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A REVIEW AND SYNTHESIS OF LATE PLEISTOCENE EXTINCTION  
MODELING: PROGRESS DELAYED BY MISMATCHES BETWEEN  
ECOLOGICAL REALISM, INTERPRETATION, AND  
METHODOLOGICAL TRANSPARENCY

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## ABSTRACT

Late Pleistocene extinctions occurred globally over a period of about 50,000 years, primarily affecting mammals of  $\geq 44$  kg body mass (i.e., megafauna) first in Australia, continuing in Eurasia and, finally, in the Americas. Polarized debate about the cause(s) of the extinctions centers on the role of climate change and anthropogenic factors (especially hunting). Since the late 1960s, investigators have developed mathematical models to simulate the ecological interactions that might have contributed to the extinctions. Here, we provide an overview of the various methodologies used and conclusions reached in the modeling literature, addressing both the strengths and weaknesses of modeling as an explanatory tool. Although late Pleistocene extinction models now provide a solid foundation for viable future work, we conclude, first, that single models offer less compelling support for their respective explanatory hypotheses than many realize; second, that disparities in methodology (both in terms of model parameterization and design) prevent meaningful comparison between models and, more generally, progress from model to model in increasing our understanding of these extinctions; and third, that recent models have been presented and possibly developed without sufficient regard for the transparency of design that facilitates scientific progress.

## INTRODUCTION

LATE Pleistocene megafaunal extinctions occurred globally over a period of roughly 50,000 years, most severely affecting mammals of  $\geq 44$  kg body mass in Australia and the Americas (Barnosky et al. 2004). Eurasian species with low reproductive rates were also hard hit, supporting the conclusion that lower maximal intrinsic rate of population growth,  $r_{max}$ , rather than large body mass per se was the decisive factor contributing to extinctions (Johnson 2002). Polarized debate about the cause(s) of the extinctions dates back to the 19th century, centering on anthropogenic effects (especially hunting) and climate (Grayson 1984), with a variety of hypotheses being proposed to account for the observed extinction patterns.

Here we address one particular facet of the broader debate: testing explanatory hypotheses through rigorous, empirically based models. Our approach clarifies the nature and limitations of one body of relevant evidence while circumventing a static, polarized debate concerning the limited archeological evidence for human predation on extinct megafauna in North America (e.g., Grayson 2001; Grayson and Meltzer 2002; Fiedel and Haynes 2004) and, even moreso, Australia (e.g., Gillespie et al. 2006; Field et al. 2008, 2013; Wroe et al. 2013). In the current review, we focus on the modeling of human predation on herbivores. Extinctions among megafaunal predators and scavengers have not been modeled, since such spe-

cies losses are assumed to inevitably result from herbivore extinctions.

Martin (1967, 1973) hypothesizes that human hunting caused the extinctions via “overkill” (i.e., hunting caused prey mortality to exceed prey natality). “Blitzkrieg” refers to an overkill scenario under which a rapidly advancing front of specialized large game hunters colonize a continent and extinguish megafaunal prey as they occupy available territory (Martin 1973). Although the broader overkill scenario retains considerable explanatory value, the blitzkrieg scenario appears increasingly unlikely (Beck 1996; Koch and Barnosky 2006; Waters and Stafford 2007; Goebel et al. 2010; but see Brook and Bowman 2004).

Hypotheses focusing on human predation as a cause of extinction have been assessed via mathematical models since the 1960s (e.g., Budyko 1967, 1974; Mosimann and Martin 1975). Initial models were useful in demonstrating that human hunting represents a credible alternative explanation to climate change. Although the first models lacked ecological realism, they led to broader acceptance that human hunting could have played a part in the extinctions (e.g., Koch and Barnosky 2006; Yule 2009), laying the groundwork for future modeling efforts. More recent models have played an important role in advancing the debate about the causes of late Pleistocene extinctions (Barnosky et al. 2004), but fundamental challenges parameterizing megafaunal

extinction models pose significant difficulties.

By updating the last in-depth review of the late Pleistocene extinction modeling literature (Wesler 1981), the current paper sheds some much-needed light on the subject so that we can better assess how human hunting might have factored into those extinctions. Our analysis suggests that existing models are consistent with multiple extinction hypotheses and emphasizes the value of minimally complex, transparent, open-access modeling efforts.

#### THE LIMITS OF MODELING: PARAMETERIZATION

It has long been recognized that mathematical models alone can prove nothing about the respective roles or relative importance of anthropogenic effects and climate in late Pleistocene megafaunal extinctions (Mosimann and Martin 1975), although this point is often overlooked. Models can, however, constrain the scope of claims about the extinctions (Choquenot and Bowman 1998) and complement the data and analytical tools at our disposal by allowing us to assess particular extinction scenarios. Recent discussion about late Pleistocene extinctions has too often lost track of those limits—in part because of misconceptions that models prove one or another extinction hypothesis (e.g., Haynes 2002; Fiedel and Haynes 2004).

