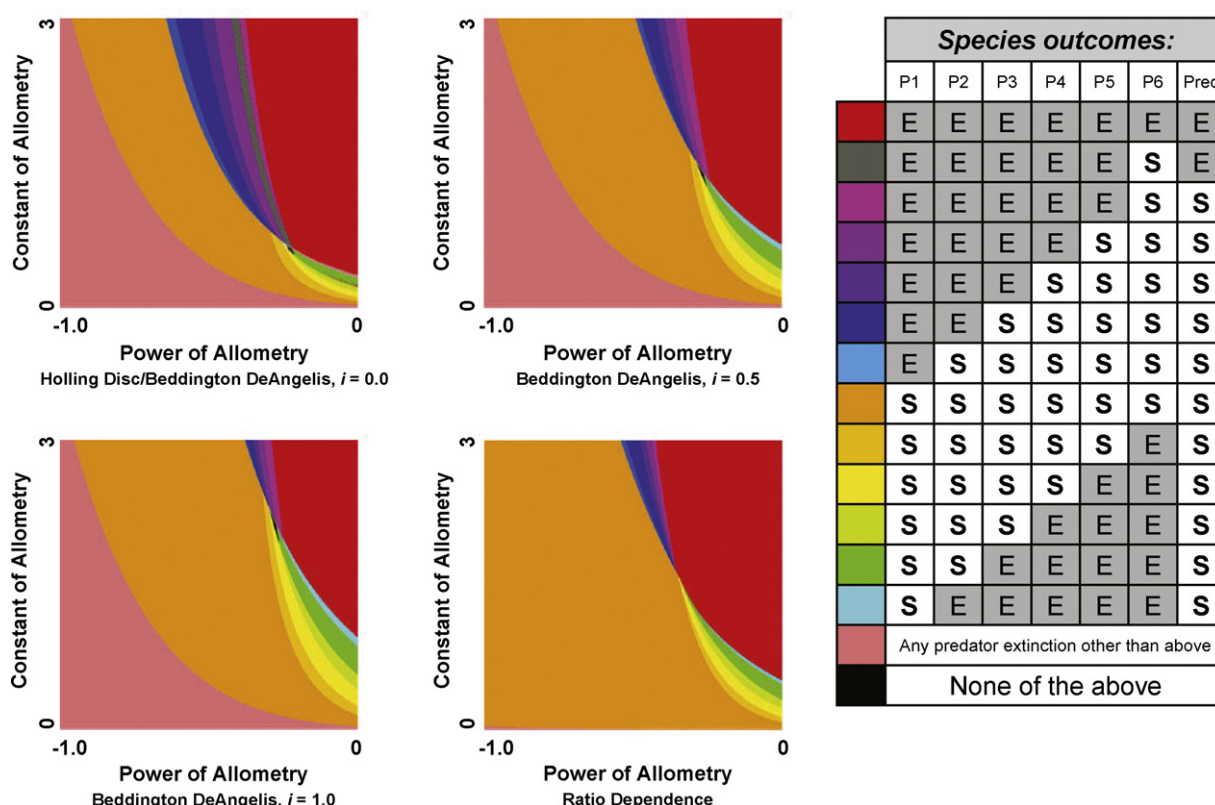


Fig. 5 – Survival–extinction outcomes.

The third module defines parameter space in two dimensions: (1) the allometric constant for capture efficiency ( $C_a$  or  $C_\alpha$ ) and (2) the allometric power for capture efficiency (PowerCE). For each combination of parameters, the module performs a numerical simulation and checks for extinction, reiterating this process until all species are extinct or all remaining species coexist for the full 500-year simulation (Fig. 4). Exploring the two dimensions of the capture efficiency allometry, this module color-codes each outcome and creates a graphical representation of system stability (Fig. 5).

All simulations were performed using *Mathematica* version 6.0.2.1 and are available on request from the corresponding author.

## 5. Results

Changes in functional response form yielded only minimal qualitative differences in survival–extinction patterns (Fig. 5). Observed differences in the juxtaposition of particular outcomes occurred in only a small portion of the total parameter space that we have no *a priori* justification for identifying as being particularly biologically relevant. Because we do not know where reality falls in the parameter space, we have no basis for suggesting that the particular outcomes associated with particular parameter combinations represent or approximate actual events.

