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**Modeling Biotic Causes of Extinction: Vertebrate Case Studies at the
Intersection of Evolutionary Ecology, Paleontology, and Conservation
Biology**

A Dissertation Presented
by

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Abstract of the Dissertation

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While the modeling of metapopulation dynamics has illuminated biotic causes of extinction and provided both useful insights and a variety of modeling tools for conservation biology, the techniques of theoretical ecology and mathematical modeling can be directed at evolutionary and ecological topics to assess extinction in so far generally overlooked ways. This dissertation investigates a series of informative modeling case studies dealing with predation and competition in vertebrate systems in order to demonstrate its potential to inform conservation biology and North American restoration.

First, I review Late Pleistocene extinction models in order to develop a more transparent, ecologically realistic alternative and a framework for future modeling efforts. The resulting analysis and model reveal serious limitations in constraining model parameters. My conclusions strongly suggest that existing Late Pleistocene extinction models should be subject to considerable skepticism, both due to their inability to account for survival-extinction patterns in North American species and their inability to differentiate between different extinction scenarios.

Second, I assess the ecological consequences of the loss of a guild's top carnivore by developing a new conceptual model of intraguild competition among North American canids. The model provides a tool for the management of carnivores and their prey and suggests: (1) that mesopredator release in North America, rather than representing a recent ecological novelty, was typical during the Pleistocene; (2) that ecological restoration efforts could in some respects benefit from excluding rather than introducing the largest predators; and (3) that restoration efforts aimed at a pre-European North American benchmark would benefit threatened mesopredator prey species, while a Pleistocene restoration strategy would provide them with little or no advantage over current conditions. These conclusions emphasize the value of a

paleoecological perspective in conservation biology and the need for caution in restoration efforts, particularly those that call for the introduction of Old World megafauna as analogs for extinct Pleistocene species.

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Christopher X.J. Jensen is a coauthor on chapter two, a review of Late Pleistocene extinction modeling literature. I undertook the primary reviewing, analytical, and writing duties, while C.X.J. Jensen assisted with the analysis.

Christopher X.J. Jensen and Aby Joseph (an undergraduate research assistant) are coauthors on chapter three, including appendices two and three, which presents a new model of Late Pleistocene extinctions we developed. I undertook primary analytical and writing duties and was responsible for providing the biological background necessary for constructing and parameterizing the model. C.X.J. Jensen provided training and technical assistance with the software (Mathematica) used in this work along with technical assistance in transforming the parameter space of Berezovskaya, Karev, and Arditi (2001). After our initial introduction to Mathematica, all three authors worked jointly to construct the basic model over the course of one semester. Over the course of a second semester, I directed A. Joseph in refining and annotating various versions of the model, interpreting preliminary results, and expanding the model. I and C.X.J. Jensen interpreted the final results.

I am the third author of appendix one, an in-press article on modeling methodology, with Lev Ginzburg as first author and C.X.J. Jensen as second author. I assisted with the revision of an initial draft for submission and then took lead responsibility for a major revision and resubmission of the manuscript. When the manuscript was accepted for publication pending moderate revision and expansion, I undertook both the revision and the additions.

I am the sole author of chapters four and five and appendix four, a book review published in *Conservation Biology*.

Chapter 1: Introduction

Raup (1991: 80) observes that extinctions plot into a “fairly smooth” but skewed distribution, in which minor extinction events are common and larger events increasingly rare. He notes that no known break in the curve justifies depicting mass extinctions as inherently different from lesser extinctions, although he does not rule out the existence of such a discontinuity. While Raup is correct from a statistical point of view, I would suggest that a biological distinction is possible. Extinctions resulting from abiotic causes could occur at nearly any point on the distributional curve, since abiotic events can vary greatly in the severity of their effects.

For instance, impacting bolides range from baseball- to Mount Everest-sized, with effects ranging from local and short-term to global and long-term spatiotemporal scales. Yet extinctions resulting from biotic causes should be restricted mainly to the portion of the curve depicting minor extinction events. Such biotic factors as predation or competition, even when their effects are severe on a few taxa, are unlikely to have the broad global and taxonomic consequences of severe abiotic factors such as climate shifts, volcanism, or bolide impacts. Thus, although evidence of mass extinctions and subsequent faunal rebounds is readily apparent in the fossil record, the less obvious but more typical background extinctions better represent “normal” extinction dynamics. Consequently, the aftermaths of such extinctions should represent the more typical suite of biological consequences. My focal task is to direct

attention toward extinctions that occur within the context of these more “normal” conditions in order to establish a baseline that will clarify the evolutionary-ecological causes and effects of extinction—work with important conservation implications.

A focus on Pleistocene extinctions and ecosystems offers several advantages for this work. One of these is a practical matter of accessibility. Most Pleistocene species remain extant, and those that are extinct are well represented in the fossil record. As the first extinctions in which humans have been implicated as a causal agent, Pleistocene extinctions also provide a unique opportunity to explore human ecological impacts.

While metapopulation modeling has illuminated biotic causes of extinction and provided both useful insights and a variety of tools for conservation biology, the techniques of theoretical ecology and mathematical modeling can be directed at evolutionary and ecological topics to assess extinction in so far generally overlooked ways. Here, I present several related projects in this vein, investigating a series of informative Pleistocene case studies dealing with predation and competition in vertebrate systems, placing a particular emphasis on mammals. My overarching goal is to assess the implications of this modeling work for conservation biology, demonstrating its potential to inform approaches to North American restoration.

My first task is to assess and refine ecological modeling of Late Pleistocene megafaunal extinctions in order to develop a more transparent, ecologically realistic model and a framework for future modeling efforts. Late Pleistocene extinctions occurred globally over approximately 50,000 years. Large (≥ 44 kg body mass) and presumably slow-reproducing mammals in Eurasia, Australia, and the Americas were

most severely affected, although several megafaunal reptile and bird species died out in Australia (Barnosky et al. 2004). While larger species suffered higher extinction rates, smaller animals were also affected—a phenomenon that has not been adequately explained. Polarized debate about the cause(s) of the extinctions dates back to the nineteenth century, centering on climate and anthropogenic effects (particularly hunting). One arena in which the Late Pleistocene megafaunal extinction debate has played out is in the area of predator-prey modeling.

My goal is to assess the approaches and conclusions of Late Pleistocene megafaunal extinction models in order to clarify the ways in which mathematical models can—and cannot—help us identify specific causal factors. To that end, my first chapter reviews the modeling literature, demonstrating that it has been undertaken in the context of a diverse but often undisciplined enterprise which has done more to inspire debate than settle it. Barnosky et al. (2004) suggest a key role for modeling in resolving the debate—calling specifically for more realistic ecological models. But such an effort requires more varied work with predator-prey modeling than Barnosky et al. (2004) acknowledge. Matters requiring fundamental attention include model assumptions (e.g., relating to functional response), model design (e.g., incorporating ecologically reasonable interactions; limiting the number of parameters), parameterization (i.e., maximizing parameter constraint), and model presentation (particularly in regard to model transparency). A brief analysis of existing modeling work clarifies the difficulties associated with its widely varying approaches.

Within the context provided by the opening chapter, my second chapter develops an hypothesis about Late Pleistocene megafaunal extinctions that

might explain the so far inexplicable loss of both larger and smaller species. I and my collaborators test the hypothesis via a seven-species predator-prey model that explores both unstudied aspects of multi-prey parameter space and the unknown parameter values for hunter-gatherer prey capture efficiencies, one of the most problematic aspects of ecological modeling of Pleistocene extinctions. The clarity inherent to this alternative approach emphasizes that modeling “evidence” does not support any particular extinction hypothesis while underlining the need in Late Pleistocene studies as well as in paleoecology and ecology more generally for lean, transparent, open-access modeling efforts. The methodology we articulate is consistent with a particular modeling philosophy and represents a project independent of but consistent with a broader, ongoing interest in modeling methodology and philosophy (Ginzburg et al. *In Press*—**Appendix 1**).

My third chapter takes a different approach, considering competition in Pleistocene ecosystems to assess the ecological consequences of predator extinction. I explore the effects of the loss of a guild’s top carnivore by developing a conceptual model of intraguild competition in one representative North American predator guild—the canids. In addition to providing a tool for the management of carnivores and their prey, the model suggests: (1) that mesopredator release in North America, rather than representing a recent ecological novelty, was typical during the Pleistocene and (2) that ecological restoration efforts could in some respects benefit from excluding rather than introducing the largest predators. More generally, the model suggests (3) that restoration efforts aimed at a pre-European North American

benchmark would benefit threatened mesopredator prey species, while a Pleistocene restoration strategy would provide them with little or no advantage over current conditions. These conclusions emphasize the value of a paleoecological perspective in conservation biology and the need for caution in restoration efforts, particularly those that call for the introduction of Old World megafauna as analogs for extinct Pleistocene species.

Uniformitarianism—the notion that the present is the key to the past—has proven to be a fruitful scientific assumption. If we wish to understand the natural processes that have shaped the world’s species and ecosystems, it is also nearly a methodological necessity. In relying on it in the pages that follow, however, I hope to demonstrate that the past can also inform the present and, perhaps, the future as well. As we face the possibility of the first mass extinction event with a clear biotic cause—i.e., the human species and its environmental impacts—a paleoecological perspective might inform both what we do now and what we will eventually attempt in the areas of conservation biology and ecological restoration.

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Chapter 2

Dismantling the Black Boxes: Constructing and Interpreting Late Pleistocene Megafaunal Extinction Models

Jeffrey V. Yule and Christopher X.J. Jensen

To be submitted to *Trends in Ecology and Evolution*

Context:

In the absence of paleontological and archaeological evidence, debate about the causes of Pleistocene extinctions has relied on predator-prey modeling as a means of establishing a viable alternative to the traditional explanation based on climate change. This chapter addresses the manner in which a growing body of modeling evidence has increasingly been misunderstood as establishing human predation as the cause of Pleistocene extinctions, particularly in the Americas while suggesting a more productive approach for future modeling efforts.

Abstract

Debate about the causes of Late Pleistocene megafaunal extinctions has long been polarized, with proponents generally gravitating toward one of two main causal hypotheses: overhunting (i.e., “overkill”) and climate change. Overkill was initially considered to be the less likely explanation, but in the 1960s and 1970s ecological modeling demonstrated the possibility of extinction via predation. Recently, ecological models have been misconstrued as offering strong support for the overkill hypothesis. We argue that this faulty conclusion results from fundamental misunderstandings about the design and interpretation of predator-prey models. We suggest, first, that the relevant models offer far less compelling evidence of overkill than many realize; second, that recent models have been developed without sufficient regard for simplicity of design and transparency; and, third, that while some model parameterizations indicate human predation as a credible cause of megafaunal extinction, these models cannot rule out extinction scenarios involving other contributing factors (e.g., anthropogenic habitat alteration, climate change). Although human hunting might well have been a significant contributing factor in many Late Pleistocene extinctions, the modeling evidence currently available supports no claim stronger than that.

Introduction

Late Pleistocene megafaunal extinctions occurred globally over a period of roughly 50,000 years, most severely affecting mammals of ≥ 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_m , rather than large body mass *per se* was the decisive factor contributing to species extinction (Johnson 2002). Polarized debate about the causes of the extinctions dates back to the nineteenth 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 (Grayson 2001; Grayson and Meltzer 2002; Fiedel and Haynes 2004). In the current review, we focus on the modeling of human predation on herbivores. Extinctions among megafaunal predator and scavengers have not been modeled, since such species losses are assumed to inevitably result from herbivore extinctions.

Martin (1967, 1973) hypothesizes that human hunting caused the extinctions via “overkill” (i.e., hunting led prey death rates to exceed prey birth

rates). “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). While the broader overkill scenario retains considerable explanatory value, the blitzkrieg scenario appears increasingly unlikely (Beck 1996; Koch and Barnosky 2006; Waters and Stafford 2007; 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 most recent models are considered important in resolving debate about the causes of Late Pleistocene extinctions (e.g., Barnosky et al. 2004), the current state of megafaunal extinction modeling fails to justify optimism. Fundamental difficulties parameterizing megafaunal extinction models pose significant difficulties, and models have become increasingly opaque, leaving interested parties in the unenviable position of having to rely on what are essentially black boxes of unknown complexity and reliability. Under the circumstances, claims that a model “supports” any hypothesis are both misleading and inaccurate.

By updating the last in-depth review of the literature (Wesler 1981), the current paper sheds some much-needed light on Late Pleistocene extinction modeling so that we can better assess how human hunting might have factored into those extinctions. Our analysis suggests that the available modeling

evidence is consistent with multiple extinction hypotheses while emphasizing the value of minimally complex, transparent, open-access modeling efforts. Overkill remains a viable hypothesis, but meaningful refinements of existing models require greater simplicity of design, more transparent presentation, and greater ecological realism.

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 1975), although this point has been often overlooked. Models can, however, constrain the scope of claims about those extinctions (Choquenot 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. Regrettably, it is extremely difficult to identify the assumptions and parameterizations needed to legitimately assess a theory using a model. 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) of prey; P , the density of

megafaunal prey populations; H , the density of human populations; and O , the rate of prey off-take by human hunters. Different theorists might formulate slightly different equations, 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. 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 (Hawkes *et al.* 1997), per capita prey off-take could have been much higher than most models assume (Brook and Bowman 2002). Alternately, the actual values might be much lower than has been assumed. The scarce archaeological 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 Aborigines relied primarily on small game, fish, and plant resources—in which case most current models would drastically overestimate per capita prey off-take. Johnson's ((Johnson 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 recent reviews of the archaeological

evidence of megafaunal predation reach nearly opposite conclusions with nearly opposite implications for parameterizing prey off-take (Grayson and Meltzer 2003; Fiedel and Haynes 2004).

Simply determining what percentage of an animal Pleistocene hunters consumed is problematic. Choquenot and Bowman (1998), for instance, follow Altman (1982) in assuming that 25% of a prey animal's bodyweight would have been lost as waste during the butchering process. In Choquenot and Bowman (1998), aboriginal hunters require 2.25 kg meat per day. By contrast, Mosimann and Martin (1975) assume that Paleoindian hunters in North America would have needed either 8.6 kg or 16.0 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 Aboriginal societies spanning continents should be treated as spatially uniform foragers. This is a difficult issue to resolve, because we know so little about Clovis and Aboriginal 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). The first Pleistocene extinction models sidestepped some of these difficulties by relying on simple structures and broad assumptions.

A Failure of Ecological Realism: Budyko and the Virtues of Transparency

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 (Mosimann 1975) and effectively culminating in Whittington and Dyke's (Whittington 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 Paleoindian dispersal that now seems unlikely (Turner 1992, Beck 1996, Steele 1998). 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. While other models (Mithen 1993,

Choquenot 1998, Alroy 2001, Brook 2002, 2004) react to Budyko's (1967, 1974) model, its greatest (and least duplicated) virtues are simplicity and 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 10,000-25,000 years—a very different expectation than that of more recent overkill scenarios, from Mosimann and Martin (Mosimann 1975) to Alroy (Alroy 2001), which predict North American extinctions within a few centuries or, at most, millennia of human arrival.

In Budyko's model, human populations grow with an assumed r_m that is unrelated to prey off-take: 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 invariant. 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 (Brook 2002). However, in the absence of the ecological feedback we favor, 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. Other things being held equal, one consequence of such feedback in Budyko's model would have been faster megafaunal extinction.

Models lacking ecological feedback need not support overkill. In modeling marsupial megafaunal extinction in *Eucalyptus* savanna, Choquenot and Bowman (Choquenot 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, but prey do. The model provides a simplified 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 became scarce (Koch and Barnosky 2006). Since the model tests a series of static Aboriginal 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 off-take 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 ecological time.

Optimal Foraging Models

Following May (1973), Belovsky (1988) provides stability analyses of several early models (e.g., Mosimann and Martin 1975; Whittington and Dyke 1984), demonstrating their inability to achieve stable coexistence between Paleoindians and their prey. Belovsky (1988) identifies the source of that instability as a lack of feedback between human and prey demographics. 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) models North America specifically. Linking human and prey demographics adds ecological realism to the models and does so 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) considers 1-2 species, while Winterhalder and Lu (1997) accounts for 2-4 (**Table 1**).