Models describing a theoretical position are relatively easy to develop. For instance, Brook and Bowman (2002, supplemental material) note that all Pleistocene overkill models depend on four terms:  $r_m$ , the maximal replacement rate (or maximal intrinsic rate of population growth, more typically abbreviated  $r_{max}$ ) of prey;  $P$ , the density of megafaunal prey populations;  $H$ , the density of human populations; and  $O$ , the rate of prey offtake by human hunters. Different modelers might formulate slightly different equations (with the logistic equation, perhaps slightly modified, being the one most commonly used), but Brook and Bowman's (2002) general point is sound. Extinction follows when  $OH > r_m P$ . As they note, although the inequality is simple, the task of assigning reliable values to its terms is not.

Consider, for instance, the parameterization of just one term:  $O$ .

Optimal foraging theory seeks to identify the sorts of adaptive hunting and gathering strategies that would arise and persist due to natural selection. The findings from that body of literature can—and have—informed predator-prey modeling. Unfortunately, our assumptions about what constitutes optimal Paleoindian hunting may be incorrect, since what is optimal for foraging success might be suboptimal in other areas of life. If the hunting of megafauna conferred sexual selection advantages to males (e.g., Hawkes et al. 1997), per capita prey offtake could have been much higher than most models assume (Brook and Bowman 2002). Similarly, factors relating to sexual selection might have led hunters to target larger, more dangerous prey in preference to vulnerable juveniles, which would be consistent with the findings of Brook and Bowman (2004) but might contradict the otherwise rational hunting strategy tested by Brook and Johnson (2006) in Australia.

Alternately, prey offtake might be much lower than has been assumed. The scarce archeological evidence of human predation on extinct megafauna in North America (and its complete absence thus far in Australia) might result not from poor preservation but from the fact that Paleoindians and Paleoaborigines relied primarily on small game, fish, and plant resources. Such a situation would be consistent with Finlayson's (2009) informed observation that the nutritional importance of meat to prehistoric humans has likely been overemphasized because animal remains (especially bones) preserve better than plant remains. If so, many current models would drastically overestimate per capita prey offtake. Johnson's (2002) demonstration that large prey were not hunted preferentially in North America and a recent optimal foraging analysis (Byers and Ugan 2005) would support assigning lower values to  $O$ . We lack any clear indication of which perspective to favor. Two reviews of the archeological evidence of megafaunal predation reach nearly opposite conclusions with nearly opposite implications for parameter-

izing prey offtake (Grayson and Meltzer 2003; Fiedel and Haynes 2004).

Simply determining what percentage of an animal Pleistocene hunters consumed is problematic. For instance, Choquenot and Bowman (1998) follow Altman (1982) in assuming that 25% of a prey animal's body weight would have been lost as waste during butchering. In Choquenot and Bowman (1998), aboriginal hunters require 2.25 kg of meat per day. By contrast, Mosimann and Martin (1975) assume that Paleoindian hunters in North America would have needed either 8.6 kg or 16 kg of meat per day, since they would have wasted more in their game-rich environment. But while Mosimann and Martin (1975) assume that abundant naïve prey would have led to wastage, others argue that Pleistocene megafauna were not naïve (e.g., Wroe et al. 2004; Koch and Barnosky 2006) and would have been dangerous enough to warrant more careful and complete use by Paleoindian hunters (e.g., Stauffer 1975; Webster 1981).

An additional complication relates to the degree to which Paleoindian or Paleoaboriginal societies spanning continents should be treated as spatially uniform foragers. This is a difficult issue to resolve, because we know so little about Paleoindian and Paleoaboriginal resource use (e.g., Grayson and Meltzer 2002). Typical assumptions of uniform resource use might or might not be correct but nonetheless constrain model outcomes. For instance, if hunting pressure on megafaunal species were reduced in the tropics and subtropics (where plant foods were more readily available) or in coastal areas (where marine species could have been important staples), then such regions might have been megafaunal refugia rather than population sinks.

Even for relatively well-understood late Pleistocene ecosystems, all parameters involve similar degrees of uncertainty. Because of this pervasive parametric uncertainty, extinction models can only demonstrate what could (or could not) have happened under a given set of assumptions and parameter values (Brook and Bowman 2002, 2004). Despite the fact that ecological modeling necessarily both involves and requires "grossly simplified versions of reality" (Brook and

Johnson 2006:40), models can at least partially account for parametric uncertainty by testing a wide range of values for unconstrained parameters. The first Pleistocene extinction models sidestepped some of these difficulties by relying on simple structures and broad assumptions.

#### INITIAL MEGAFANAL EXTINCTION MODEL FOUNDATION: MAMMOTHS

M. I. Budyko's differential equation, single-prey model of old world mammoth overkill (Budyko 1967, 1974) represents the fundamental mathematical work on Pleistocene megafaunal extinctions. One line of investigation, beginning with Mosimann and Martin (1975) and culminating in Whittington and Dyke's (1984) sensitivity analysis of the Mosimann and Martin (1975) model, adapts Budyko's basic approach to a spatially explicit model that assumes a pattern of northwest to southeast Paleoindian dispersal from Beringia that now seems unlikely (Beck 1996; Steele et al. 1998; Turner 2002). Mathematically, the major change in approach is a move from a continuous-time, differential equation model to more extinction-prone difference equations, which proceed in a series of discrete time steps. Although other models (e.g., Mosimann and Martin 1975; Mithen 1993, 1997) react to Budyko's (1967, 1974) model, its greatest (and least duplicated) virtue is transparency. The complete presentation of the model makes its assumptions and parameterizations—and their limitations—open to analysis and modification. Budyko (1967, 1974) concludes that mammoth extinction in Europe likely resulted from long-term hunting and simultaneous stresses imposed by climate shifts. As modeled, extinction would have taken at least 10,000 to 25,000 years—a very different expectation than that of more recent overkill scenarios, from Mosimann and Martin (1975) to Alroy (2001), which predict North American extinctions within a few centuries or, at most, millennia of human arrival, and Brook and Johnson (2006), which predicts similar outcomes in Australia.