Survival–extinction outcomes depend on the combined absolute magnitudes of hunting pressure ( $C_a$  or  $C_\alpha$ ) and the relative susceptibility of prey species to human hunters,

PowerCE. Total extinction occurs in the top right region of parameter space, where capture efficiency is highest and prey mass has the least influence on how easy a prey item is to capture. Predator extinction occurs in the bottom left region of parameter space, where capture efficiency is lowest and the highest mass prey species are significantly more difficult to capture. Predator–prey coexistence occurs in regions of intermediate capture efficiency. The transition from coexistence varies between functional response forms but occurs in the general region of  $\text{PowerCE} > -0.35$ , depending on the overall intensity of hunting pressure ( $C_a$  or  $C_\alpha$ ). Where  $\text{PowerCE} < -0.35$ , stepwise extinctions eliminate species from smallest to largest when hunting pressure is greatest. Where  $\text{PowerCE} > -0.35$ , stepwise extinctions eliminate species from largest to smallest at lower levels of hunting pressure. Increasing levels of predator interference lead to increasing system stability (i.e., a larger region of coexistence). At higher interference levels, the transition that dominates the region of parameter space explored is the extinction of high mass prey. At lower interference levels, the transition that dominates is the extinction of low mass prey. We observed no parameter combinations yielding the result predicted by the BKA hypothesis.

## 6. Discussion

The model we present assumes a starting human population density of 0.1 per  $\text{km}^2$  in North America, depicting a scenario in which hunters and prey form a well-mixed system.



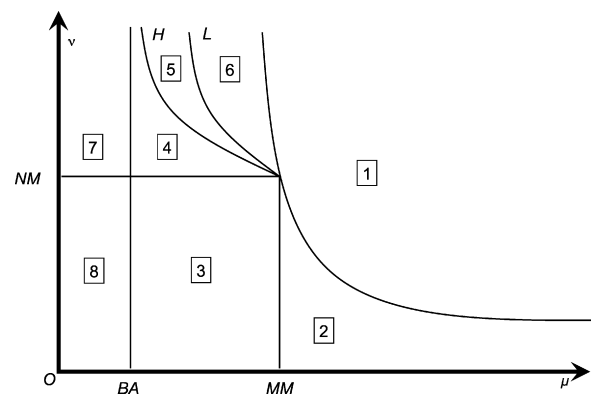
Hunters take prey nonselectively on the basis of availability (i.e., more abundant prey are more likely to be encountered and hunted than rare prey; no prey species are given particular priority). The model then explores extinction dynamics over a 500-year period of hunting. A spatially explicit model following the movements of an advancing front of hunters – as per Mosimann and Martin (1975) or Alroy (2001) – might more realistically depict some aspects of predator–prey interactions. But for present purposes our approach recommends itself for at least three reasons.

First, our goal was to examine the effects of functional response in the absence of other factors; assuming a well-mixed system achieves that goal. Second, while adding a spatially explicit component to the model might increase or decrease extinction probabilities, it would probably not affect the pattern of extinctions, and our goal was to assess patterns. Third, given the prevailing uncertainty about the time(s) and route(s) of human entry into North America and growing knowledge of both Paleoindian foraging and the duration of human–megafauna sympatry (e.g., Graf and Schmitt, 2007; Mithen, 2004; Webb, 2006), our starting assumptions may reasonably approximate reality. Under the circumstances, then, the current model allows for a preliminary assessment of functional response's potential role in clarifying Pleistocene extinction patterns.

In our simulations, the coexistence transition that occurs in the region of  $\text{PowerCE} = -0.35$  represents the tipping point between the relative importance of prey  $r_{\max}$  and predator capture efficiency. When  $\text{PowerCE} < -0.35$ , larger prey are so much more difficult to capture than smaller prey that they persist despite their relatively low  $r_{\max}$  values. Conversely, smaller species are eliminated despite their relatively high  $r_{\max}$  values because of the extremely high hunting pressure they face. When  $\text{PowerCE} > -0.35$ , larger prey are only marginally more difficult to capture than smaller prey, and their relatively low  $r_{\max}$  values cannot compensate for hunting pressure. Conversely, in this region of parameter space the relatively high  $r_{\max}$  values of smaller species are sufficient to compensate for the reduced hunting pressure they face.