Belovsky's (1988) model assumes that a single male-female Paleoindian pair colonize 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 increasing 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. While some extinctions are possible, however, the model does not duplicate Late Pleistocene extinction patterns. These results are consistent with findings from another optimal foraging model (Winterhalder et al. 1988), which demonstrate that ecosystems with few prey species are not extinction-prone. Thus, while early optimal foraging models suggest that extinction is a possibility in multi-prey systems, they do not support overkill as a likely cause of Late Pleistocene extinctions.

A later multiprey simulation (Winterhalder and Lu 1997) suggests that long-term human residence in multi-prey ecosystems with varied resources can lead both to single extinctions and the general loss of large species that occurred in the Late Pleistocene. 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 r values depend on foraging success). Winterhalder and Lu (1997) conclude that “fall-back” 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. Persistent human populations have more opportunities to encounter increasingly rare prey

individuals. For that reason, the likelihood of megafaunal extinction can actually increase 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 somewhat different methodology and in part because their authors rarely emphasize their potential contribution to the debate.

Late Pleistocene Extinction Models: Current State and Problems

Alroy (2001) presents a complex computer simulation that purports to demonstrate that human hunting was sufficient to cause Late Pleistocene megafaunal extinctions in North America. 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 or longitude per side. Prey parameters that correlate with size (e.g., r_m , 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 only slightly better than a simplest case “model” 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 (**Figure 1**). The simulation is generally effective in accounting for outcomes involving the largest (>500 kg) megafaunal species but less successful with outcomes involving smaller (<60 kg) species.

In a pair of single-prey models, Brook and Bowman (2002, 2004) evaluate Alroy’s (2001) conclusions by accounting for the likely effects of reduced prey naiveté. 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 naiveté in conjunction with changes in the parameterization of 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) from the conventional Holling Type II approach to the less extinction-prone Holling Type III. In fact, the functional response form used in Alroy (2001) is actually unique to the model and

presents a range of potential problems (e.g., at high human densities, the functional response form causes hunters to spontaneously generate prey) (Yule and Jensen, In Preparation). The Brook and Bowman perspective on prey naiveté has not been influential (but see Wroe et al. 2004), perhaps because it has limited practical implications. Only in simplified models does their suggested change in functional response have significant consequences. In Brook and Bowman (2002), overkill is not a typical outcome, while Brook and Bowman (2004) finds overkill under a variety of parameterizations.

In part, Alroy (2001) assesses his model by comparing its outcomes to those of the simple one-line method. The one-line method correctly predicts 30 of 41 (73%) actual survival-extinction outcomes, while 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 slight improvement over the one-line 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). The modeling literature (e.g., Jensen and Ginzburg 2004), however, suggests that over parameterization might be involved.

Parameterization and Over Parameterization/Over Fitting

Ecological models offer simplified depictions of ecological interactions. The idea that larger, more complex models are necessarily superior to smaller,

simpler ones, while understandable, is generally mistaken. Because they are more tractable and transparent, more minimalist models better allow ecologists to test their understanding of how ecological systems actually work by identifying the ecosystem components that are most relevant to the dynamics they wish to study.

Despite the increasing availability of the computing power necessary to run complex, highly parameterized simulations, extinction models designed to account for most or all conceivably relevant factors actually present more problems than they solve. In the face of uncertainty about parameter values, the difficulties associated with adding each new parameter to a model are not additive; they are multiplicative. Each additional parameter allows for more fine-tuning of a model to a particular data set. Over parameterized models appear highly successful because their numerous additional parameters allow for a closer but unwarranted fit to the data (e.g., Dyson 2004). Given sufficient freedom to assign parameter values, 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 over parameterized that a variety of initial conditions yield the same (perhaps desired) result. In the present context, then, if complex models suggest that overkill *per se* was either inevitable or impossible given our knowledge of Paleoindian, Aboriginal, and megafaunal ecology (Alroy 2001), we should consider carefully whether the claims are warranted or the models over parameterized. More specifically, when the details of the models are

inaccessible, over parameterization can become a potent rhetorical device which incorrectly implies that a model provides compelling proof of a position (Ginzburg and Jensen 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. Brook and Bowman (2002: 14627) rightly call for “logical, structured, and transparent” mathematical modeling of the Late Pleistocene extinctions while recognizing that model output must remain a product of the implicit and explicit assumptions on which models always rest. Regrettably, complex simulations can easily become just the sort of opaque black boxes that Brook and Bowman (2002) warn against, either literally (if they are proprietary) or practically (if they are not user friendly or if they are not made available to other investigators). Simpler, leaner models pose far fewer difficulties in this regard. For these reasons, from a utilitarian perspective several earlier models (e.g., Belovsky 1988) are in many respects superior to Alroy’s (Alroy 2001) later simulation.

Even though the Alroy simulation provides for the dynamic interaction between predators and prey, this interaction is, like the model as a whole, opaque and inaccessible to other investigators. Improved models must achieve simplicity and transparency while also allowing for more realistic feedback

between prey consumption and predator population growth. By using the minimum number of parameters necessary, such models would maintain transparency and facilitate additional analysis, criticism, and, if necessary, modification. Increasing the number of parameters in a model, even if only moving from two parameters to three, represents a significant step that should be justified (e.g., Dyson 2004). While 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.

Conclusion

The value of any ecological model lies as much in its complete, transparent presentation as in the careful interpretation of its results. Yet Late Pleistocene extinction models are typically presented as black boxes, with results summarized and some design details provided in supplemental materials without the entire models ever having been made openly available (**Table 1**). We consider the scientific community's acceptance of such fragmentary presentation to be as troubling as the lack of skepticism and scrutiny such publications face. Given the ease with which complete models can be made available online, we suggest that full transparency should be the norm rather than the exception.

Greater care is also warranted in interpreting models. An important starting point would be to recognize that "successful" predation models do not rule out the possibility that Pleistocene extinctions resulted from multiple causes.

The variety of model assumptions and parameterizations that are consistent with overkill are also necessarily consistent with extinctions resulting from multiple stresses that include predation and other factors (e.g., climate change and its effects on habitat quality and availability). Models demonstrating predation as sufficient to cause species extinctions do not rule out other contributing factors.

We advocate a minimalist approach to the design of Late Pleistocene extinction models, a point that we recognize is liable to inspire debate. We justify this methodological position on practical grounds. In the current modeling context, many relevant parameter values remain either unconstrained or poorly constrained; similarly, the effects of many assumptions remain unclear. From a methodological perspective, we advocate a stepwise approach to increasing model complexity so that complicating factors can be effectively 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 were 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 or insignificant in their effects. By this reasoning, an approach that develops more complex models in a series of steps (e.g., Brook and Bowman 2002 and Brook and Bowman 2004; Winterhalder et al,

1998 and Winterhalder and Lu 1997) should be preferred to one that incorporate numerous complicating factors simultaneously (e.g., Alroy 2001). We recognize that Alroy (2001) is the most successful current model of predation as a cause of Late Pleistocene megafaunal extinctions. Yet modelers and a range of interested parties still need to understand how the model achieves its modest improvement over assuming that more slowly reproducing species face greater risk of extinction. Initial attempts in this direction that purport to use simplified versions of the Alroy (2001) model (e.g., Brook and Bowman 2002) have done little to clarify matters—and, further, it remains uncertain whether the simplified models in question bear any significant resemblance to the Alroy model.

Finally, we agree with Barnosky et al. (2004) that more ecologically realistic models can contribute to our understanding of Late Pleistocene extinctions. As a first step in achieving that improved realism, we suggest two areas where existing research provides readily accessible and potentially valuable opportunities. First, models should account for the feedback between the hunting success and reproductive rates of hunter-gatherers. Second, Pleistocene extinction models should make fuller use of available functional response tools in representing the effects of changes in predator and prey densities on predation rates (Yule and Jensen, In Preparation). The most recent models rely on either a unique functional response form that is provided without justification or explanation (Alroy 2001) or on very basic forms (e.g., Holling 1959) that ignore the effects of predator interference (Brook and Bowman 2002).

Late Pleistocene extinction models and the debate surrounding them have recently generated far more heat than light. Nonetheless, ecological models have the potential to clarify our grasp of certain aspects of Late Pleistocene extinctions. If we abandon the black box approach and the mentality it engenders, models can achieve a larger measure of that potential. The payoffs may be more limited than some would prefer, but they will be also both far more reliable and far more instructive.

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Figure 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).

<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>Stoekoceros conklingi</i>	53	E	<i>Euceratherium collinum</i>	499	E
<i>Stoekoceros 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 niobrarenensis</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	Surviving (Extant)	=	S
<i>Equus francisi</i>	368	E	Extinct	=	E

Table 1: Overview of Ecological Models of Late Pleistocene Megafaunal Extinctions

Model	Number of Prey Species Modelled	Form of Model	Spatially Explicit?	Density Dependent Resource Growth? (e.g. logistic)	Allometrically Constrained?	Obeys Biomass Conversion Principle?	Dynamic Interaction in Predator-Prey Demographics?	Functional Response Saturation Type	Full and Transparent Presentation of Model
Budyko (1967, 1974)	1	Differential Equation	No	No	No	No	No	Unrelated to Prey Density	Yes
Mosimann and Martin (1975)	1	Difference Equation	Yes	No	No	No	No	Unrelated to Prey Density	No
Whittington and Dyke (1984)	1	Difference Equation	Yes	No	No	No	No	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
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	No	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	No	III	No
Brook and Bowman (2004)	1	Difference Equation	No	Yes	Yes	No ?	No	III ?	No
Yule et al. (IP)	6	Differential Equation	No	Yes	Yes	Yes	Yes	varied	Yes

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Chapter 3

A New Human Predation Explanation for Late Pleistocene Megafaunal Extinction Patterns in North America

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To be submitted to *Ecological Modelling*

Context:

The previous chapter provides the context for Late Pleistocene extinction modeling efforts. Here, my collaborators and I use that context to develop a model that incorporates additional ecological realism while maintaining transparency, minimalism of design, and maximal constraint of parameters.

Abstract

Although Late Pleistocene extinctions disproportionately affected larger mammalian species, a variety of smaller species were also lost. To date, no satisfactory explanation has been presented to account for observed size-based extinction patterns. Beginning with the assumption that human predation caused the extinctions, we offer the first such explanatory hypothesis, which is predicated on considering more realistic predator functional response forms. We then test the hypothesis via a one-predator, six-prey ecological model. Results indicate that altering assumptions about one cornerstone of ecological modeling (i.e., functional response) fails to produce qualitative differences in survival-extinction outcomes. This unexpected finding suggests that the ecological characteristics of Late Pleistocene extinctions remain insufficiently understood to distinguish between a variety of competing extinction scenarios involving multiple causes in combination. Although we find no support for the hypothesis we present, in light of the current limits of parameterization, we are also unable to falsify it. We conclude that the matter of causation and the conclusions of previous Late Pleistocene extinction models remain far less certain than many have assumed.

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.

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 as first articulated by Martin (1967) and later refined and modeled by Mosimann and Martin (1975). Such an interpretation of the modeling evidence is, at best, premature. Alroy's (2001) model performs only 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 (**Figure 1**).

In part, Alroy (2001) assesses his model by comparing its outcomes to those of the simple one-line method. The one-line method correctly predicts 30 of 41 (73%) of actual survival-extinction outcomes, while the Alroy 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 (**Chapter 1**). However, because the complex model is not an open access resource, it remains unclear how the simulation achieves this slight improvement over a simplest case approach. Critiques of popular modeling approaches (e.g., Jensen and Ginzburg 2004), suggest that the improvement might result from over parameterization—but it is unclear what factor or combination of factors produces the improvement.

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 the megafauna under human hunting pressure. But a simple model that performs well from the outset is generally a more significant achievement than a highly

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

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_m), increased home range size, reduced population size) (e.g., Johnson 2002). Amongst the heaviest species (i.e., ≥ 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 ≤ 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, Karev, and Arditi'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. The original BKA parameter space has been rescaled so that the x-axis represents the ratio of prey r_m to predator r_m ; the y-axis remains unchanged in defining α , the capture efficiency of human hunters in dealing with prey (**Figure 2; Appendix 2**).

Within the yellow parameter space, predator and prey coexist, while extinctions occur within the white parameter space. Because r_m correlates inversely 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_m values for predator and prey are identical. The dotted line represents the simplest possible version of the assumed relationship between capture efficiency and r_m /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. For human hunters the line must both start 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.

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_m 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 (**Figure 3**).

The specific parameter values for α 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. While the lack of parameter values precludes specificity, the relationship we identify offers a simple, reasonable empirical prediction of general anticipated extinction patterns. That is, although modelers lack α 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 precision than prevailing parameteric uncertainty can justify. It is a simpler modeling tool but one that has the potential to work.

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 differential equations. We analyzed this model to predict extinction patterns at various values of predator capture efficiency, a or α (**Figure 4**). To determine whether functional response choices incorporating predator interference 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 excludes predator interference), Beddington-DeAngelis (a simple derivative of the Holling Disc Equation that incorporates a predator interference parameter, i), and Ratio Dependence (which assumes complete sharing of prey among predators, an assumption consistent with a technologically sophisticated, cooperatively foraging omnivores exploiting available prey) (**Table 1**).

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_m (**Figure 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), developing a module that computes prey parameter values (e.g., r_m , carrying capacity) based on input of their masses. One key allometry remains undefined: the relationship between prey mass and predator efficiency in capturing prey. Our goal 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

$\frac{1}{\text{time} \cdot \text{individual}}$. Under ratio dependence, capture efficiency is denoted by α and

is measured in units of $\frac{1}{\text{time}}$. 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_α , which differ between the two functional response forms, as follows:

$$a = C_a m_i^{PowerCE} \quad (1)$$

$$\alpha = C_\alpha m_i^{PowerCE} \quad (2)$$

Without assuming that $C_a = C_\alpha$, we explored various estimates of C_a , C_α , and $PowerCE$ by testing a wide range of parameter 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 proved problematic for the Ratio-Dependent model. The Ratio-Dependent functional response contains the rational expression:

$$\frac{\alpha \frac{N}{P}}{1 + \alpha h \frac{N}{P}} \quad (3)$$

Because the predator abundance, P , approaches zero for a variety of parameterizations, the expression $\frac{N}{P}$ also approaches infinity, causing the numerical simulation algorithm to produce error messages. Despite these messages, we consider the simulation outputs trustworthy, since errors occur at population sizes below our extinction thresholds and, therefore, in irrelevant sections of our simulated time series.

All simulations were performed using *Mathematica* version 5.2.0.0 and are available on request. See **Appendix 3** for more information on the specific calculations and code employed in these simulations.

Results

No qualitative difference in survival-extinction patterns results from changes in functional response form (**Figure 5**). Survival-extinction outcomes depend on the combined absolute magnitudes of hunting pressure, C_a , 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. Predator extinction occurs in the bottom left region of parameter space, where capture efficiency is lowest. Species coexistence occurs in regions of intermediate capture efficiency. The transition from coexistence occurs in the region of $PowerCE > -0.5$, depending on the overall intensity of hunting pressure (C_a). Where $PowerCE < -0.35$, stepwise extinctions eliminate species from smallest to largest when hunting pressure is greatest. Where $PowerCE > -0.35$, stepwise extinctions eliminate species from largest and 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.

Regardless of functional response form, under biologically reasonable parameter combinations all simulations yield the same general pattern of survival-extinction outcomes (**Figure 5**). In moving through parameter space from lower to higher values of both C_a and $PowerCE$, the progression is: predator extinction, coexistence of all species, loss of the two largest prey species, followed consecutively by loss of the three, four, and five largest prey species, and, finally, the extinction all species. We observed no parameter combinations yielding the result predicted by the BKA hypothesis.

Discussion

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

We do not observe all five possible intermediate outcomes between coexistence and complete extinction, because the two smallest prey species either survive or go extinct together. We suspect that the very similar sizes of the two species lead them to share the same fate. Additional simulations outside the scope of the current project would allow us to test that explanation.

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_m 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. This outcome may represent evidence that the functional response dynamics of obligate predator-prey systems do not apply to multi-prey systems.

We are left to explain the inability of models to match observed survival-extinction outcomes. If our results are correct, differences in functional response cannot account for these shortcomings. One possible explanation is 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.

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. 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 this 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 (**Figure 1**). Given our limited knowledge of the biological characteristics of extinct species, however, such a model would be unfalsifiable. We are left to conclude that allometric constraint in Late Pleistocene extinction modeling involves serious 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 resolution.