In Budyko's model, human populations grow with an assumed  $r_{max}$  that is unrelated to prey offtake: hunter population growth is

not linked to mammoth consumption. Instead, an exponential growth rate of 0.01% per year (far below the 2–4% values generally used in more recent models) is imposed and held constant. We would argue that models in which human populations wax or wane depending on the amount of food they consume would be both more instructive and ecologically realistic (e.g., Ginzburg 1998), although some disagree with this position (e.g., Brook and Bowman 2002). However, in the absence of the ecological feedback we favor some other density-dependent limits on human population growth (none of which are features of Budyko's model) the exponential growth of a predator population inevitably leads to the extinction of as many prey species as are present in a model. The only meaningful question that remains relates to how long it will take for extinction to occur.

Mithen's (1993, 1997) Leslie matrix models incorporate environmental stressors to continue Budyko's (1967, 1974) exploration of mammoth extinctions in both Europe (Mithen 1993) and North America (Mithen 1997), concluding that mammoth extinction would not have required a blitzkrieg scenario. Because mammoth  $r_{max}$  is relatively low, yearly prey offtake in the 2–5% range (consistent with opportunistic hunting rather than megafaunal specialization) is sufficient to cause extinction. However, Mithen (1993, 1997) does not rule out multiple extinction stressors operating simultaneously, since human hunting and climatic shifts were sufficient to cause extinctions both independently and in tandem under a wide variety of scenarios. Unlike previous modeling efforts (e.g., Budyko 1967, 1974; Mosimann and Martin 1975), Mithen's (1993, 1997) models achieve coexistence of human and mammoth populations under several parameter combinations. Thus, Mithen's (1993, 1997) models are the first to demonstrate that prey extinction is a possible but not inevitable mathematical conclusion.

#### SINGLE-PREY MODELS IN OTHER CONTEXTS

In modeling marsupial megafaunal extinction in Australian *Eucalyptus* savanna, Choque-

not and Bowman (1998) rely on a first-order differential equation model of a single-predator, single-prey system. Human hunters have no rates of intrinsic population increase (human population is determined using estimates of prehistoric populations), but prey do. The model provides a limited refutation of overkill—at least to the extent that it could have occurred locally within one human generation. The results are problematic, however. Larger prey—despite their lower reproductive rates—are not as extinction-prone as smaller species, perhaps due to low parameter values assigned to human population densities or the assumption that hunting efficiency declines as prey becomes scarce (Koch and Barnosky 2006).

Since the model tests a series of static Paleoaboriginal population densities against prey populations, it also lacks any dynamic connection between predator and prey. Once again, humans have an imposed, constant effect on prey, and there are no consequences for either falling short of or exceeding the minimal prey offtake needed to maintain their population. Choquenot and Bowman's (1998) model does not lead to local overkill in the short term, but due to the lack of feedback between prey consumption and predator population growth it cannot be instructive over longer spans of time. Implicit in the modeling approach used in Choquenot and Bowman (1998) is a significant question that has not been addressed: should models use population estimates or independently reproduce estimated human population trends in order to be considered valid? Presumably, an actual record of population fluctuations would lead to a more accurate depiction of what would have happened under particular starting assumptions, but prehistoric population estimates remain uncertain.

In a pair of single-prey models, Brook and Bowman (2002, 2004) evaluate Alroy's (2001) conclusions by accounting for the likely effects of prey naïveté. The first, simplified model (Brook and Bowman 2002) considers reduced prey vulnerability as a single complicating factor. The second (Brook and Bowman 2004) addresses reduced prey naïveté in conjunction with sensitivity analysis of pa-

rameters related to human and prey dynamics, prey offtake, and habitat quality. Brook and Bowman's approach changes assumptions about functional response (i.e., the rate at which predators capture prey as prey and predator densities change) and attempts to explore a continuum of functional responses between Holling Types II and III using the Michaelis-Menten equation, although the functional response form presented in their supplemental material does not appear to produce this continuum.

The Brook and Bowman perspective on prey naïveté has not been influential (but see Wroe et al. 2004). Thus far, their suggested change in functional response has had significant consequences only in a single-prey modeling context (i.e., Brook and Johnson 2006). In Brook and Bowman (2002), overkill is not a typical outcome, while Brook and Bowman (2004) find overkill under a variety of parameter combinations. However, the opacity of Brook and Bowman (2004) is problematic. As with previous modeling efforts (e.g., Mosimann and Martin 1975; Alroy 2001), unclear presentation of the model's design features and functionality and the absence of code prevents independent replication of both the model and its results.