We find no support for the hypothesis that ratio-dependent functional response offers a superior explanation for Late Pleistocene extinction patterns. All functional response variants demonstrate that the “single line” hypothesis provides a reasonable baseline explanation for the extinction of either larger or smaller prey species, depending on the relative magnitudes of hunting pressure and prey  $r_{\max}$  but not simultaneously in a manner that would provide a closer match to observed extinction patterns. This negative finding raises a matter of considerable importance in a broader modeling context. Appropriate functional response choice is considered to be critical for achieving ecologically realistic outcomes in predator–prey models (e.g., Skalski and Gilliam, 2001; Fenlon and Faddy, 2006). Yet our results indicate a predator–prey context in which survival–extinction outcomes are relatively insensitive to varied functional response choice.

We are left to explain the inability of all models to match observed survival–extinction outcomes. If our results are correct, differences in functional response cannot account for these shortcomings. Our results may represent evidence that the functional response predictions of obligate predator–prey



**Fig. 6 – Original representation of Ratio-Dependent parameter space from Berezovskaya et al. (2001).**

systems do not apply to multi-prey systems. It is also possible that predation alone cannot account for Late Pleistocene extinction patterns, which would lend credence to extinction scenarios involving predation along with other anthropogenic or climate-related causes. It may also be that adding additional complexity to the models (e.g., spatially explicit movement of prey and predators, initial species abundance estimates based on fossil data) would increase the fidelity of model predictions.

That our simulations fail to match historical survival–extinction patterns could also expose the limits of parameterizing such models. While we agree that allometric relationships between body mass and relevant life history traits underpin Late Pleistocene extinctions (Johnson, 2002; Brook and Bowman, 2005) and represent the best available means of constraining Late Pleistocene extinction models, we observe no fundamental differences in mass-based survival–extinction outcomes in the models we assess. We suggest the possibility that the best tool available to us in constraining parameter values may be insufficient. Allometric relationships resolve in log scale regressions of a wide range of values—a level of resolution that allows for one to two orders of magnitude of uncertainty when assigning parameter values to organisms of a particular mass range. Allometries are liable to break down in the relatively small range between the smallest (21 kg) and largest (5827 kg) prey species we consider here (Table 2). Such uncertainty allows for a wide range of plausible outcomes, irrespective of functional response choice.

The one-line method follows biological intuition in explaining higher extinction risk to be a consequence of the lower maximal reproductive rates characteristic of larger species. One plausible explanation for the failure of the current model would be to assume that species violating expectations were in one or more respects also biologically idiosyncratic in violating allometric assumptions. Given the freedom to assume that particular prey species violate allometric assumptions for one or more parameters, it would be possible to exactly match observed survival–extinction outcomes (Fig. 1). But assuming idiosyncratic parameter values without any empirical basis would represent an egregious form of over-fitting. Given our limited knowledge of the biological characteristics of extinct species, such a model would be unfalsifiable. We are left to conclude that allometric constraint