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 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 would have influenced capture efficiency (**Chapter 2**). Our models consider a range of possible capture efficiencies but offer no additional insights into how this uncertain parameter might be constrained.

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 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 unrelated to functional response.

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 there are no significant consequences for adopting different functional response forms in this modeling context. Such a result suggests to us a need for considerable caution in both the design and interpretation of Late Pleistocene extinction models. 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.

Although the BKA hypothesis assumes that human predation caused megafaunal extinctions, it neither supports the overkill hypothesis nor refutes alternative climate-based explanations. It merely suggests that, under some parameterizations, human predation could have resulted in extinctions among larger and smaller prey species. Thus the BKA-derived conjecture remains consistent both with overkill scenario and extinctions resulting from a broader range of anthropogenic causes including but not limited to hunting, either in

conjunction with or in isolation from climatic effects. We would argue that the same qualification should be applied to other recent modeling efforts (e.g., Alroy 2001).

Figure 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).

<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	Surviving (Extant)	=	S
<i>Equus francisi</i>	368	E	Extinct	=	E

Figure 2: Berezovskaya-Karev-Arditi Ratio-dependent Parameter Space and Its Predicted Extinction/Coexistence Zones, where α is the predator's capture efficiency of the prey species, r_{prey} is the prey species' maximal rate of population increase; μ is the predator's death rate in the absence of prey; and $r_{predator}$ 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.

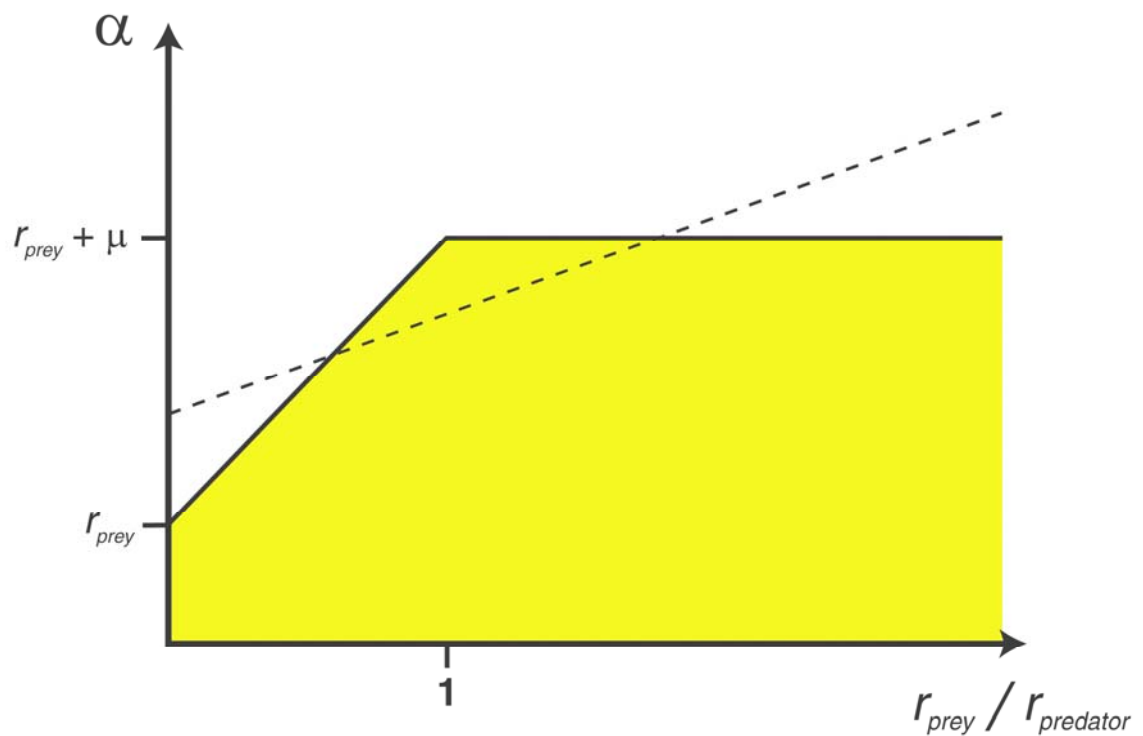


Figure 3: Two-Line Method of Predicting Late Pleistocene Mammalian Extinctions. This simplified, intuitive approach achieves two more correct outcome matches than Alroy's (2001) opaque and much more complex method. Data from Alroy (2001).

<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		Surviving (Extant) =	S	
<i>Equus francisi</i>	368	E		Extinct =	E	

Figure 4: Model Flow Chart

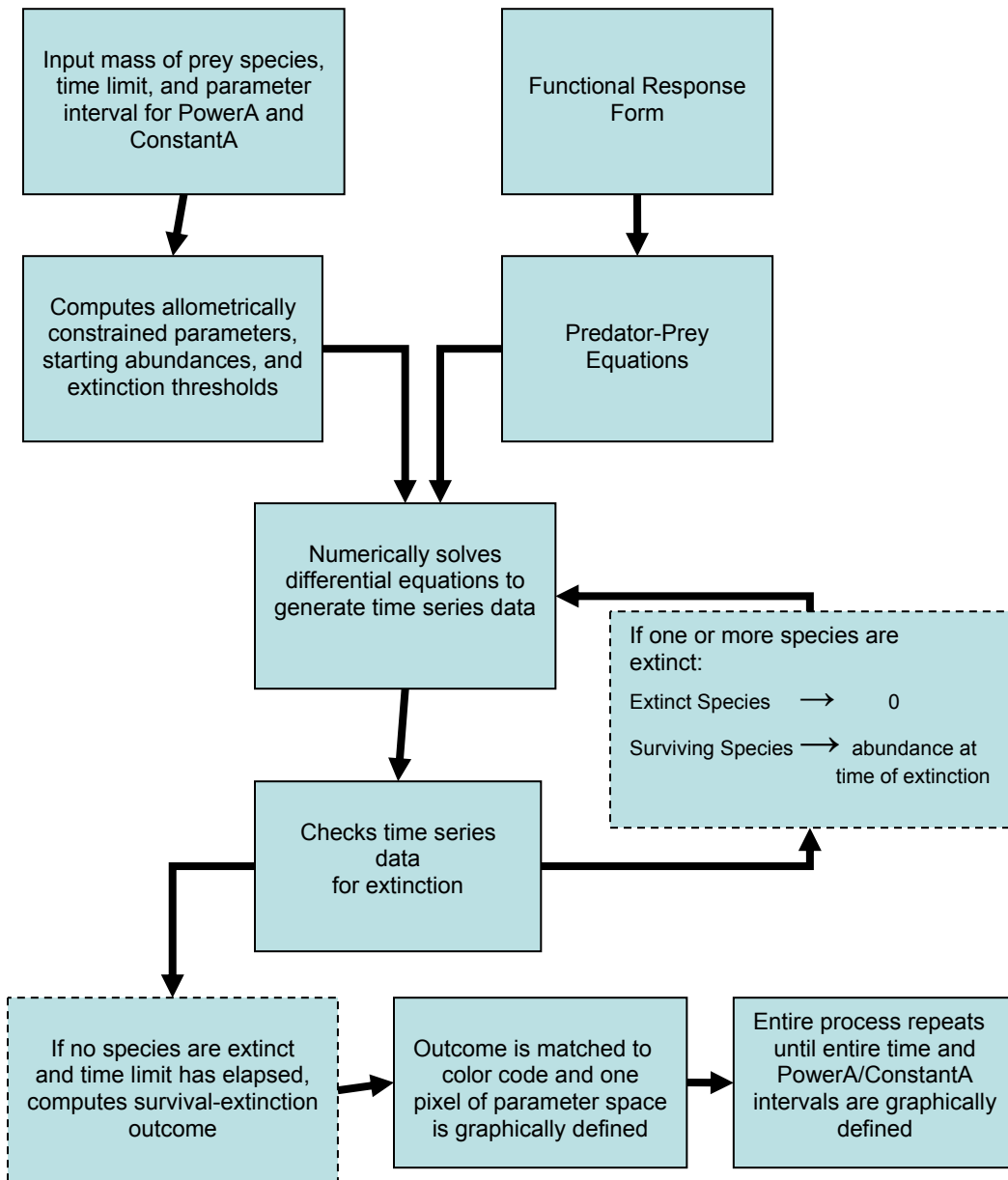


Figure 5: Survival-Extinction Outcomes. Bracketed numbers represent, from left to right, six prey and one predator species; 0 = extinct and 1 = surviving.

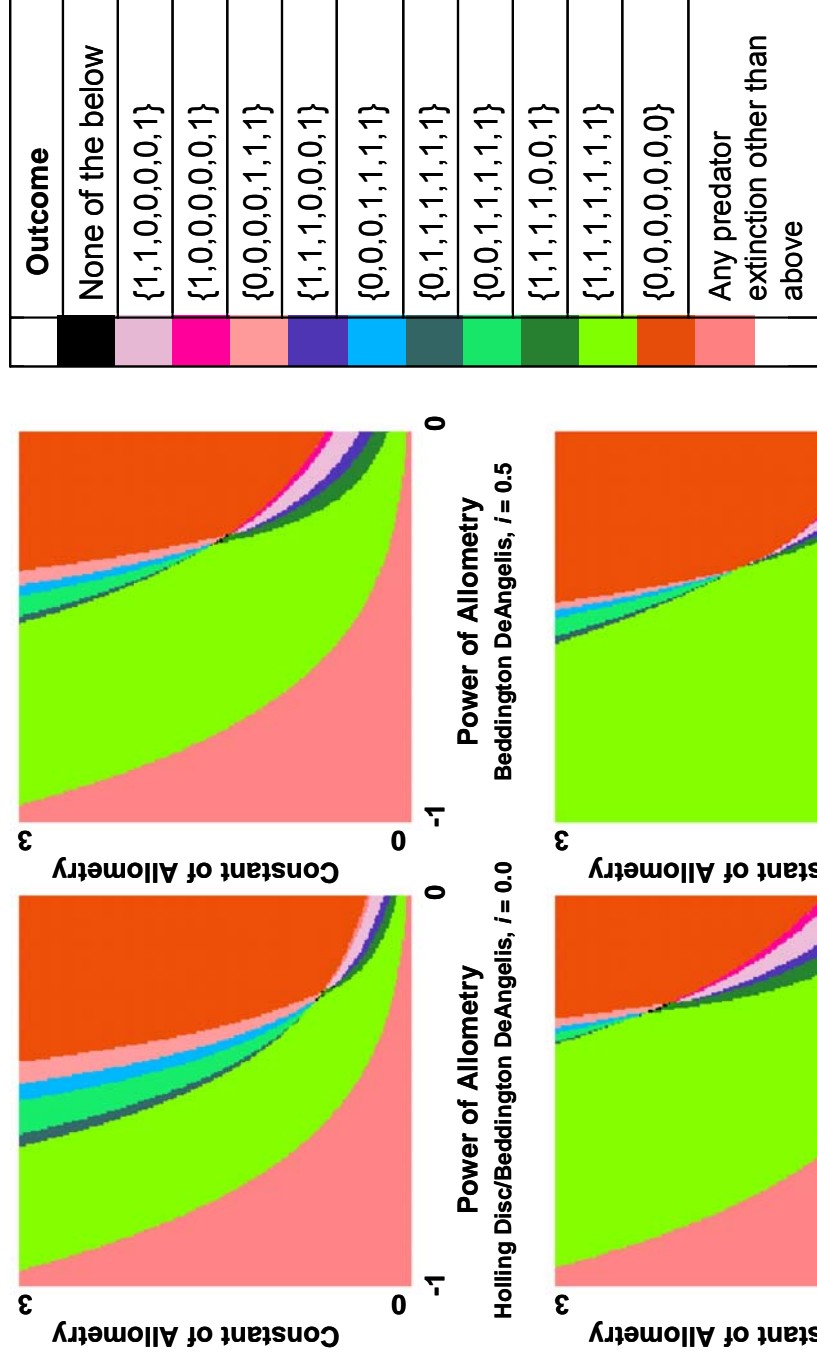


Table 1: Late Pleistocene Extinction Model Functional Response Assumptions

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. (Chapter 1)	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

Table 3: Parameterizations — Allometric Constraints and Assumptions

Parameter	Allometric Power Assumed	Source
r_m (maximal rate of population increase)	- 0.36	Caughley and Krebs (1983)
K (carrying capacity)	- 0.75	Damuth 1987
e (conversion efficiency)	1.0	Assumption: all herbivore flesh has equal per kg nutritional value
h (handling time)	1.0	Assumption: time to prepare and digest herbivore flesh is proportional to its mass
a or α (capture efficiency)	Unknown	The parameter our model explores

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Chapter 4

Extinction as Predator Removal: Intraguild Competitive Cascades, Mesopredator Release, and a Paleoecological Perspective for Ecological Restoration

Jeffrey V. Yule

To be submitted to *Ecological Restoration*

Context:

Pleistocene extinctions and paleoecology have broader relevance for conservation, management, and restoration than my previous chapters address. My final chapter explores that broader relevance through its presentation of a new model of carnivore competition.

Abstract

Recognition that Paleoindians and Native Americans significantly altered the ecosystems they occupied suggests that North American restoration efforts might be better directed toward a pre-human Pleistocene standard rather than the pre-Columbian (i.e., before European contact) benchmark that has long been typical. Some grasp of the relevant ecological details will be necessary to settle the matter. The difficulty is in synthesizing paleobiological and neontological data into tractable formats to illuminate both vanished ecosystems and contemporary restoration practice. The current paper takes a step in this direction by presenting a new ecological model of one representative North American predator guild: the canids. The model reconstructs some aspects of Late Pleistocene, Holocene, and historical ecosystems and provides a tool for the management of carnivores and their prey. The model suggests that mesopredator release in North America might have been typical during the Pleistocene, that ecological restoration efforts aimed at a Pleistocene benchmark could in some respects benefit from excluding rather than introducing the largest predators, and that restoration efforts aimed at a pre-Columbian benchmark would benefit threatened mesopredator prey species, while a Pleistocene restoration strategy would provide them with little or no advantage over current conditions. These conclusions emphasize the value of a paleoecological perspective in conservation biology and ecological restoration.

Introduction

Any restoration plan requires some benchmark towards which to direct efforts and against which to evaluate success. Currently, the most general North American restoration benchmark is under scrutiny. Recognition that Paleoindians and Native Americans significantly altered the ecosystems they occupied (e.g., Cronon 1983, Flannery 2001, Martin and Szuter 1999) has led to suggestions that North American restoration might be better directed toward a pre-human Pleistocene standard rather than the pre-Columbian (i.e., pre-European contact) benchmark that has long been typical (e.g., Donlan et al. 2005, Flannery 2001, Martin and Burney 1999). An improved grasp of the relevant ecological details will be necessary to determine whether such an approach is practical rather than merely esthetically or philosophically attractive (Yule 2006—**Appendix 3**). The difficulty is in synthesizing paleobiological and neontological data into tractable formats capable of illuminating both vanished ecosystems and contemporary restoration and conservation practice. The current paper takes a step in this direction by presenting a new ecological model of one representative North American predator guild: the canids. The model was developed to answer the question: “Can our understanding of predator ecology and paleoecology inform our decisions about whether to pursue a pre-human Pleistocene or a pre-Columbian standard for restoration and conservation?”

To help answer that question, the new model depicts the competitive dynamics and ecological consequences of a particular carnivore group’s interactions. The term “guild” typically refers to organisms that occupy

overlapping niches and experience a high degree of resource overlap. Thus, a variety of species, not all of them closely related (e.g., foxes, coyotes, badgers, and raptors) might constitute the small predator guild in a particular area. The term “guild” can also refer to a group of phylogenetically related species that occupy overlapping niches and use similar morphologies and behaviors in utilizing resources. I will use the term primarily in this latter sense in referring to North American canids as a guild, focusing particularly on both extant species (gray wolves, coyotes, and foxes) and one extinct species (dire wolf).

In cases of interspecies competition within carnivore guilds, the larger competitor typically prevails. In an effort to illuminate the relevant ecological dynamics at issue with North American carnivores both during and since the late Pleistocene, I relied on this general principal to develop a conceptual model. Subsequently, I surveyed the literature on interspecific carnivore competition to gather data against which to assess the model and its utility for contemporary restoration.