A subsequent single-prey model by Brook and Johnson (2006) takes an underutilized approach to late Pleistocene extinctions by considering age-specific prey vulnerability in an Australian context. Focused on the largest Australian megafaunal species *Diprotodon optatum*, the results of the model indicate that human hunting alone would have been sufficient to cause prey extinction if vulnerable juveniles were targeted. The model's assessment of age structure in megafaunal extinction provides useful insights into the consequences of differential susceptibility to hunting of long-lived,  $K$ -selected prey species populations with low  $r_{max}$  values and long maturation times. Moreover, unlike previous Australian efforts (i.e., Choquenot and Bowman 1998), the Brook and Johnson (2006) model establishes and assesses the consequences of a dynamic connection between predator and prey populations. In doing so, Brook and Johnson (2006) test varying assumptions about

functional response (including Holling Type II and Type III), observing varying times to extinction under different starting assumptions. Generally, Brook and Johnson (2006) bear out the results of Mithen (1993, 1997), albeit in a different context and with a different focal prey species: megafaunal prey offtake at or below 5% per year can lead to extinction.

#### AGGREGATE MEGAFANAL MODELS

Mosimann and Martin's (1975) model is the first published simulation to test overkill as an explanatory hypothesis for North American extinctions. This spatially explicit difference equation model simulates a front of Paleoindian hunters moving southeast across North America over generational time. The model restricts hunter diet to extinct, large mammal prey. Although the simulation begins with a tribe of hunters in Canada and runs for 700 years, hunters overrun archeologically confirmed hunting sites within several hundred years. However, the model proceeds on problematic assumptions. Human dispersal and reproduction are inconsistently linked to hunting success. Geometric population growth occurs only in the presence of prey without regard to successful prey offtake. Range extension results under two scenarios: a gradual front advance (when prey is present) and a jump advance (when prey is absent). Jump advances only occur when prey has been completely exhausted from an area and continue until new prey is located. After a jump advance, prey cannot recolonize an abandoned area, because the model assumes humans have unfavorably altered the landscape. Since the model's hunters have no hunting success-linked constraints on their reproduction and range extension and since prey cannot recolonize vacated habitat, prey extinction is a foregone conclusion.

Accordingly, the model is less a test of the overkill hypothesis than an exploration of a particular colonization scenario (Whittington and Dyke 1984). Following May (1973), Belovsky (1988) provides stability analyses of Mosimann and Martin (1975) and the Whittington and Dyke (1984) sensitivity analysis of Mosimann and Martin (1975), demonstrating the model's inability to achieve sta-

ble coexistence between Pale Indians and prey. Belovsky (1988) identifies the source of that instability as a lack of feedback between humans and prey populations. A recurrent concern (Choquenot and Bowman 1998; Brook and Bowman 2002) is that under such conditions, unless some other density-dependent factors limit human population growth and allow for coexistence between humans and prey species, extinctions are inevitable; only their timing is at issue. However, if prey offtake does not influence predator population growth or carrying capacity, it is necessary to clarify what factors do. To date, published models typically lack such details. It is reasonable to imagine scenarios under which the linkage between prey and predator populations might be either more or less direct, but models need to explain the conditions that dictate a particular linkage (or lack thereof) between prey consumption and predator population growth.

Alroy (2001) surmounts this limitation in a complex computer simulation. Human prey and predator dynamics are coupled, with humans assumed to be nonselective hunters. Forty-one megafaunal prey species are differentiated and individually parameterized, while secondary resources (plants, small game) are left undifferentiated and assumed to be of equal nutritional value to preferred large prey (i.e., secondary resources amount to an additional prey item). The model is spatially explicit and follows individual species outcomes within grid cells of one degree of latitude and longitude per side. Prey parameters that correlate with size (e.g.,  $r_{max}$ , population density) are constrained allometrically, while other parameter values are taken from the literature. Unconstrained parameter values—e.g., hunting ability, the equivalent of Brook and Bowman's (2002, supplemental material)  $O$ —are varied over a wide range of simulations, and the result that most closely matches historical outcomes is presented as the best-fit scenario.

Alroy's results have sometimes been interpreted (e.g., Koch 2006) as lending strong support to the overkill hypothesis. Such an interpretation is, at best, premature. Alroy's (2001) complex simulation performs better

than a simplest case mass threshold approach that separates 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. Although the simulation is generally effective in accounting for outcomes involving the largest (> 500 kg) megafaunal species, it is less successful with outcomes involving smaller (< 60 kg) species.

In part, Alroy (2001) assesses his model by comparing its outcomes to those of the simple mass threshold method, which correctly "predicts" 30 of 41 (73%) actual survival-extinction outcomes; by contrast, the Alroy model correctly predicts 32 of 41 (78%) outcomes (Alroy 2001). Given the model's complexity, it remains unclear how the simulation achieves this improvement over the mass threshold method. 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 *S. onusrosagris*; Alroy, personal communication). Critiques of model design (e.g., Ginzburg and Jensen 2004) suggest that the model may be overparameterized.