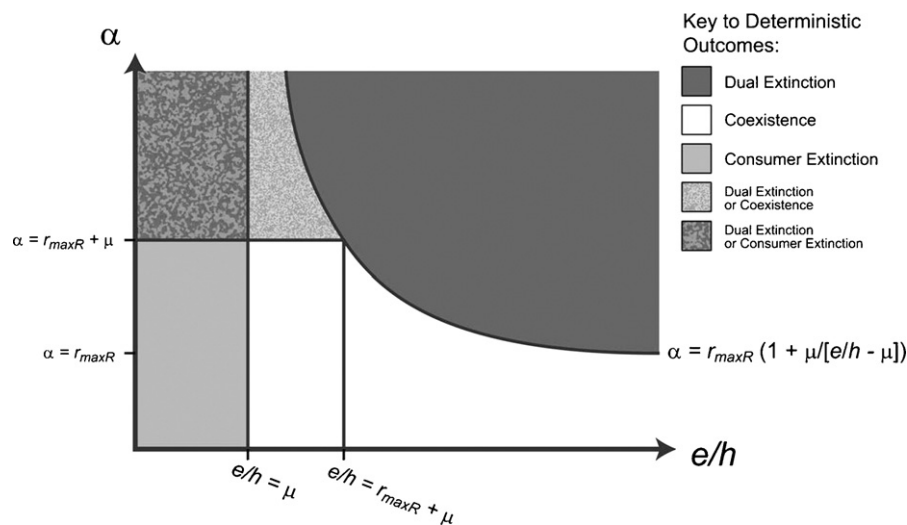


Fig. 7 – Preliminary back-transformation of Berezovskaya et al. (2001) parameter space, where  $\alpha$  is the capture efficiency,  $\mu$  is the predator death rate,  $h$  is the handling time,  $e$  is the conversion efficiency, and  $r_{\max R}$  is the maximum intrinsic growth rate of the prey. Note that certain regions of parameter space have variable outcomes that depend on initial conditions.

in Late Pleistocene extinction modeling involves serious and perhaps insurmountable limitations, a novel observation. Analysis of experimental predator–prey time-series trajectories are often insufficient to distinguish between alternative functional responses (Lundberg and Fryxell, 1995; Jost, 1998). Logic suggests that parameterizations based solely on allometric patterns would allow for even less certainty.

Capture efficiency remains the most problematic parameter in Pleistocene extinction modeling. It can neither be computed by studying extant hunter-gatherers (who occupy relatively depauperate ecosystems and, to varying degrees, rely on modern technologies) nor estimated by studying archaeological evidence (which cannot provide the temporal resolution necessary to compute rates of prey offtake) (Winterhalder and Lu, 1997). Nor is it clear how prey naiveté influenced capture efficiency. Opinion is split as to whether

megafauna were naïve and therefore particularly vulnerable to newly arrived human predators (e.g., Mosimann and Martin, 1975) or not (e.g., Wroe et al., 2004; Koch and Barnosky, 2006). Our models consider a range of possible capture efficiencies, and in so doing encompass this wide range of opinion. But our research reveals no additional insights into the constraint of the capture efficiency parameter.

We suggest that Late Pleistocene extinction modeling should be subject to considerable skepticism both in terms of its ability to explain survival–extinction patterns and, more broadly, to support or refute particular extinction scenarios. Given the parameteric uncertainty involved, we consider it highly unlikely that Late Pleistocene extinction models will be capable of differentiating between extinction scenarios resulting from either single or multiple causes. We find no support for our hypothesis, because we observe no

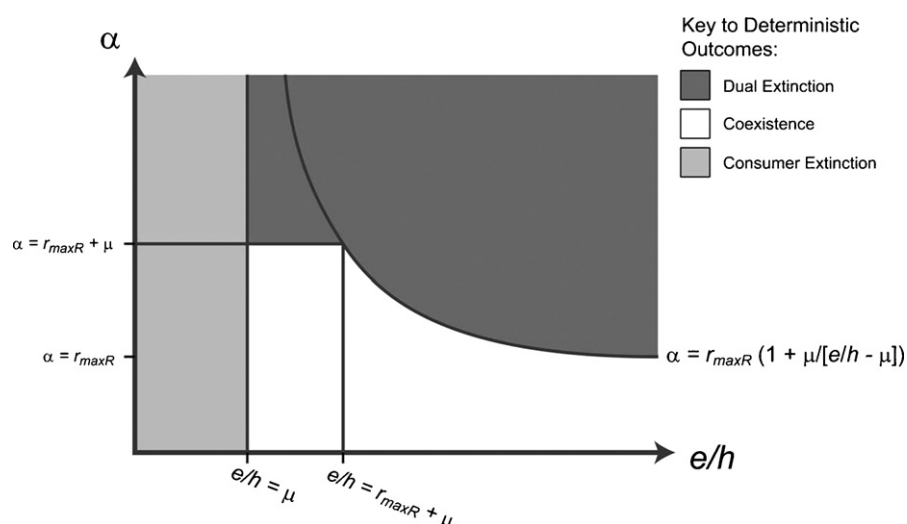


Fig. 8 – Simplification of Fig. 7 parameter space that assumes initial conditions which produce extinction prevail over those that produce coexistence.