The resulting model represents North American canid guilds during three periods: the pre-human Pleistocene, the pre-Columbian, and the recent (i.e., twentieth century) in order to provide a tool for restoration and the management of carnivores and their prey. It also suggests conclusions that could initially appear counterintuitive: (1) that mesopredator (i.e., middle-sized predators) release in North America, rather than representing an ecological novelty, might have been typical during the Pleistocene and (2) that ecological restoration efforts aimed at a Pleistocene benchmark could in some respects benefit from

excluding rather than introducing the largest predators. In addition, the model suggests (3) that restoration efforts aimed at a pre-European North American benchmark would benefit threatened mesopredator prey species, while a Pleistocene restoration strategy would provide them with little or no advantage over current conditions. These conclusions emphasize the value of a paleoecological perspective in conservation biology and the need for caution in restoration efforts, particularly those that call for the introduction of Old World megafauna as analogs for extinct Pleistocene species (e.g., Flannery 2001; Donlan et al. 2005). Since the major conservation challenge for the foreseeable future will be the limited availability of wildlife habitat, priority should be given to protecting extant North American species and understanding their ecology. Such a prioritization will inform the decision about whether a pre-Columbian or pre-human Pleistocene standard is preferable for North American restoration. Megafaunal introductions, should they ever be deemed desirable, would necessarily follow this more fundamental ecological research.

Mesopredator Release and Intraguild Competition

Terborgh and Winter (1980) suggest that the loss of top carnivores on Panama's Barro Colorado Island allowed populations of mesopredators to flourish, leading to the extirpation of their avian prey. Subsequently, a generalized mesopredator release hypothesis gained empirical support (e.g., Crooks and Soulé 1999). Based both on initial data (Wilcove 1985) and

accumulating evidence of mesopredator release, Wilcove (1999) treats mesopredator release as a fact of North American ecology. The absence of wolves, bobcats, and mountain lions from the Eastern U.S. contributes significantly to the region's unusually large populations of opossums, raccoons, and skunks, which suppress populations of their prey species (e.g., resident and Neotropical migrant songbirds), increasing their extinction risk.

From a historical perspective, both accelerated habitat fragmentation and the loss of these top predators is relatively recent. Nonetheless, a brief examination of competition within the context of predator paleoecology does not support the notion that mesopredator release is solely a modern ecological novelty, as the nest predation literature assumes (e.g., Rogers and Caro 1998). Instead, available evidence about intraguild competition amongst carnivores suggests that similar ecological release prevailed throughout much of the Pleistocene.

Competition amongst predator species takes many forms, with varying consequences for the competitively inferior species—almost always the smaller competitor. The most severe consequence of competitive encounters is death via intraguild predation. Theory predicts (Holt and Polis 1997) that intraguild predation can have strong effects on subordinate competitors' population dynamics, a claim with empirical support among carnivores, particularly canids (e.g., Carbyn et al. 1994; Peterson 1995; White and Garrott 1999). Less severe manifestations of competition (e.g., theft of kills by larger competitors) also influence the population dynamics of subordinate competitors (Creel et al. 2001).

Canid intraguild competition helps determine the relative abundance of the species within the guild via a competitive cascade. In regions where extant canids are all present, the result is a three-species pattern in which each member species suppresses populations of its next smaller competitor (Macdonald and Sillero-Zubiri 2004). Gray wolves suppress or exclude coyote populations (Peterson 1995; Creel et al. 2001) and, in turn, coyotes suppress or exclude foxes (Voigt and Earle 1983; Sargeant et al. 1987; Ralls and White 1995). Similarly, larger fox species, such as red fox, suppress smaller competitors, including arctic fox (Hersteinsson and Macdonald 1982; Tannerfeldt et al. 2002) and kit fox (Ralls and White 1995). Because of this competitive dynamic, regional wolf removal allowed for coyote range expansion in Alaska's Kenai Peninsula and the prairies of the central U.S. and Canada (Thurber et al. 1992). Conversely, wolf reintroduction to Yellowstone National Park led to a significant decline in both the number of coyote packs and the total number of coyotes (Crabtree 1998), while Isle Royale's coyote population was eliminated within a decade of wolf recolonization (Peterson 1977).

Observation suggests that such cascades arise because between any pair of sympatric canids, increasing similarity in body size predicts increasing competition. While wolves do kill foxes, they more frequently kill coyotes (Peterson 1977; Ballard et al. 2003). Typically, red foxes are also more numerous in areas where wolves depress coyote populations (Macdonald and Sillero-Zubiri 2004). This evidence supports the contention that wolf-coyote and coyote-fox competition are typically more pronounced than wolf-fox competition

(e.g., Peterson 1995). The fact that wolves do not typically consume the coyotes they kill (Ballard et al. 2003) suggests competition rather than hunger as the primary motivation for this intraguild predation.

Given these starting conditions, wolf eradication in the contiguous 48 United States should have led to an increase in coyote populations and a decrease in fox populations (Macdonald and Sillero-Zubiri 2004). Data are consistent with this scenario. Although some exceptions occur at smaller spatial and temporal scales, wolf and coyote population densities typically follow an inverse relationship (Carbyn 1982; Thurber et al. 1992; Peterson 1995). So, too, do those of coyotes and red foxes (Linhart and Robinson 1972; Sargeant et al. 1987; Peterson 1995).

The consequences of this dynamic do not appear to have been extended to a fuller consideration of pre-human Pleistocene ecosystems—perhaps because a lack of paleoecological perspective has led ecologists to consider a three-species pattern of canid sympatry to be typical (Johnson et al. 1996; Crabtree and Sheldon 1999). Yet for much of the Pleistocene, a four-species pattern of canid sympatry probably prevailed, consisting of the historically familiar three-species pattern with the extinct dire wolf acting as an additional dominant predator. If so, the suppression of North American wolf populations during the nineteenth and twentieth centuries should have led to a situation for smaller canids and their prey that paralleled the one that prevailed during much of the Pleistocene.

Observations of large carnivore interactions in ecosystems supporting exceptionally high predator diversity such as occur in Africa (e.g., Estes 1991) coupled with functional morphological analysis of fossil carnivores (Kurtén and Anderson 1980; Van Valkenburgh 1989, 1995, 1999) suggest that dire wolves once similarly suppressed populations of their next smaller canid guildmates. The dire wolf's large size, robust build, and hyena-like dentition suggest that it was North America's dominant canid—a conclusion perhaps supported by the abundance of its fossils in Rancho La Brea's asphalt deposits (Wang et al. 2004). Although uncertainties about wolf species designations and distributions (e.g., Kurtén and Anderson 1980; Theberge 2000) make identification of the next smaller species difficult, in many areas the Gray or Timber Wolf, *Canis lupus*, is a likely candidate. Working from this starting point and making the simplifying assumption of negligible effects on canids from non-canid predators, I suggest three ecological scenarios for canids, which are broadly representative of what other guilds of predatory mammals experienced (**Figure 1**). For smaller canids (and, by extension, for their prey), the historically recent guild structure closely resembles that of the Pleistocene before megafaunal extinctions. The situation that prevailed after megafaunal extinctions and before European arrival in North America represents the novelty.

The current analysis does not contradict the argument that contemporary mesopredator release poses a threat to North American bird populations. I merely mean to point out that some paleoecological context could allow for a better-informed perspective on restoration and conservation challenges—and,

perhaps, more effective responses. For instance, although ecologists view mesopredator release as a recent consequence of habitat fragmentation, the dynamics of intraguild competition suggest that it might have been typical of pre-human North American ecosystems. Part of the reason Late Pleistocene mesopredator release was not problematic for prey species under threat today probably relates to the formerly abundant, heterogeneous habitat that was available. But the dynamics of intraguild competition among predators was also likely to have played an important role by suppressing populations of key predator species.

Conclusion

The conservation biology implications are noteworthy. From a restoration perspective, for instance, some ecological features of lost Pleistocene ecosystems could in some respects be more readily approximated not by introducing the largest Old World megafaunal predators (e.g., lions, tigers) as analogues for the largest missing species, as some have suggested (e.g., Flannery 2001; Donlan et al. 2005). Instead, maintaining historically occurring top North American predators (e.g., gray wolves) at populations below carrying capacity would mimic some of the competitive and predator-prey conditions that prevailed when dire wolves were the dominant canids—yielding a Pleistocene-minus-one-tier guild structure.

Ecosystems containing analogues for the largest extinct megafauna would be readily distinguishable from those that do not. Nonetheless, a simple management strategy (e.g., one involving predator culling) could approximate three-fourths of the Pleistocene canid guild structure—and presumably abundances of canid prey species—potentially restoring some of Pleistocene North America’s trophic and species abundance characteristics. Such an approach would also benefit threatened mesofaunal prey species. On the other hand, introducing a new top tier of predators to approximate lost species would do little or nothing to reduce the threat to mesopredator prey—a problematic situation for the foreseeable future given the lack of wildlife habitat. While I have focused on the example of canids, the same logic of intraguild competition should apply more generally to carnivores, suggesting a means of restoring or approximating significant aspects of Pleistocene North American ecology.

Although actual carnivore guilds would likely be more speciose (e.g., including felids and ursids as well as canids) at any given competitive level, they would reflect the same broad patterns of size dominance and subsequent cascades of population suppression and release. It follows, then, that the direct effects on predators and the indirect effects on prey resulting from competitive suppression and release could inform decisions about restoration and species management. The particulars will necessarily be context-dependent, however. Since the number of different size classes of competitors varies from location to location, the same species might be the mesopredator of one community and the

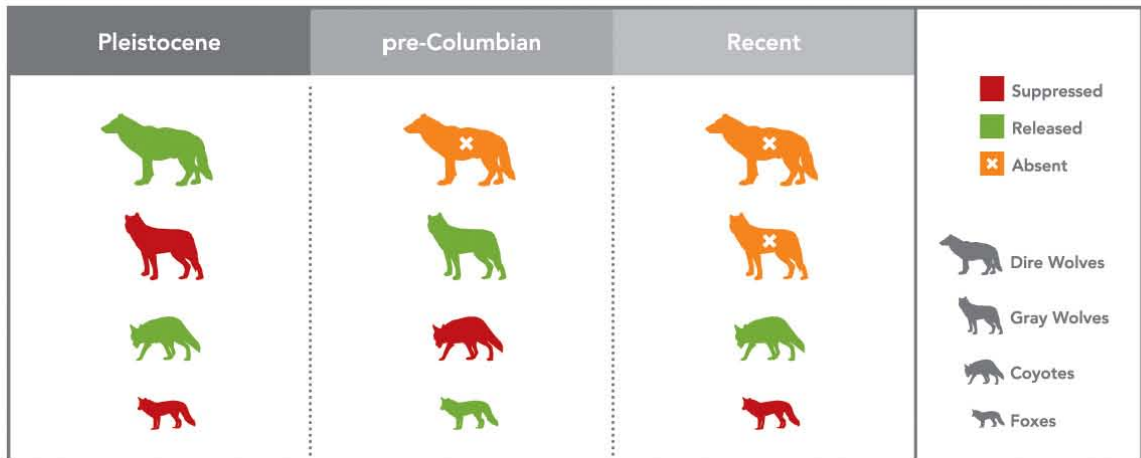
top predator of another. Nonetheless, understanding the overall competitive dynamic will allow for better context-specific decision-making.

Conservation biologists have recognized the potential importance of interspecific, intraguild competition—suggesting, for instance, that management strategies could take advantage of intraguild predation in general or mesopredator release in particular (for a recent review see Müller and Brodeur 2002). The current suggestion that a paleoecological perspective on intraguild competition has implications for ecological restoration, however, appears to be novel and deserving of additional investigation. More broadly, a paleoecological perspective would provide benefits in a variety of restoration and conservation biology contexts, including estimating the ecological effects for interacting species of potential conservation strategies (e.g., Soulé et al. 2003), informing discussions of what constitutes “good” restoration (Higgs 1997), or, more specifically, determining how restoration can best proceed in North America. For now, the take-home message is a reminder to proceed with caution. Restoration of North American ecosystems to some approximation of their historical condition might prove to be preferable to megafaunal introductions; at the very least, the current example suggests that efforts aimed at a pre-Columbian benchmark for restoration should be given priority over attempts at working toward a Pleistocene standard.

Acknowledgments

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Figure 1: Three Canid Competition Scenarios. Depicted are the states (in terms of presence in or absence from the guild) and effects (population suppression resulting from competition or population release resulting from lack of competition) each species experienced due to the actions—or absence—of a next larger competitor. In each of the three different periods (i.e., the Pleistocene, pre-Columbian, and Recent columns), species mass decreases from top to bottom. Note the similarities between the “Pleistocene” and “Recent” scenarios for the smaller canids (coyotes and foxes).



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Chapter 5

Canids, Neotropical Migrant Birds, and Conservation: Tests Using Data from the Greater Yellowstone Ecosystem Confirm an Intraguild Canid Competition Model

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To be submitted to *Conservation Biology*

Context:

In order to ground truth the model presented in Chapter 4, I obtained raw data from two different data sets to test the models assumptions and predictions. The following chapter consists of two sections “A” (which presents the tests of model assumptions) and “B” (which presents the test of model predictions). Each section should be read concurrently.

Abstract

Data from the Greater Yellowstone Ecosystem allow for a strong preliminary test of the assumptions and predictions of my intraguild canid competition model (**Chapter 4**). I test model assumptions by examining data on canid intra- and interguild competition, using data on inter- and intraguild killing of predators as a measure of competition. I test model predictions using neotropical migrant songbird (NMS) census data. I use a Before-After Control-Impact (BACI) ANOVA to determine whether the data are consistent with the hypothesis that NMS have experienced ecological release as a consequence of wolves suppressing mesopredator populations. Analysis confirms that both model assumptions and predictions are consistent with available data.

Introduction

A strong preliminary test of the assumptions and predictions of my intraguild competition model (**Chapter 4**) requires data from a monitored region that meets three criteria. First, it must provide data on a newly reintroduced top canid carnivore, with specific information available about the timing of the reintroduction. Second, abundance data for neotropical migrant songbirds (NMS) must be available for periods both before and after the reintroduction. Third, control data on NMS populations in similar areas where top carnivore reintroductions have not occurred must be available. Gray wolf reintroductions to Yellowstone National Park in 1995 and 1996 provide just such an opportunity. Reintroduced wolves have been intensively monitored, allowing for the

quantification of their competitive interactions with both canid and noncanid predators. Annual North American Breeding Bird Survey (BBS) routes provide the necessary NMS census data. Three routes overlap recently established wolf territories within Yellowstone National Park, while an additional three routes in national forests elsewhere in the Greater Yellowstone Ecosystem function as effective control sites for comparative purposes.

Methods

A. Test of Model Assumptions

Following wolf reintroduction to Yellowstone National Park in 1995 and 1996, wolf predation on herbivores was intensively monitored for two 30-day periods per year, in March and from mid-November through mid-December (e.g., Phillips and Smith 1997; Smith 1998). As a corollary to that effort, beginning in 1999 data on wolf kills of predators were also recorded. Because inter- and intraspecific killing represent the most extreme manifestations of competition, these data provide a means of quantifying the degree of competition occurring both within the canid guild and between canids and non-canid predators. To quantify competition, I culled data on wolf kills from Yellowstone Wolf Project Annual Reports (Smith et al. 1999, 2000, 2001, 2003, 2004 2005; Smith and Guernsey 2002) (**Table 1**). I then determined whether the data were in accord with the three key assumptions of my intraguild competition model (**Chapter 4**): (i) that the majority of competition faced by canids should come from within the canid guild; (ii) that competition between canids of the same or adjacent size

classes should be maximal; and (iii) that competition between non-adjacent size classes (i.e., the largest and smallest canids) should be minimal.

B. Test of Model Predictions

My canid competition model predicts that the introduction of a new top predator to a system would lead to the ecological suppression of mesopredators and the release of their prey (**Chapter 4**). Given that prediction, one effective test of the model would be to assess the effects of wolf introduction on the abundance of mesopredator prey species, such as the neotropical migrant songbirds. Such a test would require specific information on the timing of wolf reintroduction, pre- and post-reintroduction NMS census data for areas where wolves were reintroduced, and control NMS census data for the same time period from comparable areas where wolves were absent. The goal would be to undertake a before- and after- analysis to reveal, first, whether any significant interaction exists between the presence of wolves and NMS abundance and, second, if one exists, whether it is in the predicted direction.