Yule et al. (2009) represents the first return to multiprey system modeling in North America following Alroy (2001). Yule et al. (2009) simulates human predation on a subset of individually parameterized North American fauna in an allometrically constrained model. Although the six-species prey assemblage is smaller than Alroy's (2001), selected species characterize a range of mass categories sufficient to overlap the mass threshold predictor of survival-extinction outcomes. In addition to allometrically defined parameters, the model also explores two unconstrained parameters: hunting pressure and prey susceptibility. Although functional response is considered to be critical for achieving ecologically realistic characterizations of predator-prey interactions both in general (e.g., Skalski and Gilliam 2001; Fenlon and Faddy 2006; Williams 2008) and in regard to late Pleistocene extinction modeling (e.g., Brook and Bowman 2002; Brook and Johnson 2006), Yule et al. (2009) is one of the first modeling exercises to explore the conse-

quences to predator-prey dynamics of varying functional response choice. Prior to Yule et al. (2009), no multiprey models and only one single-prey model (Brook and Johnson 2006) tested the effect of varying functional response forms. Yule et al. (2009) models system dynamics under three different functional response forms: Holling Type II; Beddington-DeAngelis (a simple derivative of the Holling Disc Equation incorporating a predator interference parameter,  $i$ , which provides a measure of the time spent by predators interacting with one another rather than hunting); and Ratio Dependence (which assumes complete sharing of prey among predators). Contrary to prevailing expectation, Yule et al. (2009) found that varying functional response choice had minimal consequences for survival-extinction outcomes. As with previous modeling efforts, the extinction of the largest megafaunal species was easily explained, while the loss of intermediate mass species was not.

An additional conclusion of Yule et al. (2009) is that although allometric constraint of late Pleistocene extinction model parameters remains the best available form of constraint, it nonetheless involves serious limitations. Using a life-history approach to calculate probabilistic extinction risk, Zuo et al. (2013) reaches a similar conclusion, noting the limitations of allometric constraint in deterministic predator-prey models and the relative potential of analyzing variation around established values (e.g., published mass estimates of extinct mammals) and allometric calculations based on that data. Zuo et al.'s (2013) probabilistic modeling of extinction risk may more accurately explain extinction patterns among both megafaunal and smaller mammals on the basis of such traits as instantaneous mortality rate and age of first reproduction.

In a distinctly different context, Prescott et al. (2012) uses a generalized linear model to determine whether climate change, human arrival, or both provide the best fit to observed extinctions on five landmasses (North America, South America, Palearctic Eurasia, Australia, and New Zealand). To account for prevailing uncertainties about climate change and the dates of human arrival in different

regions, the model tests 330,000 different possible combinations, concluding that extinctions can best be explained as having resulted from both climatic and anthropogenic factors. Nonetheless, human arrival appears to better explain extinction than climate change. However, the Prescott et al. (2012) model suggests that climate cooling played a larger role in extinctions than climate warming, although the late Pleistocene was a period of warming. Prescott et al. (2012) is a statistical model that seeks to identify a best fit to data sets rather than a predator-prey, foraging, or economic maximization model, but its findings are of interest both in and of themselves and for the baseline they provide. Future work in this area might prove valuable in providing independent checks of other modeling efforts.

#### THE MAXIMIZATION APPROACH: OPTIMAL FORAGING AND ECONOMIC MODELS

Belovsky's (1988) analyses of early models (e.g., Mosimann and Martin 1975; Whittington and Dyke 1984) demonstrate their inability to achieve stable coexistence between Paleoindians and their prey, noting that a lack of feedback between human and prey demographics perpetuates system instability. Optimal foraging models provide a viable alternative to the first late Pleistocene megafaunal extinction models by explicitly accounting for that feedback and allowing for the temporal variation in human diet that is otherwise difficult to model.

Foraging models do not typically assess particular regional conditions (e.g., Winterhalder et al. 1988; Winterhalder and Lu 1997), although Belovsky (1988) specifically models North America. Linking human and prey demographics adds ecological realism to the models while considering at least as many prey species as other models of the time. As with Mosimann and Martin (1975), for instance, Belovsky (1988) treats prey as an aggregate category while also differentiating between hunted and gathered food. Similarly, Winterhalder et al. (1988) consider one to two species, while Winterhalder and Lu (1997) account for two to four (Table 1).

Belovsky's (1988) model assumes that a single male-female Paleoindian pair colonize