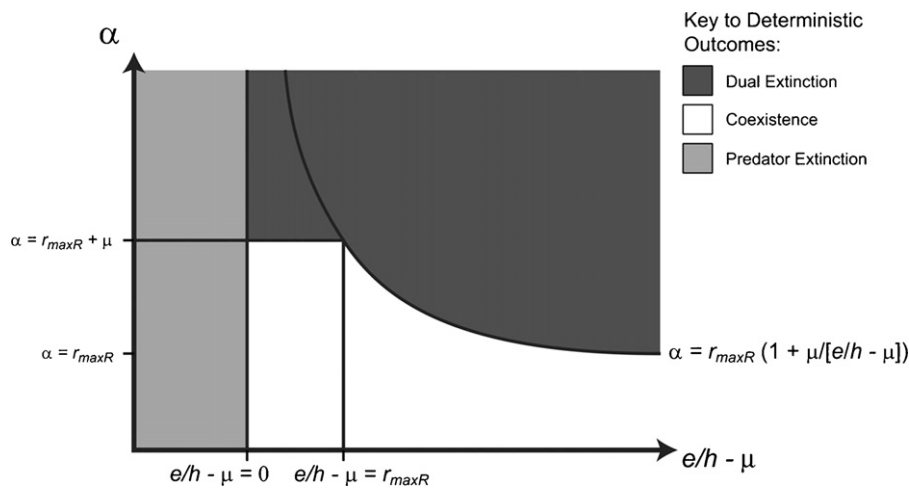


Fig. 9 – Result of transforming the x-axis of parameter space (defined as  $e/h$ ) by subtracting predator death rate,  $\mu$ .

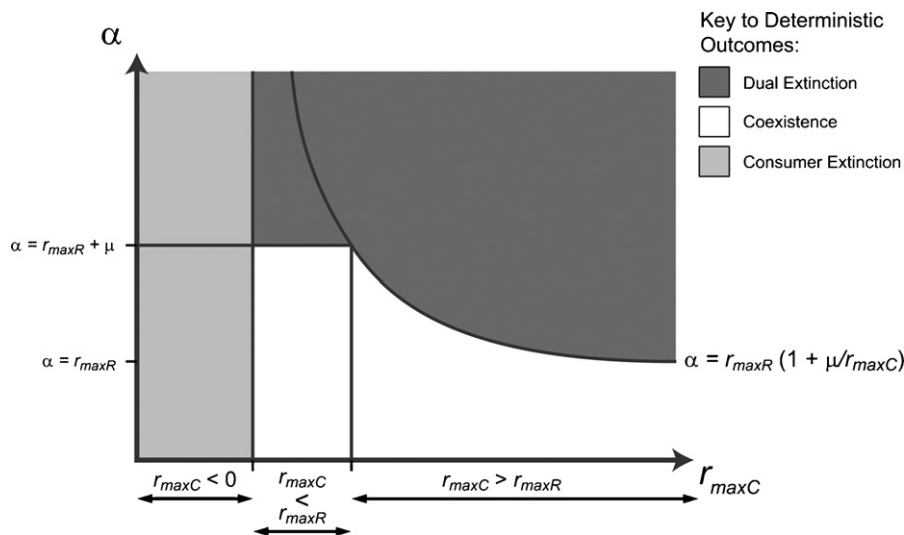


Fig. 10 – Reinterpretation of x-axis as  $r_{\max C}$ , maximum intrinsic growth rate of predators. The resulting three regions represent areas where predator populations either decline ( $r_{\max C} < 0$ ), grow more slowly than their prey ( $r_{\max C} < r_{\max R}$ ), or grow more rapidly than their prey ( $r_{\max C} > r_{\max R}$ ).

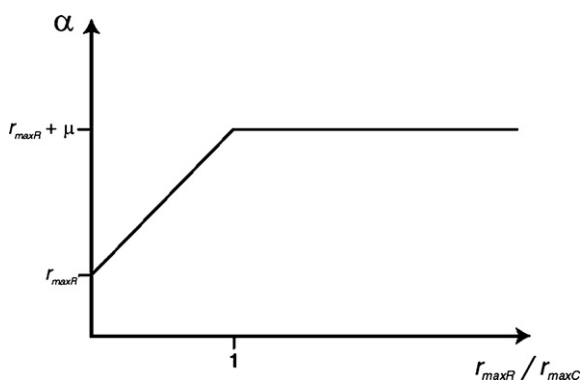


Fig. 11 – Final transformation: the x-axis is inverted and multiplied by  $r_{\max R}$  to produce an axis that explains stability in two regions of parameter space.

significant differences in outcomes resulting from altered functional response predictions. Under the circumstances, however, we cannot differentiate between three possible explanations for our negative result: (1) that our initial hypothesis is correct, (2) that some other functional response form might better explain Late Pleistocene survival–extinction patterns, or (3) that observed survival–extinction patterns are either unrelated or only partially related to functional response.