An entire class of analytical framework, Before-After Control-Impact (BACI) analyses, was developed for addressing questions of exactly this sort. BACI analysis was initially developed for assessing unplanned environmental impacts (e.g., oil spills, chemical spills) in which it was important to determine whether the impacts in question had significant ecological effects and, if so, in what direction (Green 1979). Such situations commonly involve one or more of the following difficulties: limited pre-impact data, limited control data, uncertainty

about the timing of the impact, and limited power (Green 1979; Smith 2002)—none of which apply here. Relative to other contexts in which BACI techniques are applied, the current situation is nearly ideal in allowing for statistical analysis of the relevant trends. Pre-impact, post-impact, and control NMS census data are available, and the timing of wolf reintroduction is known. Due to the nature of the data available, the BACI methodology can be readily and profitably adapted to the current question.

The annual North American Breeding Bird Survey (BBS) follows multiple 24.5-mile road routes. Beginning 30 minutes before local sunrise during peak breeding season, observers on each route stop at 0.5-mile intervals for a three-minute point count of all birds seen or heard within a 0.25 mile radius. Three North American Breeding Bird Survey Routes (001, NE Entrance; 030, Mammoth; and 901, Yellowstone) in the Wyoming portion of Yellowstone National Park fall within recently established wolf territories. Three additional survey routes outside of Yellowstone but within the Greater Yellowstone Ecosystem (GYE) that do not overlap wolf territories provide controls. Control route 071 (Soda Lake) is in Bridger National Forest; control routes 041 (Bald Mountain) and 042 (Crazy Woman) are in Bighorn National Forest.

Data from these routes are particularly amenable to analysis via a BACI, two-way ANOVA, with wolf reintroduction representing a press impact (Underwood 1994; Smith 2002). The proposed analysis highlights the interaction of interest: between Location (wolf versus non-wolf) and Period (pre- versus post-wolf reintroduction). Given the nature of the analysis, the available data also

preclude potential difficulties of limited statistical power. Three routes overlap areas where reintroduced wolves initially established territories. Experiments or surveys designed specifically to test the canid competition model would ideally involve greater replication to insure the availability of sufficient data. What represents sufficient data, however, is largely a matter of context. The requirements for a BACI analysis to discern pattern in the noisy temporal variance of population data are modest (Underwood 1994). From a BACI perspective, the replication available here is exceptional in providing both sufficient spatial and temporal replication necessary for a powerful design (Stewart-Oaten et al. 1986; Underwood 1994). I predicted that a significant interaction would exist between Location and Period and, more specifically, that wolf reintroduction would correlate with an increase in mean NMS abundance relative to that in control areas.

To test this hypothesis I found a total of 10 neotropical migrant songbird species with breeding ranges overlapping Yellowstone National Park (**Table 2**) and more than one of the BBS routes used in this study. All species are open cup nesters, although the heights at which they nest vary from ground level to high canopy. The canid intraguild competition model (Chapter 3) predicts that the suppression of mesopredators resulting from wolf reintroduction should lead to increases in the size of NMS populations when compared to areas where wolves are absent. The model focuses on aggregate, community-level properties resulting from the ecological suppression or release of various size classes of predators and prey (**Chapter 4**). For that reason, I assumed *a priori* that it would

be most appropriate to treat NMS as a single, aggregate functional group. Such an approach is not only reasonable in a BACI context but also necessary, because the bird census data available preclude a strong test of interaction between the putative impact (i.e., wolf reintroduction) and subsequent changes in NMS abundance at the level of single species. Approaching the data in this aggregate manner also results in a more conservative test, since any species exhibiting an alternative response would reduce the power of the analysis.

Wolf reintroduction took place in 1995 and 1996, a two-year impact. The years 1978-1994 provide “before” data; the years 1997-2006 provide “after” data; and 1995-1996 data were excluded from the analysis. Because count data follow

a Poisson rather than normal distribution, I transformed it using the $Y' = \sqrt{Y + \frac{1}{2}}$

function ($\frac{1}{2}$ was added to each value to accommodate the many zeros in the data set; Sokal and Rohlf 1995). In all other respects, the data met the conditions of the analysis. Although serial correlation represents a potential problem with BACI analyses that can depress p -values and result in Type I errors (e.g., Conquest 2000; Murtagh 2000), inspection of the raw data revealed marked annual variation, suggesting that serial correlation was unlikely to be a problem in this particular case.

JMP version 5.1 was used for all analyses.

Results

A. Test of Model Assumptions

Consistent with the model assumption that most canid competition is intraguild, the majority (78.08%) of predators killed by wolves were canids of the same or adjacent size class. 52.05% of total kills were coyotes; 26.03% of total kills were wolves; and there was no evidence that wolves killed foxes (i.e., 0.0% of total kills foxes). A minority (21.92%) of all predators killed were non-canids, with no single species representing $\geq 5\%$ of total predators killed. Large non-canid predators (brown bear and cougar), which are typically killed as cubs, together represent 8.22% of total predators killed by wolves. Treated as aggregate groups, smaller mammalian predators (badger, skunk) and predatory/scavenging birds (golden eagle, raven, short-eared owl) each represent 6.85% of total predators killed.

Wolf mortality has been monitored since their reintroduction to Yellowstone. In the study area no predators other than wolves are known to have killed wolves. A less serious consequence of competition between predators is loss of prey. Although the data have not been systematically recorded or reported in Yellowstone, this form of competition from non-canids appears to be more significant for wolves. Brown bears routinely displaced wolves—particularly those of the smallest pack, Mollie's—from prey (bison) in 1997, 2000, and 2002. Reflecting the competitive superiority of wolves over cougars, wolves also displaced cougar from prey (elk) in 2004.

B. Test of Model Predictions

The ANOVA revealed a highly significant interaction between Location and Period in the direction predicted by the model (**Table 3; Figure 1**). Pre-wolf reintroduction NMS abundances were not significantly different between the control and wolf reintroduction locations. After wolf reintroduction, wolf reintroduction areas exhibited a slight NMS population increase, while, in contrast, NMS abundances declined markedly in control areas.

Discussion

A. Test of Model Assumptions

These data suggest that the model's assumptions are reasonable. In systems where the same predatory species co-occur, similar patterns should hold—with one exception. The mean number of instances of wolves killing other wolves would likely be higher. The data for the first years after reintroduction record relatively few cases of wolves killing other wolves (a mean of 0.75 wolves killed per year from 1998-2001) with the number increasing subsequently (a mean of 5.0 wolves killed per year from 2002-2005). This discrepancy in means likely results from minimal intraspecies competition during the years it took wolves to approach carrying capacity, a period that was probably extended due to wolf mortality resulting from automobile collisions and culling of nuisance individuals.

B. Test of Model Predictions

The presence of a significant interaction between Location and Period (**Table 3**) and the direction of the observed changes in NMS abundances (**Figure 1**) are consistent with the model's predictions. Possibly, the ecological effects resulting from the presence of wolves acted to buffer the factors that led to a decline in mean NMS abundance in control areas. Such an explanation, while reasonable, must remain conjectural.

Nonetheless, the results of the current analysis are noteworthy. The BBS provides the best available data to test for changes in NMS populations in the wake of North American canid reintroduction. Yet these data involve potential limitations. The most significant of these relates to the fact that BBS routes follow roadways and census disturbed habitat that may not adequately reflect NMS population trends elsewhere in Yellowstone National Park or the Greater Yellowstone Ecosystem. Possibly, wolf-reintroduction effects would have been less evident in these areas. If so, this analysis is presumably conservative in that the data would underestimate any positive effect of wolves on NMS abundances.

Conclusions

A. Test of Model Assumptions

Model assumptions are robust to comparison with available data, particularly data from a restoration context, for which the model was designed. These results suggest that the model's starting assumptions are valid.

B. Test of Model Predictions

Conquest (2000) correctly emphasizes the value of prudence in interpreting BACI analysis results. The challenges involved in interpreting BACI analyses represent in microcosm the interpretive challenges inherent to biometry in general. Even if analyses reveal significant differences in pre- and post-impact means, such results are not sufficient to indicate a causal relationship between the impact in question and the observed effects on measured means. That the model's predictions are in such close accord with existing data lends support to its potential validity. Keeping in mind the dictum that "all models are wrong, but some models are useful" (Anderson and Woessner 1992), however, a more restrained conclusion is prudent. Accordingly, then, I conclude that the results of the current analysis lend additional support to the notion that the model might have utility in the wildlife restoration and management context for which it was developed.

Figure 1

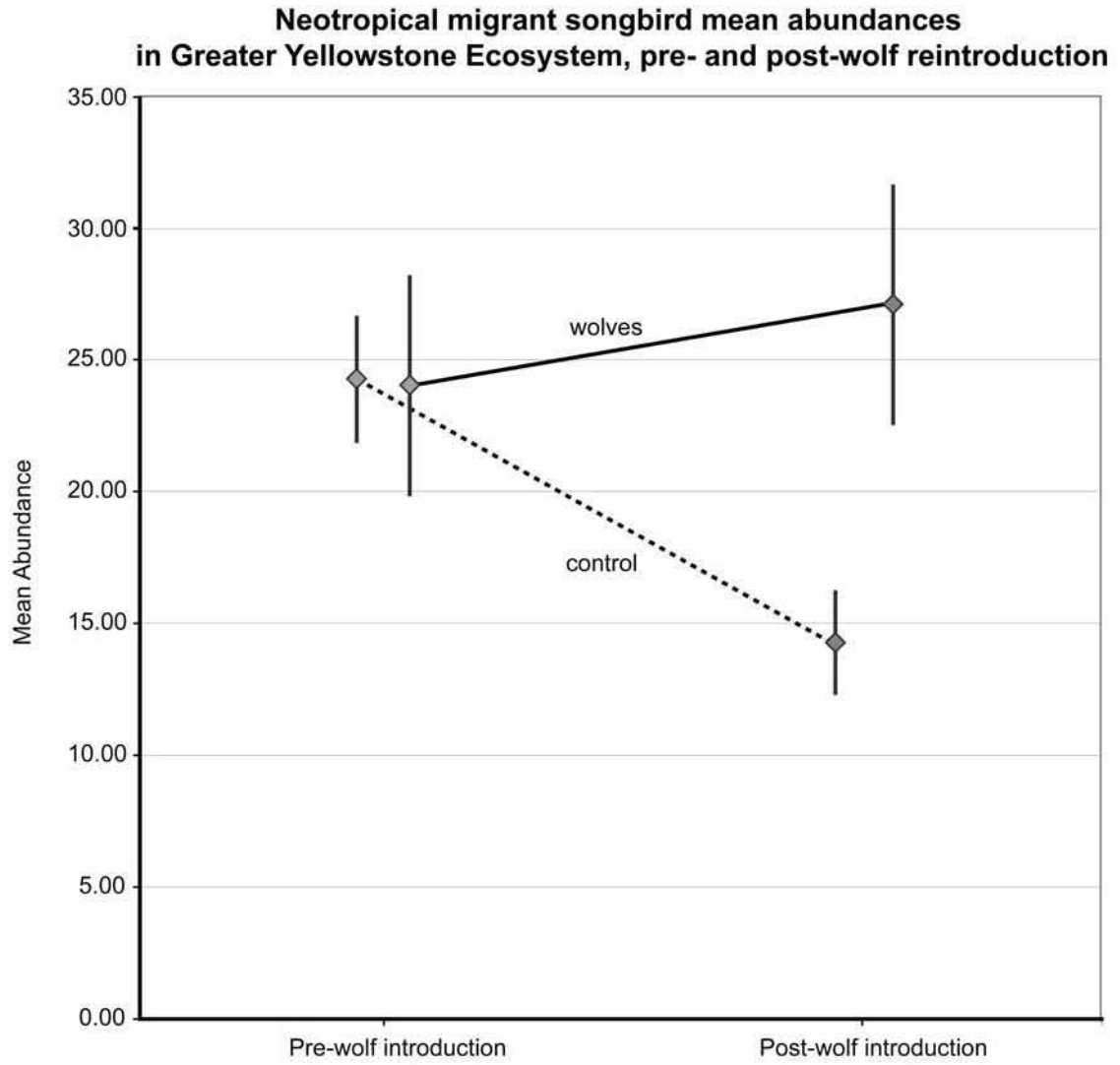


Table 1: Predator species killed by wolves 1998-2005

Predator Species	Number Killed	Percentage of Total Predators Killed
Wolf	19	26.03
Coyote	38	52.05
Fox	0	0.00
Brown Bear	3	4.11
Cougar	3	4.11
Badger	3	4.11
Skunk	2	2.74
Raven	3	4.11
Golden Eagle	1	1.37
Short-eared Owl	1	1.37

Data from Smith et al. (1999, 2000, 2001, 2003, 2004 2005) and Smith and Guernsey (2002)

Table 2: Species included in test of model predictions

Name	Latin Binomial
American Redstart	<i>Setophaga ruticilla</i>
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Dusky Flycatcher	<i>Empidonax oberholseri</i>
Gray Catbird	<i>Dumetella carolinensis</i>
MacGillivray's Warbler	<i>Oporornis tolmiei</i>
Plumbeous Vireo	<i>Vireo plumbeous</i>
Warbling Vireo	<i>Vireo gilvus</i>
Western Wood-Peevee	<i>Contopus sordidulus</i>
Yellow Warbler	<i>Dendroica petechia</i>

Table 3: ANOVA for two-factor BACI design with replication

Source	SS	df	F	P
Location: Control-Wolves	5.89425	1	0.0572	0.8228
Route[Location]	434.908	4		
Period: Before-After	0.04887	1	0.0515	0.8221
Year[Period]	24.9786	26		
Interaction: Location x Period	5.15834	1	6.2370	0.0144
Error	71.12648	86		
Total	598.84550	119		

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Appendix 1

Aiming the “Unreasonable Effectiveness of Mathematics” at Ecological Theory

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In Press, *Ecological Modelling*

Context:

Broadly speaking, my interests in and perspective on the philosophy and methodology of ecological modeling is foundational to my work, just as it is for any modeler. This project addresses the fundamental modeling question: “What level of generality is appropriate for a model?” In important respects, this paper articulates many fundamental aspects of the approach I take in all of my previous chapters

Abstract

A good theory is focused without being blurred by extraneous detail or overgenerality. Yet ecological theories frequently fail to achieve this desirable middle ground. Here, we review the reasons for the mismatch between what theorists seek to achieve and what they actually accomplish. In doing so, we argue on pragmatic grounds against mathematical literalism as an appropriate constraint to mathematical constructions: such literalism would allow mathematics to constrain biology when the biology ought to be constraining mathematics. We also suggest a method for differentiating theories with the potential to be “unreasonably effective” from those that are simply overgeneral. Simple axiomatic assumptions about an ecological system should lead to theoretical predictions that can then be compared with existing data. If the theory is so general that data cannot be used to test it, the theory must be made more specific.

Introduction

As a language capable of describing patterns, mathematics has unmatched explanatory power (Steiner, 1978; Colyvan, 2001). Mathematical theory’s consistent success in the physical sciences inspired Eugene Wigner to celebrate the “unreasonable effectiveness of mathematics” in a famous 1959 lecture (Wigner, 1967). In many so-called exact sciences, mathematics has illuminated natural laws, allowing clear principles to be formulated.

Ecologists differ over whether it is appropriate to emulate these accomplishments: while some believe that “Principles of Ecology” are within our reach (Lawton, 1999; Turchin, 2001; Berryman, 2003; Colyvan and Ginzburg, 2003b), others maintain that the physical sciences provide a poor model for progress in biological fields (O’Hara, 2005). If we are to harness the unreasonable effectiveness of mathematics for ecology’s benefit, how should we go about it? What lessons can we learn from the mathematical successes of other scientific fields? What special properties of ecology create pitfalls for those attempting to use mathematical approaches?

We maintain here that it is crucial for ecological theories to remain in focus: general enough that their predictions and explanations extend beyond a single data set or system but specific enough that their predictions and explanations do not become trivial (**Figure 1**). Although we remain optimistic that mathematics can yield increased understanding in ecology, many current uses of mathematics remain uninformative: theories are either too specific (**Figure 1c**) or too general (**Figure 1e**). The most useful theories emphasize explanation over description and incorporate a “limit myth” (i.e., they describe a pure situation without extraneous factors, as with the assumption in physics that surfaces are frictionless). Ecological theories commonly do not meet the above criteria. Using our specific knowledge of predator-prey interaction theory, we review the reasons for this misfit and explore the possibilities and problems associated with the use of mathematics. We argue for a specific approach to constraining mathematical

constructs in ecology and suggest a set of rules for those who wish to use mathematics to illuminate ecological principles.