TABLE 1  
An overview of published late Pleistocene megafaunal extinction models

Model	Number of prey species modeled	Form of model	Spatially explicit?	Density-dependent resource growth? (e.g., logistic)	Allometrically constrained?	Dynamic interaction in predator-prey demographics?	Obeys biomass conversion principle?	Functional response saturation type	Full and transparent presentation of model
Budyko (1967, 1974)	1	Differential equation	No	No	No	No	N/A	Unrelated to prey density	Yes
Mosimann and Martin (1975)	1	Difference equation	Yes	No	No	No	N/A	Unrelated to prey density	No
Whittington and Dyke (1984)	1	Difference equation	Yes	No	No	No	N/A	Unrelated to prey density	No
Belovsky (1987, 1988)	2 (hunted food, gathered food)	Difference equation	No	Yes (gathered food)	N/A	Yes	Yes	Special case	Yes
Winterhalder et al. (1988)	1 or 2	Difference equation	No	Yes	N/A	Yes	Yes	Special case	No
Mithen (1993)	1	Difference equation	No	Partially	No	No	N/A	Unrelated to prey density	No
Mithen (1997)	1	Difference equation	No	Partially	No	No	N/A	Unrelated to prey density	No
Winterhalder and Lu (1997)	Up to 4	Difference equation	No	Yes	N/A	Yes	Yes	Special case	No
Choquenot and Bowman (1998)	1	N/A	No	Yes	Yes	No	N/A	II	No
Alroy (2001)	42	Difference equation	Yes	Yes	Yes	Yes	Yes	Unique form	No
Brook and Bowman (2002)	1	Difference equation	Yes	Yes	Yes	No	N/A	III	No
Brook and Bowman (2004)	1	Difference equation	No	Yes	Yes	No	N/A	Modified Michaelis-Menten	No
Brook and Johnson (2006)	1	Difference equation	No	Yes	Yes	No	N/A	Varied	No
Bulte et al. (2006)	1 or 2	Difference equation	Yes	Yes	No	Yes	Yes	Unrelated to prey density	Yes
Yule et al. (2009)	6	Differential equation	No	Yes	Yes	Yes	Yes	Varied	Yes

the Americas via Beringia, as per the scenario presented in Mosimann and Martin (1975), and that these foragers are nutrient maximizers (i.e., they increase fitness by maximizing nutritional intake; Belovsky 1987). Belovsky (1988) concludes that hunter-gatherers in low primary productivity environments overexploit neither prey nor gathered resources. In ecosystems with high primary productivity (e.g., tallgrass prairie, river floodplains), some prey extinctions result and gathered food resources become less abundant. Although extinction is possible, the model does not duplicate actual late Pleistocene survival-extinction patterns. These results are consistent with findings from another optimal foraging model (Winterhalder et al. 1988), which demonstrates that communities with few prey species are not extinction-prone.

A later multiprey simulation (Winterhalder and Lu 1997) suggests that long-term human residence in multiprey ecosystems with varied resources can lead both to single extinctions and the general loss of large species typical of late Pleistocene communities. Under the assumption that humans hunt game of any size class as they encounter it, their model tests parameterizations of human foraging efficiency, prey population ecology (using the logistic growth equation), and human population ecology (using a modified logistic growth equation in which human  $r$  values depend on foraging success). Winterhalder and Lu (1997) conclude that “fallback” resources (e.g., tubers or small mammals that are not among the top-ranked food items) could allow hunter-gatherer populations to persist when preferred resources (i.e., larger prey) are unavailable. Since persistent human populations have more opportunities to encounter increasingly rare prey individuals, the likelihood of megafaunal extinction actually increases under conditions of broad foraging. Although optimal foraging models invalidate a common misconception—that specialization on megafaunal prey is more likely than generalized foraging to cause prey extinction (Koch and Barnosky 2006)—there has been no recent work in the area. The relevance of optimal foraging models to the dialogue about late Pleistocene extinctions is sometimes

overlooked—in part because these models rely on a different methodology and in part because their authors rarely emphasize their potential contribution to the debate.

Although optimal foraging theory provides a useful set of methods to describe ecological interactions, it does not account for human behaviors not driven strictly by nutritional considerations. This limitation led to economic modeling, which represents an alternative to optimal foraging theory. Economic models were first used to assess extinctions in an attempt to explain the impact of commercial fisheries during the late 1960s (Smith 1968, 1969; Gould 1972; Clark 1973). Although this initial theoretical work sought to maximize profit in a context distinct from ecology, it reveals the potential of economic factors to explain how humans overuse natural resources. If instant profit can be maximized by harvesting the last member of an animal population, Clark (1973) suggests that extinction will follow for species whose maximum reproductive rates do not exceed the minimum threshold required to withstand exploitation. However, variables such as profit, which are inherently subjective and group-specific, are difficult to model for vanished societies since it is impossible to objectively constrain parameter values; consequently, profit has limited value as a component of late Pleistocene megafaunal extinction modeling.

Bulte et al. (2006) presents a model that uses an alternative to profit—utility—as a primary indicator of human satisfaction. Bulte et al. (2006) assumes that Paleoindians would have maximized utility—an assumption in economic modeling roughly equivalent to the assumption in optimal foraging modeling that food gathering would be optimized—with utility accounting for the consumption of both food and other goods (e.g., tools, cloth). Bulte et al. (2006) concludes that Paleoindian overhunting could have caused megafaunal extinctions with smaller mammals playing a significant role as alternative food sources when megafaunal populations declined, which is consistent with Winterhalder and Lu’s (1997) optimal foraging model. However, the Bulte et al. (2006) model does not provide species-

specific results (i.e., the model cannot be assessed by comparing its results to actual survival/extinction outcomes). In addition, the indirect influence of small mammal populations on megafauna may result from peculiarities of the Bulte et al. (2006) model's design relating to the unrealistically limited number of values tested for human and prey population growth rates and carrying capacities. For instance, if the model presented in Bulte et al. (2006) were to assess a wider range of reasonable assumptions relating to species-specific population growth rates and/or carrying capacity sharing (e.g., by allowing more groups of prey species to share habitat), its survival/extinction outcomes might more closely approximate real world survival/extinction patterns.