## 7. Conclusion

We present a simple, transparent hypothesis based on functional response choice that offers a general explanation for how human predation might have led to extinctions among larger and smaller prey species in Late Pleistocene North

America—an area where previous models have been unsuccessful. The numerical simulations we present do not fully support that hypothesis. Even using the best available methods for constraining parameterizations, the model we present suggests that the consequences of adopting different functional response forms in this modeling context are minimal. Such a result suggests to us a need for considerable caution in both the design and interpretation of Late Pleistocene extinction models.

Our findings suggest that simple predator–prey models alone – irrespective of functional response formulation – cannot explain the observed pattern of extinction and survival that emerges from the Late Pleistocene. Our simulations explored all reasonable allometric relationships between body mass and prey vulnerability but could not explain the particular susceptibility to extinction displayed by both the smallest and largest mammals modeled. This finding suggests that other factors need to be considered in order to fully explain these patterns. Including the full suite of 41 prey species, allowing for movement of predators and prey over space, assigning prey densities based on the fossil record, or various other modifications may improve the fit of the model. But such refinements must be made in a stepwise fashion so that the importance of each factor can be understood. In addition, any such additions must be based on reliable data and maximally constrained so as to avoid over-fitting.

We conclude that the difficulties with parameterization in Late Pleistocene extinction models are considerably more serious and pervasive than an occasional poorly computed value in one model or another (e.g., [Slaughter and Skulan, 2001](#)). For the foreseeable future, predator–prey models of Late Pleistocene ecosystems are unlikely to be precise enough to differentiate between different extinction scenarios, particularly those in which multiple factors (e.g., climate, hunting, anthropogenic habitat alteration) might be involved.

## Appendix A. Transformation of Berezovskaya, Arditi, and Karev (2001) parameter space

In their original publication ([Berezovskaya et al., 2001](#)), Berezovskaya, Arditi, and Karev present the parameter space of Ratio Dependence using their original transformed variables ([Fig. 6](#)).

These variables can be back-transformed into the more familiar parameters employed in predator–prey equations to indicate the qualitative outcomes expected within each region of the space ([Fig. 7](#)).

We further simplify this space by assuming that the initial conditions that produce extinction will always prevail over those that produce coexistence. This assumption is reasonable for assessing long-term stability: eventually most systems will venture into the region that produces extinction, so we only define coexistence in regions that persist at any set of initial conditions ([Fig. 8](#)).

In the previously discussed versions of parameter space, the x-axis is defined as  $e/h$ . We transform this axis by subtracting the predator death rate,  $\mu$  ([Fig. 9](#)). This transformation has two desirable effects: (1) it redefines the origin on the x-axis such that predators only persist in the system in the positive

region of the axis and (2) the x-axis becomes  $e/h - \mu$ , which has important biological meaning. In order to understand the meaning of this axis, we must first consider the inverse of handling time,  $1/h$ . This quantity represents the maximum consumption rate of predators. If we multiply this maximum growth rate by the conversion efficiency we get  $e/h$ , the maximum reproductive output of predators. Subtracting the death rate of predators, we obtain the maximum net growth rate of predators,  $e/h - \mu$ . The x-axis can therefore be interpreted as  $r_{\max C}$ , the maximum intrinsic growth rate of predators.

Using this new interpretation of the axis, three important regions of the  $r_{\max C}$  axis emerge ([Fig. 10](#)). These three regions represent areas where predator populations either decline ( $r_{\max C} < 0$ ), grow more slowly than their prey ( $r_{\max C} < r_{\max R}$ ), or grow more rapidly than their prey ( $r_{\max C} > r_{\max R}$ ).