Laws, Postulates, and Principles

Newton's competitor Leibnitz developed a conception of gravity similar to but more general than the familiar Newtonian version. Rather than specifying a particular relationship between gravitational force and distance from the sun (as Newton did), Leibnitz suggested that gravitational force declined monotonically with distance. The idea was correct but not useful because it suggested no specific applicable function. The specific function Newton proposed (an inverse square decline in gravitational force with distance) led to the potentially falsifiable prediction of elliptical planetary orbits. This historical example demonstrates that generality is guaranteed to be safe but not practically useful. However uncomfortable it might be to take a risk and postulate a specific relationship, specificity at least has a chance of being useful. Generalities are too imprecise to serve as building blocks for productive theories.

Formulating basic principles for constructing theories necessarily involves striking a balance between generalities, which are safe but potentially useless, and specific statements, which are risky but potentially useful. Theories that are either too general or too specific are unlikely to be useful. Two of us have already described the errors associated with overly specific theories (Ginzburg and Jensen, 2004); here we address the problem of overly general theories.

A statement that will serve as a foundational principle must be precise and informative. We know of only one such unanimously agreed upon principle in ecology: the Malthusian law of exponential growth, a simple statement stressing the multiplicative character of reproduction. It is called a law in most textbooks even though populations cannot grow exponentially for long. It has all the features of a "good" law: it describes what happens in the absence of extraneous factors, establishing a baseline that sets the stage for developing theories aimed at more biologically relevant situations. The similarity of this law to Newton's first law of inertia (uniform motion in the absence of forces) has been observed (Ginzburg, 1986; Turchin, 2001).

Differences of opinion surface when theorists describe the ecological processes that lead to deviations from exponential behavior. Here, we consider as examples sets of principles proposed by Berryman (2003) and postulates suggested by Turchin (2001). Although there is nothing erroneous in either set, both suffer from a substantial degree of overgenerality that might render them unsuitable to serve as the foundation for effective theory. The problem with overly general statements is that they are trivially correct but do not lead to predictions specific enough to be checked against evidence.

An example from each of the two sets serves to demonstrate the risk in being too general. Turchin (2001) suggests generalizing the biomass conversion postulate (Ginzburg, 1998) to make it a more general inequality rather than an equality. In its original, specific form the postulate suggests that the rate of

consumer reproduction is a function of its consumption rate. Such a rule imposes a particular symmetry on predator-prey theories, forcing a linkage between the so-called functional and numerical responses. Turchin suggests a more general one-sided inequality: a consumer cannot derive more from what is consumed than the consumed resource contains. Theories positing this more general assumption have excessive flexibility, since they are not constrained by the conversion postulate that the specific statement requires. It is hard to disagree with a more general statement if one agrees with a special case. Nonetheless, from a practical point of view, the specific formulation is more useful in constructing theories because it places a reasonable and reasonably precise biological constraint on theoretical constructions.

Berryman (1999) suggested a set of principles substantially similar to Turchin's. He later articulated the general view (Berryman, 2002) that ecology, like physics, may not need its own laws since both disciplines are subject to general system theory, which describes interactions and feedbacks in any dynamical system. But such a claim is problematic. While system theory could be used to describe elements of ecology or physics, it would do so in such general terms as to provide little practical foundation. We would like to know, for instance, how fast gravitational force declines with distance or how predator consumption and reproduction rates relate to one another. These specifics make theoretical physics different from theoretical ecology; that both involve "interactions" containing "feedback" is true but not sufficiently informative.

Although we are hesitant to advance examples from outside our area of expertise, we can suggest contexts in which the perspective we offer here might be useful. In reviewing the last several years of 'Ecological Modelling' in search of safe, overly general models, we found a potential candidate in a community ecology model (Salles et al., 2006). In addition, we identified a pair of relevant methodological discussions, one dealing with systems ecology modelling (Schizas and Stamou, 2007) and the other with individual-based modelling (Aumann, 2007).

A qualitative perspective on a four-species community by Salles et al. (2006) does little more than confirm that the authors developed a model whose outcomes coincide with the limited number of observed real world outcomes. While such a finding represents an important—and necessary—preliminary achievement, the result's generality is not very informative. Of course, examples of appropriate model generality are typical of 'Ecological Modelling'. Rather than focus attention on a diverse range of such efforts, we thought it might be more useful to point out a particular recent perspective on modelling methodology that is consistent with our analysis. To that end, we suggest Aumann (2007), which articulates a general approach to developing simulations while grounding that methodology in appropriately specific work on species-habitat interactions.

We would also point out that the current paper provides a potentially useful perspective for a variety of modeling enterprises. In addressing the manner in which systems ecology modelling appropriately addresses physiochemical or biological phenomena, Schizas and Stamou (2007) face the

central methodological issue of interest to us: what level of model generality is sufficient and what level is excessive? While we would not presume to answer that question for them, we hope that the current discussion might provide a useful perspective.

In our own work we certainly try to be clear and specific about our assumptions in developing simple, testable theories (Ginzburg and Colyvan, 2004). This self-imposed discipline forces us away from the safety of generality and into the riskier territory of specific prediction. We accept the resulting risk in the hope that our approach will give us a chance to make progress.

Assumption Selection and Generality

Mathematical theories are based upon axiomatic assumptions. In ecology, assumptions usually follow from intuition about the way in which biological systems function. An important contribution of ecological theorists is to explain how particular sets of assumptions lead to theoretical predictions. The resulting theoretical predictions aid in assessing the quality of particular assumptions and models by allowing for comparison between model predictions and empirical observations. Selecting appropriate assumptions to underlie a model is crucial, because the behavior of more complex models can vary drastically under different assumptions.

Modern predator-prey theory is built upon the foundation laid by Lotka (1925) and Volterra (1926) and is generally formulated on the basis of a Rosenzweig and MacArthur (1963) model. Inherent to this family of models is the assumption of prey dependence: the per capita consumption rate of the predator is a function of prey abundance and does not depend on predator abundance. Two mathematical discoveries—the paradox of enrichment (PoE) and the enrichment response (ER)—illuminated key predictions of this model (Rosenzweig, 1971; Oksanen et al., 1981).

The PoE predicts that a simple obligate predator-prey system might be destabilized by increases in the carrying capacity of the basal trophic level. As such, the PoE remains the chief mechanism by which traditional predator-prey models explain dual extinction of predator and prey owing to overconsumption. Although most ecology textbooks feature the PoE, it enjoys almost no experimental support in either laboratory or natural systems (Arditi and Berryman, 1991; Jensen and Ginzburg, 2005). Although the general ecological community may not be attuned to this problem, the community of theoretical ecologists is acutely aware of the discrepancy and has exerted significant effort to explain why the PoE is rarely (if ever) observed (Jensen and Ginzburg, 2005).

Most explanations for the absence of the PoE begin with the assumption that the phenomenon could exist. This assumption is equivalent to establishing prey dependence as an axiom. With the Rosenzweig-MacArthur model as a basis, additional terms are added to depict ecological phenomena that, if present in experimental systems, might explain the failure to observe the PoE. These phenomena represent an array of possible ecological scenarios including the presence of: i) multiple prey species varying in edibility (Phillips, 1974; Leibold,

1989; Kretzschmar et al., 1993; Abrams and Walters, 1996; Genkai-Kato and Yamamura, 1999); ii) density dependence of the predator death rate parameter (Gatto, 1991); iii) refuges and immigration (Abrams and Roth, 1994); iv) spatial heterogeneity (Nisbet et al., 1998; Petrovskii et al., 2004); v) life-history traits that enable consumers to buffer the effects of low prey densities (McCauley et al., 1999); and vi) prey possessing inducible defenses (Vos et al., 2004).

We contend that at the most fundamental level ecology ought to utilize mathematics in exactly this manner. A simple axiomatic assumption (e.g., prey dependence) about an ecological system should lead to theoretical predictions that can then be compared with existing data. If the data contradict those predictions, theory must be modified. Where we depart from most ecological theorists is at this last step: deciding how theory should be modified.

Although their specific mechanisms vary, all explanations outlined above for the absence of the PoE posit an additional causative mechanism. As such, they run the risk of being too specific (**Figure 1c**); it seems unlikely that any one of the suggested factors could be influential in all systems, and so any explanation of why the PoE cannot be observed is liable to be specific to the system in question. One way to address this problem would be to construct a massive model that incorporates the potential for all conceivable mechanisms; yet while such a model would be applicable to all systems, its extreme generality would prevent it from being useful (**Figure 1e**).

We wonder why a more obvious step has not been taken: if basic theory can only explain existing data via formulations that are either too specific or too general, perhaps basic theory needs to be revised. Specifically, we wonder why the prey-dependent assumption has not been replaced with a different assumption: predator dependence. Predator dependence, which can come in a variety of forms (Leslie, 1948; Hassell and Varley, 1969; Beddington, 1975; DeAngelis et al., 1975; Arditi and Ginzburg, 1989; Jensen et al., *In Press*; Ginzburg et al., *In Submission*), dampens or completely removes the effect of enrichment on stability (Huisman and DeBoer, 1997) without invoking overly specific or overly general model formulations.

The enrichment response (ER) also illuminates the effects of increasing carrying capacity but considers these effects over food chains of varying lengths. As with the PoE, a preponderance of empirical evidence does not support the existence of ER (Jensen and Ginzburg, 2005), and the results of laboratory and natural experiments are more consistent with predator-dependent models of trophic chain enrichment (Arditi and Saiah, 1992; Bohannan and Lenski, 1997; Kaunzinger and Morin, 1998). Not surprisingly, many theorists have also turned to increased-complexity explanations in attempting to preserve the prey-dependent assumption in spite of its poor predictive power.

Pragmatism

The validity of the principles underlying a theory determines whether or not it will be effective in predicting actual ecological outcomes. Unfortunately, inspecting these principles directly might only reveal internal logical

inconsistencies without indicating a given theory's usefulness. A simple pragmatic rule (i.e., check the consequences of the model against data) remains most reliable. Such a comparison is not as simple as it might seem, as the danger of overfitting covered in our previous review (Ginzburg and Jensen, 2004) represents only one of many hurdles that must be overcome.

Theories never work perfectly; each incorporates, to use a famous expression of Quine's (Quine, 1976; 1980; 1995), a "limit myth" (a description and consideration of a pure situation that ignores extraneous factors—for example, a body falling in the absence of air resistance or the interaction of a single predator species with a single prey species in the absence of any others). To illustrate this idea, we use the example of the tension between the two limit myths of predation theory (prey dependence and ratio dependence), which is described in Abrams and Ginzburg (2000). Qualitatively, two main arguments favor a ratio-dependent limit: the absence of the paradox of enrichment and the equilibrium behavior of trophic chains in response to increased basal productivity (Arditi and Berryman, 1991; Ginzburg and Akçakaya, 1992; Akçakaya et al., 1995). Both have been reviewed above and can be explained within the framework of a more traditional prey-dependent limit myth if the model includes additional complexity. Since complex predator-prey webs are the norm in nature, few opportunities are available to test the predictions of simple models (i.e., those that depict obligate predator-prey pairs). One approach to adjudicating the debate between prey- and ratio-dependent explanations is to directly measure functional responses. Doing so most commonly reveals predator dependence (a more general intermediate situation between the two limit myths), although pure ratio-dependence is also an occasional result (Skalski and Gilliam, 2001). The question we wish to ask is not which of the two extremes is correct, because we know that both are wrong. Instead, we wish to determine which of the two simplified views is more useful if we have to make a practical judgment today, before all the details of the intermediate mechanism are fully understood. Pragmatism dictates that we temporarily adopt the ratio-dependent myth, because it produces a rough, qualitatively correct outcome based on a simple model. Direct measurements of functional responses reject prey dependence more frequently than they do ratio dependence (Jost, 1998; Jost and Ellner, 2000; Jost and Arditi, 2001; Skalski and Gilliam, 2001).

We make the choice to follow our philosophy of risk-taking by being specific with basic assumptions fully understanding the risk. We believe that, of the two extremes, ratio dependence is preferable. The more general intermediate choice would be even better, but it requires at least another parameter. There is typically so little data that using one more parameter leads to overfitting—a potentially serious problem since we can barely find data for the simpler extreme cases (Jost, 1998).

There is safety in making no judgment at all, a not uncommon ivory-towerish behavior. But while no academic jobs will be gained or lost as a result of this choice, numerous practical judgments on ecosystem management depend on it. Ecological theory is likely to have practical applications with potentially

important consequences. We suggest that it is preferable to use theory in combination with available data to advance ecological understanding now even though in doing so we may risk making occasional errors.

Applying Appropriate Constraint to Mathematical Constructions

Biology should constrain our mathematical constructions. While mathematics provides an incredibly vast set of possible equations, logic dictates that only a small subset of these equations can represent a given ecological phenomenon. A large number of constructions, while mathematically sound, should be excluded based on their inconsistency with biology. While most ecologists would agree with such a principle, deciding how best to put it into practice remains a contentious issue. Among ecological theorists, a number of constraints have been forwarded; most proposed theories obey some constraints but rarely all. We consider two proposed constraints on predator-prey theories: (i) instantaneous processes and (ii) biomass conversion.

Many ecological theorists believe that continuous equations should be used only in models of instantaneous processes (Murdoch et al., 2003). Models that include processes interpretable as being strictly instantaneous are called “mechanistic,” while those that do not are derided as “phenomenological.” We call this formalism the “fallacy of instantism” and consider it a particular example of mathematical literalism (Jensen et al., *In Press*). We reject the use of mathematical literalism to constrain mathematical constructions on simple grounds: literalism allows mathematics to constrain biology when biology ought to be constraining mathematics. Proponents of instantism and other forms of literalism fail to appreciate the metaphorical nature of models (Hilborn and Mangel, 1997) and unnecessarily exclude models with potentially great explanatory power.

The biomass conversion principle described above allows ecology to logically constrain mathematics. For a set of predator-prey equations to obey the principle, a predator’s numerical response must be a function of its functional response (Ginzburg, 1998). In biological terms, reproduction must be a function of consumption. While such constraint will strike most ecologists as reasonable, a number of popular models violate the biomass conversion principle (Turchin, 2003).

Applying either too much or too little constraint to our mathematical constructions produces the same undesirable result: because we end up choosing from an incomplete or over-complete list of models, we greatly increase our risk of missing the most reasonable mathematical construction. While the application of logical constraints provides an important first step in avoiding this pitfall, we contend that the best means of determining which constraints should be excluded is to devise and perform experiments that explore contrasting model predictions.