THE DIFFICULTIES OF COMPARISON:  
MODEL TRANSPARENCY,  
PARAMETERIZATION, AND OTHER VEXING  
ISSUES

The wide array of methodologies and varying complexity of Pleistocene megafaunal extinction models makes direct comparison between them difficult (Table 1). Although each method might lend itself to a particular application (e.g., single-prey models by extending our understanding of individual species' susceptibility to extinction via predation; multiprey models by providing snapshots of simplified ecological interactions), incompatibility between models—and, by extension, the hypotheses they test—limits how they extend our understanding of Pleistocene extinctions. The most valuable result of existing modeling work might only be realized once progress in each individual area allows either for ground truthing or providing independent checks of the others.

The current state of affairs, in which different types of models have fundamentally different aims and functionality, raises an important question: by what measure can ecologists, modelers, and other interested parties determine whether or not a model is successful? In brief, the most successful models of late Pleistocene extinction are those that present their methods and functionality transparently and, by doing so, provide insights into the ecological dynamics they as-

sess. To many, Alroy (2001) represents the most successful model of predation as a cause of late Pleistocene extinctions by virtue of the large number of species it includes, its overall accuracy in accounting for species survival/extinction outcomes, its coupling of predator and prey demographics, and the complexity of its operation. However, complex models are not necessarily superior to their simpler counterparts. Rather, complexity becomes a valuable attribute of models only after foundational efforts provide a clear rationale for that complexity, including a clear elucidation of how model complexity reasonably improves the model's ability to produce observed outcomes (Grimm and Railsback 2012).

More minimalist, fully presented models better allow ecologists to test their basic understanding of how ecological systems work before going on to develop subsequent models that incorporate more complicating factors. For this reason, a model that incorporates stepwise fine-tuning and refinements allows ecologists to assess the consequence of each variable's effect on outcomes. In that regard, models that are the end product of multiple, peer-reviewed efforts are more likely to be successful than alternative, stand-alone efforts—if for no other reason than because their transparency allows for a higher degree of confidence in their credibility.

Outside of stepwise model development, disparity in parameterization (either in terms of assigning different values to the same parameters or by disagreeing about the number of unconstrained parameters models can include) reduces the likelihood that each new model will yield an incremental increase in our understanding of late Pleistocene extinctions. Given sufficient freedom to assign parameter values or incorporate additional parameters into a model, what might appear to the broader scientific community (or the hopeful modeler) as a robust model (i.e., one whose outcomes are relatively insensitive to altered starting parameter values) could be a model so overparameterized that a variety of initial conditions yield the same (perhaps desired) result. Overparameterized models appear highly successful because their numerous additional parameters allow for a clo-

ser but unwarranted fit to the data (e.g., Dyson 2004). The number of parameters on which a model relies can serve as an indirect measure of how much effort (i.e., trial and error) went into fitting the model to the data (Ginzburg and Jensen 2004); since the answers modelers seek are often known in advance (e.g., scenarios yielding or failing to yield megafaunal extinction), the obvious risk is of some conscious or subconscious fitting of the model to the data. Simpler, initial models that benefit from subsequent refinements pose far fewer difficulties in this regard.

Increasing the number of parameters in a model, even if only moving from two parameters to three, represents a multiplicative rather than additive increase in complexity that must be justified (e.g., Dyson 2004). Although this basic position has been advanced as an aesthetic argument (Ginzburg and Jensen 2004) and is implicit in presentations of some models (e.g., Choquenot and Bowman 1998), its practical implications for extinction modeling should not be underestimated. If complex, multiparameter models suggest that overkill was either inevitable or impossible given our knowledge of Paleoindian, Paleoaboriginal, and megafaunal ecology or climate change, we should consider carefully whether the claims are warranted or the models overparameterized.

Model transparency and parameterization are overlapping concerns and should be viewed as such. When the details of a model's design or functionality are inaccessible, overparameterization can become a potent rhetorical device that incorrectly implies that a model provides compelling proof of a position (Ginzburg and Jensen 2004). Ultimately, parameter disparity leaves little room for meaningfully comparing multiple extinction models and, as a result, little room for modeling to advance our understanding of late Pleistocene extinctions. If such disparity occurs in opaquely presented models, those models provide no foundation on which to build.

It would be almost impossible to reconstruct the majority of models assessed in this review on the basis of information included in articles and supplemental materials. De-

tails are frequently lacking, from the general (e.g., overviews of model design and functionality, including specific inputs and outputs; clear statements regarding the linkage, if any, between human hunting success and human population growth rate) to the specific (e.g., the exact formulae used to represent particular aspects of ecology). Without the transparency necessary to completely reconstruct a given model, research departs from the best practices of scientific inquiry that allow for disciplinary communities to test and refine that research—an unfortunate state of affairs given that even small changes in code or method (whether resulting from typographical errors during coding or misunderstanding the source material used in developing model components) can dramatically influence results without ever being detected by reviewers. As a consequence, the results of nontransparent models are unverifiable. Therefore, it is critical that models be presented in complete form in online supplementary material or, at the very least, made available by request (Grimm et al. 2006); the peer review process needs to do a better job of holding authors to this responsibility.

