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

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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.

1. Introduction

Late Pleistocene megafaunal extinctions occurred globally over a period of roughly 50,000 years, most severely affecting large (≥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.

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

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).