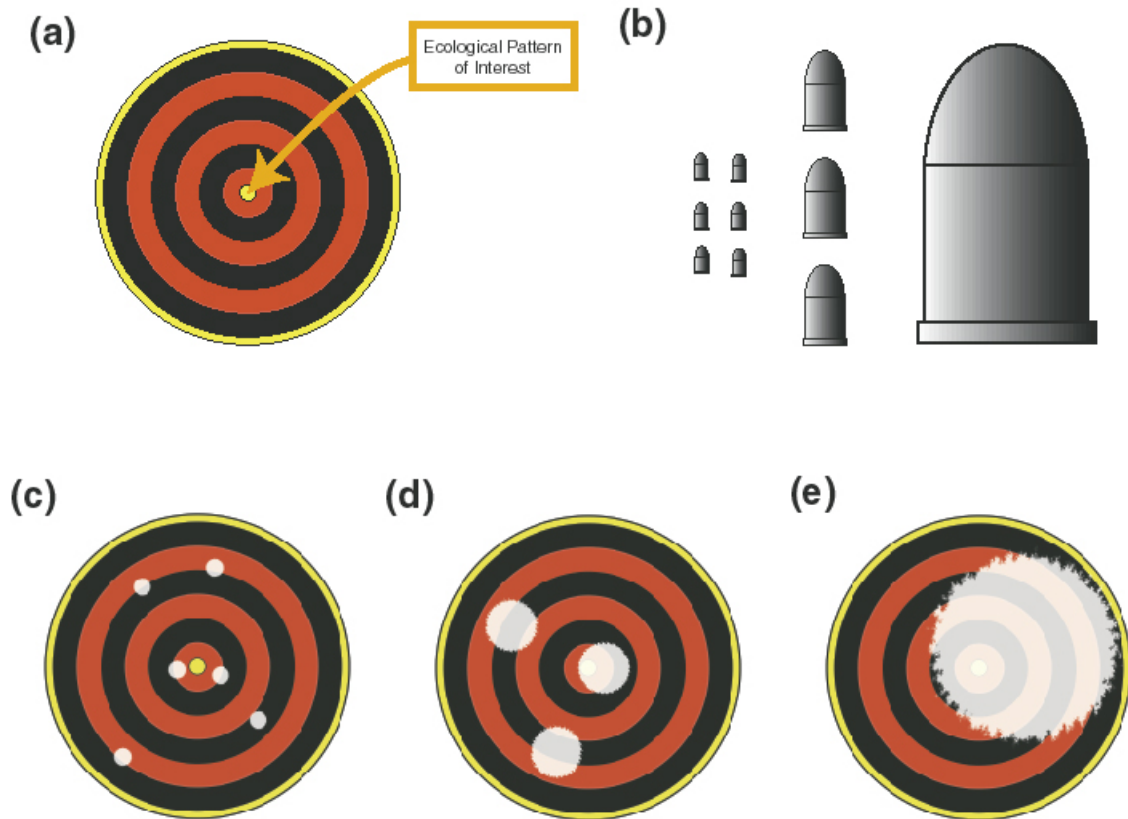
Conclusion

Ecologists face a difficult task in assessing the vast array of available models. Some shortcomings can be readily apparent. For instance, the degree of overfitting can be measured fairly easily by comparing available data with the number of parameters in a given theory (Colyvan and Ginzburg, 2003a; Ginzburg and Jensen, 2004). Other potential shortcomings are less easily quantifiable, including i) determining the appropriate degree of literalism to use in interpreting mathematical concepts in service of ecology, ii) identifying the point at which a theory becomes too general to be useful, and iii) assessing the extent to which a theory enjoys empirical support. Nonetheless, selecting the correct intermediate level of abstraction to increase theory effectiveness is not simply a matter of personal aesthetic preference. As we have demonstrated, some elements of that selection process can be logically addressed to separate “unreasonably effective” theories from those that are simply unreasonable. We conclude that an ecological theory that is in focus with evidence will have to be rough and approximate. Recognizing that such a state of affairs exists is potentially helpful rather than problematic, however. As we face an ever-increasing number of ecological crises, social demand will be for crude, imperfect descriptions of ecological phenomena now rather than more detailed, complex understanding later.

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Figure 1: Maintaining the balance between specificity and generality in ecological theories.



(a) Ecological theorists “target” particular ecological patterns or phenomena. Resulting theories can either “hit the bullseye” (i.e., capture the phenomenon perfectly) or strike some distance from the target.

(b) Theories are like artillery shells of varying caliber: not all can strike a particular target with equal accuracy. Overly specific theories are like small caliber rounds, while overly general theories are like large caliber rounds. More specific theories always outnumber general theories; at the extreme, the most general theory encompasses all possible specific theories.

(c) If an overly specific theory is used to approach a particular ecological phenomenon, the chance of it capturing the phenomenon correctly is very small, even as multiple competing theories are employed.

(d) A theory that correctly balances specificity and generality has the potential to properly capture the ecological phenomenon. Notice that being of the “right

caliber” does not guarantee that a theory will be “on target”: some theories may contain the correct level of specificity but still fail to capture the ecological phenomenon of interest.

(e) Overly general theories may capture the phenomenon but encompass so many other possible ecological patterns as to be of little practical use. In order to maintain some confidence in a theory, we need to believe that it could be wrong; overly general theories have the undesirable quality of being “correct” over too large a range of possible ecological phenomena.

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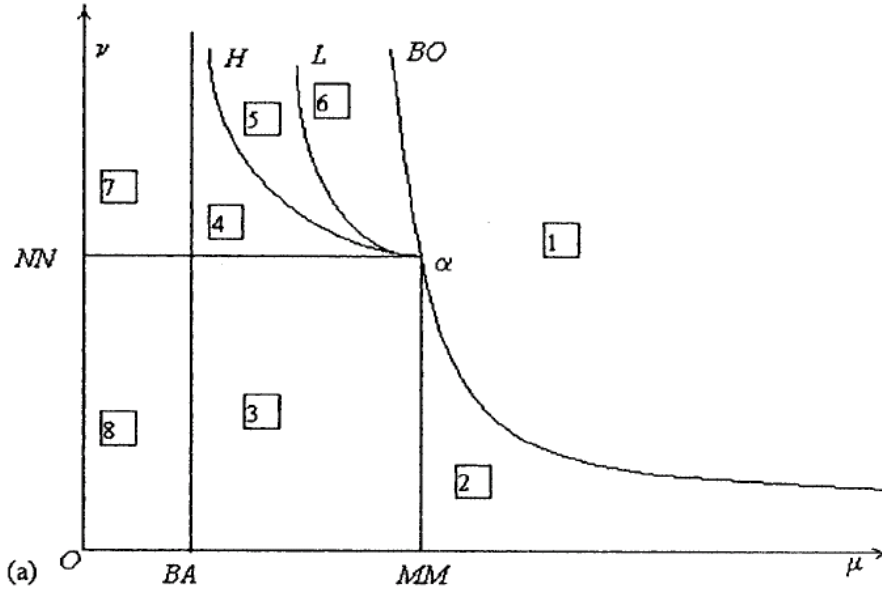
Appendix 2

Transformation of Berezovskaya, Arditi, and Karev (2001) Parameter Space

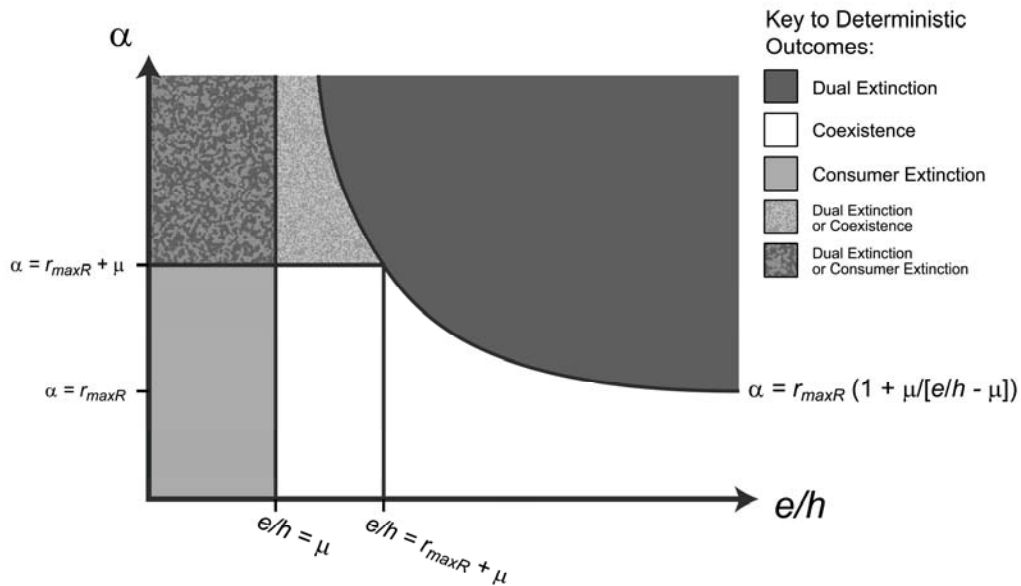
Context:

This appendix provides and explains the step-by-step process involved in converting Berezovskaya, Arditi, and Karev's (2001) parameter space into a form usable in predator-prey modeling.

In their original publication (Berezovskaya et al. 2001), Berezovskaya, Arditi, and Karev present the parameter space of ratio dependence using their original transformed variables:

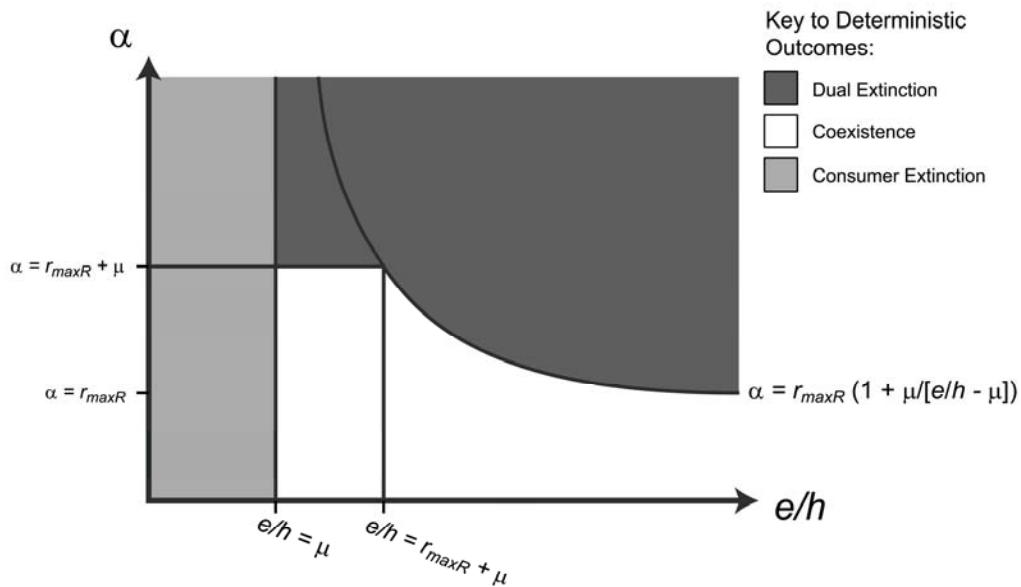


These variables can be back-transformed into the more familiar parameters employed in predator-prey equations. The parameter space below includes these common parameters and indicates the qualitative outcomes expected within each region of the space:

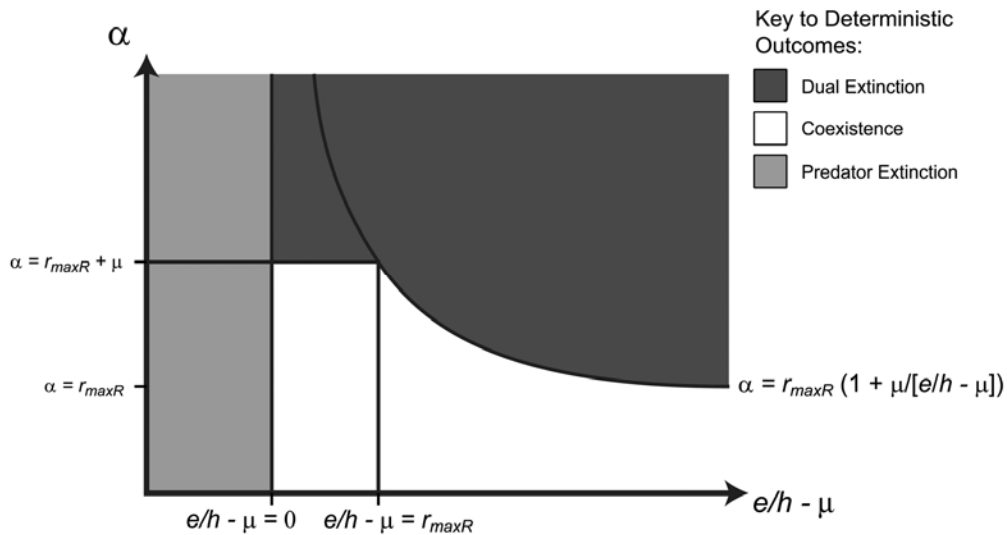


Here, α is the capture efficiency, μ is the predator death rate, h is the handling time, e is the conversion efficiency, and r_{maxR} is the intrinsic growth rate of the prey. Note that certain regions of parameter space have variable outcomes that depend on initial conditions.

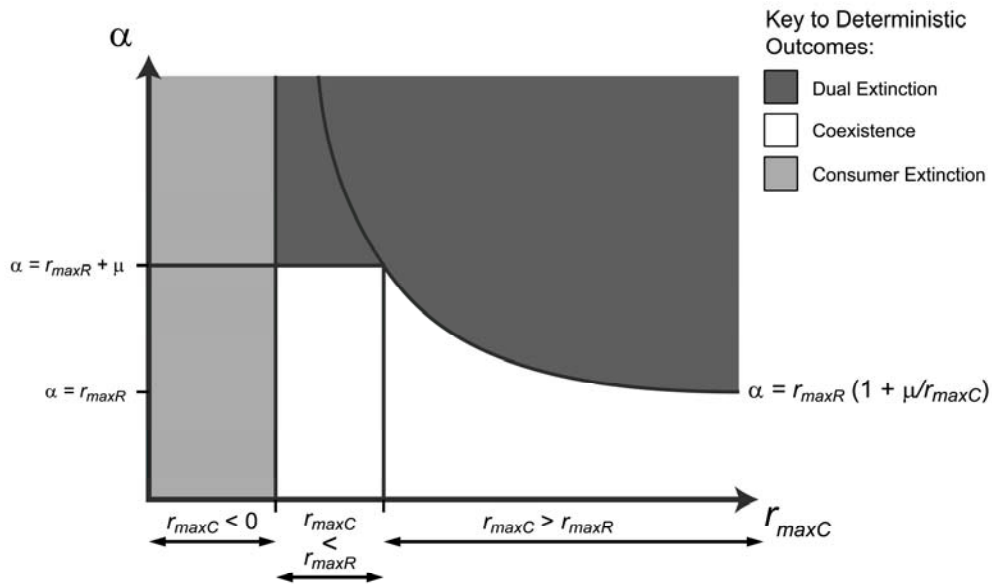
We further simplify this space by assuming that the initial conditions which produce extinction will always prevail over those that produce coexistence. This assumption is reasonable for assessing long-term stability: eventually most systems will venture into the region that produces extinction, so we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



In the versions of parameter space shown above, the x-axis is defined as e/h . We transformed this axis by subtracting the predator death rate, μ :



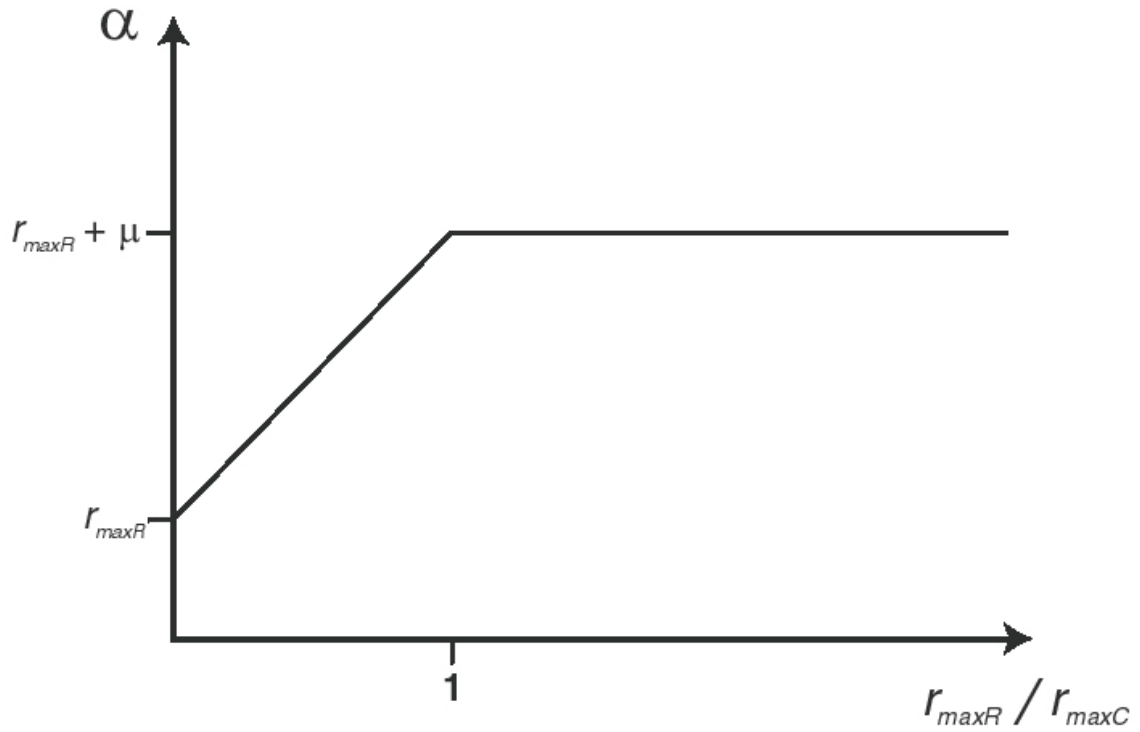
This transformation has two desirable effects: 1) it redefines the origin on the x-axis such that predators only persist in the system in the positive region of the axis; and 2) the x-axis becomes $e/h - \mu$, which has important biological meaning. In order to understand the meaning of this axis, we 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_{maxC} , the maximum growth rate of predators. Using this new interpretation of the axis, three important regions of the r_{maxC} axis emerge:



These three regions represent areas where predators die faster than they can reproduce ($r_{maxC} < 0$), predators grow more slowly than their prey ($r_{maxC} < r_{maxR}$), and predators grow more rapidly than their prey ($r_{maxC} > r_{maxR}$).