Unlike the situation in biological bench work, in which only techniques and results can be reported, modelers can present their exact work in its entirety. No parallel exists in other areas of biology, yet this significant area of comparative methodological advantage remains virtually unutilized. The insufficient presentation of models—which leaves interested parties incapable of using valuable scientific artifacts forensically—represents the key reason for this unnecessary and unfortunate state of affairs in late Pleistocene extinction modeling.

#### CONCLUSION: MODEL DESIGN AND INTERPRETATION

Late Pleistocene extinction models, the debate surrounding them, and the manner in which they have been mobilized as evidence in the context of existing debates have often generated more heat than light. That situation and some initial inconsistencies in modeling approach and methodology are not necessarily cause for surprise or alarm,

however. Assessments of the sustainability of contemporary wildlife harvests involve corresponding uncertainty and lack of uniformity (Weinbaum et al. 2013) despite the fact that they address species, hunting strategies, and technologies that are far better known than their late Pleistocene counterparts. Possibly, probabilistic life-history-based extinction models of the sort recently developed by Zuo et al. (2013) will prove to be the best available means of assessing late Pleistocene extinctions. In addition or as an alternative, the methods of analyzing the sustainability of wildlife harvests could also play a role.

Nonetheless, predator-prey and other conventional but potentially more complex ecological models could clarify our understanding of late Pleistocene extinctions. Relative to its modest beginnings, the state of late Pleistocene extinction modeling is much improved, with progress on multiple fronts providing a solid foundation for future work. Modeling efforts that constitute elements of organized research programs rather than single, stand-alone projects will likely prove most successful. Such programs will necessarily benefit from starting small. Despite the increasing availability of the computing power necessary to run complex, computationally intensive extinction simulations, models designed to account—in a first iteration—for most or all conceivably relevant factors actually present more problems than they solve.

For practical reasons, we advocate an approach predicated on incremental increases in model complexity. Many relevant parameter values remain either unconstrained or poorly constrained; similarly, the effects of many assumptions remain unclear. From a methodological perspective, a stepwise approach to increasing model complexity allows complicating factors to be assessed individually—a task that is difficult or impossible when multiple complicating factors are simultaneously added to a model. We explain our reasoning by way of analogy. If a chef's goal is to improve a recipe by making use of new ingredients, the most productive approach would be to add one or a very few new elements and immediately assess their effects. Whether or not the alternative approach of simultaneously adding a large

number of ingredients was successful, the method could not be instructive, since it could not reveal which particular additions were significant and which insignificant. By this reasoning, an approach that develops more complex models in a series of steps should be preferred to one that incorporates numerous complicating factors simultaneously.

Brook and Bowman (2002:14627) rightly call for “logical, structured, and transparent” mathematical modeling of late Pleistocene extinctions while recognizing that model output must remain a product of the implicit and explicit assumptions on which models rest. Regrettably, complex simulations can easily become just the sort of opaque black boxes that Brook and Bowman (2002) warn against. All code used in published models should be presented or, at the very minimum, available in its entirety upon request with rapid turnaround time in response to such requests. In addition, we would slightly extend the request for full transparency offered by Grimm et al. (2006) in requiring that published models include flow charts that provide overviews of their inputs and functionality.

We agree with Barnosky et al. (2004) that more ecologically realistic models can increase our understanding of late Pleistocene extinctions. As a first step in achieving that improved realism, we suggest that models continue to account for the feedback between hunting success and hunter-gatherer reproduction. We also suggest three areas for improving ecological realism. First, additional exploration of the consequences of varying functional response assumptions in larger species assemblages would be instructive. Second, models can begin to assess interspecific competition between predator and/or prey species. Third, models that include nonhuman predators and their potential effects on survival-extinction outcomes provide a promising and completely untested area of investigation. Singly or in combination, any of these factors might explain the extinction of some smaller species.

Finally, the effective analysis and presentation of model results represents a critical and too often overlooked complement to effec-

tive model design. An important starting point is recognizing that “successful” single-cause models (whether of predation or climate change) do not rule out the possibility that Pleistocene extinctions resulted from multiple causes. The variety of model assumptions and parameterizations consistent either with overkill or climate change is also necessarily consistent with extinctions resulting from multiple stresses that include both and, possibly, additional factors as well (e.g., changes in habitat quality resulting from climate change and/or human activity). Indeed, from what we understand about the ways in which multiple stressors simultaneously push species to extinction (e.g., Raup 1991), extinctions resulting from multiple factors might well represent the rule and single-culprit events the exception. The long-

term goal of late Pleistocene modeling might well be to rigorously test the explanatory power of models that include both predation and climate change, both in regard to their match to actual survival/extinction outcomes and in terms of their ability to account for particulars relating to the timing and ecological details of extinctions.

In the future, models must build on a foundation of transparency. As technology enhances our ability to produce more ambitious, computationally intensive models, we must take care to avoid opacity and irreproducibility. To successfully advance our understanding of late Pleistocene extinctions, investigators must do a better job of encouraging and facilitating additional analysis, criticism and, if necessary, modification of their work.

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