To further understand how the prey and predator maximum growth rates affect system stability, we make a final transformation. We invert the x-axis and multiply it by the maximum growth rate of prey, producing an axis that explains stability in two regions ([Fig. 11](#)). To the left of the point where  $r_{\max R}/r_{\max C} = 1$ , predators grow more rapidly than their prey. To the right of  $r_{\max R}/r_{\max C} = 1$ , predators grow more slowly than their prey.

## REFERENCES

- Alroy, J., 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306, 70–75.
- Berezovskaya, F., Karev, G., Arditi, R., 2001. Parametric analysis of the ratio-dependent predator–prey model. *J. Math. Biol.* 43, 221–246.
- Brook, B.W., Bowman, D.M.J.S., 2004. The uncertain blitzkrieg of Pleistocene megafauna. *J. Biogeogr.* 31, 517–523.
- Brook, B.W., Bowman, D.M.J.S., 2005. One equation fits overkill: why allometry underpins both prehistoric and modern body size-biased extinctions. *Popul. Ecol.* 47, 137–141.
- Budyko, M.I., 1967. On the causes of the extinction of some animals at the end of the Pleistocene. *Soviet Geography* 8, 783–793.
- Budyko, M.I., 1974. *Climate and Life*. Academic Press, New York, 508 pp.
- Caughley, G., Krebs, C.J., 1983. Are big mammals simply little mammals writ large? *Oecologia* 59, 7–17.
- Damuth, J., 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* 31, 193–246.
- Fenlon, J.S., Faddy, M.J., 2006. Modelling predation in functional response. *Ecol. Model.* 198, 154–162.
- Ginzburg, L.R., Jensen, C.X.J., 2004. Rules of thumb for judging ecological theories. *Trends Ecol. Evol.* 19, 121–126.
- Graf, K.E., Schmitt, D.N. (Eds.), 2007. *Paleoindian or Paleoarchaic? Great Basic Human Ecology at the Pleistocene/Holocene Transition*. University of Utah Press, Salt Lake City, 300 pp.
- Grayson, D.K., 1984. Nineteenth-century explanations of Pleistocene extinctions: a review and analysis. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 5–39.
- Johnson, C.N., 2002. Determinants of loss of mammal species during the Late Quaternary “megafauna” extinctions: life



- history and ecology, but not body size. *Proc. R. Soc. Lond. B Biol.* 269, 2221–2227.
- Jost, C., 1998. Comparing Predator–Prey Models Qualitatively and Quantitatively with Ecological Time-Series Data. Institut National Agronomique Paris-Grignon, Paris-Grignon.
- Koch, P.L., 2006. Review of Twilight of the Mammoths by Martin. *P.S. Science* 311, 957.
- Koch, P.L., Barnosky, A.D., 2006. Late quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* 37, 215–250.
- Lundberg, P., Fryxell, J.M., 1995. Expected population density versus productivity in ratio-dependent and prey-dependent models. *Am. Nat.* 146, 153–161.
- Martin, P.S., 1967. Prehistoric overkill. In: Martin, P.S., Wright, H.E. (Eds.), *Pleistocene Extinctions: The Search for a Cause*. Yale University Press, New Haven, pp. 75–120.
- Mithen, S., 2004. *After the Ice: A Global Human History, 20,000–5000 BC*. Harvard University Press, Cambridge, 622 pp.
- Mosimann, J.E., Martin, P.S., 1975. Simulating overkill by Paleoindians. *Am. Sci.* 63, 304–313.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, 352 pp.
- Skalski, G.T., Gilliam, J.F., 2001. Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology* 82, 3083–3092.
- Slaughter, R.J., Skulan, J., 2001. Did human hunting cause mass extinction? *Science* 294, 1459–1462.
- Webb, S.D. (Ed.), 2006. *First Floridians and Last Mastodons: The Page-Ladson Site in the Aucilla River*. Springer, The Netherlands, 613 pp.
- Winterhalder, B., Lu, F., 1997. A forager-resource population ecology model and implications for indigenous conservation. *Conserv. Biol.* 11, 1354–1364.
- Wroe, S., Field, J., Jermin, L.S., 2004. Megafaunal extinction in the Late Quaternary and the global overkill hypothesis. *Alcheringa* 28, 291–331.