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:



To the left of the point where $r_{maxR} / r_{maxC} = 1$, predators grow more rapidly than their prey. To the right of $r_{maxR} / r_{maxC} = 1$, predators grow more slowly than their prey.

Appendix 3

Calculations and Code Used in Simulations

Context:

This appendix provides and explains the Mathematica code used in our simulations.

Simulations were performed using a Mathematica notebook composed of three modules. The first module performed numerical simulations of differential equations representing the interaction between human predators and up to six prey species. Functional response forms, which appear in red below, were varied between simulations. The body masses and initial abundances of each prey species are input parameters. This module, as shown below, uses allometric relationships to determine the remaining model parameters:

```

TabledDataOutputMaker[mass1_, mass2_, mass3_, mass4_, mass5_,
  mass6_, powera_, ca_, n1i_, n2i_, n3i_, n4i_, n5i_, n6i_, pi_, i_] :=
Module[
  {FR1, FR2, FR3, FR4, FR5, FR6, diffn1, diffn2, diffn3,
    diffn4, diffn5, diffn6, pt, system, parsystem, predprey, curve,
    prey1, prey2, prey3, prey4, prey5, prey6, predator, prey1list,
    prey2list, prey3list, prey4list, prey5list, prey6list, predatorlist},
  rn1 = 1.5 ((mass1) ^ (-0.36));
  rn2 = 1.5 ((mass2) ^ (-0.36));
  rn3 = 1.5 ((mass3) ^ (-0.36));
  rn4 = 1.5 ((mass4) ^ (-0.36));
  rn5 = 1.5 ((mass5) ^ (-0.36));
  rn6 = 1.5 ((mass6) ^ (-0.36));
  a1 = ca ((mass1) ^ powera);
  a2 = ca ((mass2) ^ powera);
  a3 = ca ((mass3) ^ powera);
  a4 = ca ((mass4) ^ powera);
  a5 = ca ((mass5) ^ powera);
  a6 = ca ((mass6) ^ powera);
  e1 = 0.001 ((mass1) ^ 1);
  e2 = 0.001 ((mass2) ^ 1);
  e3 = 0.001 ((mass3) ^ 1);
  e4 = 0.001 ((mass4) ^ 1);
  e5 = 0.001 ((mass5) ^ 1);
  e6 = 0.001 ((mass6) ^ 1);
  K1 = 95.5 ((mass1) ^ (-0.75));
  K2 = 95.5 ((mass2) ^ (-0.75));
  K3 = 95.5 ((mass3) ^ (-0.75));
  K4 = 95.5 ((mass4) ^ (-0.75));
  K5 = 95.5 ((mass5) ^ (-0.75));
  K6 = 95.5 ((mass6) ^ (-0.75));
  h1 = 0.00261 ((mass1) ^ 1);
  h2 = 0.00261 ((mass2) ^ 1);
  h3 = 0.00261 ((mass3) ^ 1);
  h4 = 0.00261 ((mass4) ^ 1);
  h5 = 0.00261 ((mass5) ^ 1);
  h6 = 0.00261 ((mass6) ^ 1);
  FR1 = (a1 n1[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] +
    a3 h3 n3[t] + a4 h4 n4[t] + a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t];
  FR2 = (a2 n2[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] + a3 h3 n3[t] + a4 h4 n4[t] +
    a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t];
  FR3 = (a3 n3[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] + a3 h3 n3[t] + a4 h4 n4[t] +
    a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t];
  FR4 = (a4 n4[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] + a3 h3 n3[t] + a4 h4 n4[t] +
    a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t];
  FR5 = (a5 n5[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] + a3 h3 n3[t] + a4 h4 n4[t] +
    a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t];

```

```

FR6 = (a6 n6[t] / (1 + a1 h1 n1[t] + a2 h2 n2[t] + a3 h3 n3[t] + a4 h4 n4[t] +
a5 h5 n5[t] + a6 h6 n6[t] + i p[t])) p[t] ;
diffn1 = n1'[t] == (rn1 n1[t] (1 -  $\frac{n1[t]}{K1}$ )) - FR1 ;
diffn2 = n2'[t] == (rn2 n2[t] (1 -  $\frac{n2[t]}{K2}$ )) - FR2 ;
diffn3 = n3'[t] == (rn3 n3[t] (1 -  $\frac{n3[t]}{K3}$ )) - FR3 ;
diffn4 = n4'[t] == (rn4 n4[t] (1 -  $\frac{n4[t]}{K4}$ )) - FR4 ;
diffn5 = n5'[t] == (rn5 n5[t] (1 -  $\frac{n5[t]}{K5}$ )) - FR5 ;
diffn6 = n6'[t] == (rn6 n6[t] (1 -  $\frac{n6[t]}{K6}$ )) - FR6 ;
pt = p'[t] == e1 FR1 + e2 FR2 + e3 FR3 + e4 FR4 + e5 FR5 + e6 FR6 - 0.067 p[t] ;
system = {diffn1, diffn2, diffn3, diffn4, diffn5, diffn6, pt};
parsystem = Join[system, {n1[0] == n1i, n2[0] == n2i,
n3[0] == n3i, n4[0] == n4i, n5[0] == n5i, n6[0] == n6i, p[0] == pi}];
predprey = NDSolve [parsystem, {n1, n2, n3, n4, n5, n6, p}, {t, 1, 501}];
curve = Flatten[predprey];
prey1 = n1[t] /. curve[[1]];
prey2 = n2[t] /. curve[[2]];
prey3 = n3[t] /. curve[[3]];
prey4 = n4[t] /. curve[[4]];
prey5 = n5[t] /. curve[[5]];
prey6 = n6[t] /. curve[[6]];
predator = p[t] /. curve [[7]];
prey1list = Table[prey1, {t, 1, 501, 1}];
prey2list = Table[prey2, {t, 1, 501, 1}];
prey3list = Table[prey3, {t, 1, 501, 1}];
prey4list = Table[prey4, {t, 1, 501, 1}];
prey5list = Table[prey5, {t, 1, 501, 1}];
prey6list = Table[prey6, {t, 1, 501, 1}];
predatorlist = Table[predator, {t, 1, 501, 1}];
{prey1list, prey2list, prey3list, prey4list, prey5list, prey6list, predatorlist}
]

```

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 population of human predators.

The second module analyzes these lists and looks for extinction events, which are defined as any population that decreases to 5% or less of its carrying capacity:

```

OutcomeGenerator[mass1_, mass2_, mass3_,
mass4_, mass5_, mass6_, ca_, powera_, pi_, i_, exT_] :=
Module[
{ },
Outcome = {1, 1, 1, 1, 1, 1, 1};
changedoutcome = TRUE;
K1 = 95.5 ((mass1) ^ (-0.75));
K2 = 95.5 ((mass2) ^ (-0.75));
K3 = 95.5 ((mass3) ^ (-0.75));
K4 = 95.5 ((mass4) ^ (-0.75));
K5 = 95.5 ((mass5) ^ (-0.75));
K6 = 95.5 ((mass6) ^ (-0.75));

```



```

newpi = pi;
newn1i = K1;
newn2i = K2;
newn3i = K3;
newn4i = K4;
newn5i = K5;
newn6i = K6;
exT1 = 0.05 K1;
exT2 = 0.05 K2;
exT3 = 0.05 K3;
exT4 = 0.05 K4;
exT5 = 0.05 K5;
exT6 = 0.05 K6;
While[changedoutcome == TRUE,
  TotalList = TabledDataOutputMaker[mass1, mass2, mass3, mass4, mass5, mass6,
    powera, ca, newn1i, newn2i, newn3i, newn4i, newn5i, newn6i, newpi, i];
  Prey1List = Part [TotalList, 1];
  Prey2List = Part [TotalList, 2];
  Prey3List = Part [TotalList, 3];
  Prey4List = Part [TotalList, 4];
  Prey5List = Part [TotalList, 5];
  Prey6List = Part [TotalList, 6];
  PredList = Part [TotalList, 7];
  changedoutcome = FALSE;
  ExtCheckn1[t_] := If[(Part[Outcome, 1] == 1 && Part[Prey1List, t] < exT1),
    Outcome = ReplacePart[Outcome, 0, 1]; changedoutcome = TRUE];
  ExtCheckn2[t_] := If[(Part[Outcome, 2] == 1 && Part[Prey2List, t] < exT2),
    Outcome = ReplacePart[Outcome, 0, 2]; changedoutcome = TRUE];
  ExtCheckn3[t_] := If[(Part[Outcome, 3] == 1 && Part[Prey3List, t] < exT3),
    Outcome = ReplacePart[Outcome, 0, 3]; changedoutcome = TRUE];
  ExtCheckn4[t_] := If[(Part[Outcome, 4] == 1 && Part[Prey4List, t] < exT4),
    Outcome = ReplacePart[Outcome, 0, 4]; changedoutcome = TRUE];
  ExtCheckn5[t_] := If[(Part[Outcome, 5] == 1 && Part[Prey5List, t] < exT5),
    Outcome = ReplacePart[Outcome, 0, 5]; changedoutcome = TRUE];
  ExtCheckn6[t_] := If[(Part[Outcome, 6] == 1 && Part[Prey6List, t] < exT6),
    Outcome = ReplacePart[Outcome, 0, 6]; changedoutcome = TRUE];
  ExtCheckp[t_] := If[(Part[Outcome, 7] == 1 && Part[PredList, t] < exT),
    Outcome = ReplacePart[Outcome, 0, 7]; changedoutcome = TRUE];
  StepT = 0;
  While[(changedoutcome == FALSE && StepT < 501), StepT = StepT + 1;
    ExtCheckn1[StepT];

    ExtCheckn2[StepT];
    ExtCheckn3[StepT];
    ExtCheckn4[StepT];
    ExtCheckn5[StepT];
    ExtCheckn6[StepT];
    ExtCheckp[StepT]
  ];
  If[Part[Outcome, 1] == 0, newn1i = 0, newn1i = Part[Prey1List, StepT]
  ];
  If[Part[Outcome, 2] == 0, newn2i = 0, newn2i = Part[Prey2List, StepT]
  ];
  If[Part[Outcome, 3] == 0, newn3i = 0, newn3i = Part[Prey3List, StepT]
  ];
  If[Part[Outcome, 4] == 0, newn4i = 0, newn4i = Part[Prey4List, StepT]
  ];

```



```

If[Part[Outcome, 5] == 0, newn5i = 0, newn5i = Part[Prey5List, StepT]
];
If[Part[Outcome, 6] == 0, newn6i = 0, newn6i = Part[Prey6List, StepT]
];
If[Part[Outcome, 7] == 0, newpi = 0, newpi = Part[PredList, StepT]
]
];
Outcome
]

```

Once an extinction event is discovered, all other abundances are set to the abundance at the time of the extinction event.

The third and final module explores parameter space in two dimensions: 1) the allometric constant for capture efficiency (C_a); and 2) the allometric power for capture efficiency ($Power_{CE}$). For each combination of parameters, the module performs a numerical simulation and checks for extinction, reiterating this process until all species are extinct or remaining species coexist (see Chapter 2, Figure 4). Exploring the two dimensions of the capture efficiency allometry, this module color-codes each outcome and creates a graphical representation of system stability (see Chapter 2, Figure 5):

```

PleistoceneSpace[mass1_, mass2_, mass3_, mass4_, mass5_, mass6_,
  aLow_, aHigh_, aStep_, pLow_, pHigh_, pStep_, pi_, i_, exT_] :=
Module[
  {},
  TotalArray = {};
  a = aLow - aStep;
  While[(a < aHigh),
    a = a + aStep;
    power = pLow - pStep;
    TempArray = {};
    While[(power < pHigh),
      power = power + pStep;
      PointOutcome =
      OutcomeGenerator[mass1, mass2, mass3, mass4, mass5, mass6, a, power, pi, i, ex
    ThisColor = Hue[0, 0, 0];
    If[PointOutcome == {0, 0, 1, 1, 0, 0, 1}, ThisColor = Hue[0.15]];
    If[PointOutcome == {0, 0, 0, 0, 0, 0, 0}, ThisColor = Hue[0.05, .95, .90],
      If[Part[PointOutcome, 7] == 0, ThisColor = Hue[0.00, .5, 1.0]]];
    If[PointOutcome == {1, 1, 1, 1, 1, 1, 1}, ThisColor = Hue[0.25]];
    If[PointOutcome == {1, 1, 1, 1, 1, 0, 1}, ThisColor = Hue[0.6]];
    If[PointOutcome == {1, 1, 1, 1, 0, 0, 1}, ThisColor = Hue[0.35, .7, .5]];
    If[PointOutcome == {1, 1, 1, 0, 0, 0, 1}, ThisColor = Hue[0.7, .7, .7]];
    If[PointOutcome == {1, 1, 0, 0, 0, 0, 1}, ThisColor = Hue[.9, .2, .9]];
    If[PointOutcome == {1, 0, 0, 0, 0, 0, 1}, ThisColor = Hue[0.90]];
    If[PointOutcome == {0, 0, 0, 0, 0, 1, 1}, ThisColor = Hue[1, .7, .8]];
    If[PointOutcome == {0, 0, 0, 0, 1, 1, 1}, ThisColor = Hue[0.00, 0.4, 1]];
    If[PointOutcome == {0, 0, 0, 1, 1, 1, 1}, ThisColor = Hue[0.55]];
    If[PointOutcome == {0, 0, 1, 1, 1, 1, 1}, ThisColor = Hue[0.4, .9, .9]];
    If[PointOutcome == {0, 1, 1, 1, 1, 1, 1}, ThisColor = Hue[0.5, 0.5, 0.4]];
    If[PointOutcome == {1, 1, 0, 0, 1, 1, 1}, ThisColor = Hue[0.3, .99, .6]];
    If[PointOutcome == {1, 0, 0, 0, 0, 1, 1}, ThisColor = Hue[0.20, 0.7, 0.9]];

```

```
TempArray = Join[TempArray, {ThisColor}]
];
TotalArray = Join[TotalArray, {TempArray}]
];
Show[Graphics[RasterArray[TotalArray], AspectRatio -> Automatic]]
]
```

Appendix 4

Book Review

Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America

(University of California Press, 2005)

Jeffrey V. Yule

Conservation Biology 20(2006): 1327-1328

Context:

My dissertation focuses on one component of a broader discussion involving not only science but also ethics and policy. This review provides some broader conservation biology context for my research by addressing some of these related subjects and their interrelationships.

Twilight of the Mammoths is an intriguing but not entirely effective combination of three disparate parts: memoir of scientific discovery, analysis of competing Late Pleistocene extinction hypotheses, and call for radical North American restoration. These various threads are united in falling within the broad interests of the author, who is justifiably well-known for his overkill hypothesis (i.e., that human overhunting caused Late Pleistocene megafaunal extinctions) and for exploring the conservation biology implications of Pleistocene and Holocene extinctions. While the book is inconsistent, the author's informed, passionate perspective remains worthy of consideration.

The first two chapters introduce overkill and provide an overview of pre-human Pleistocene faunas. Subsequent chapters address related topics. These include the importance of ground sloth dung and packrat midden analysis to Pleistocene studies; the paleobiology of ground sloths, which Martin considers to be the hallmark American megafaunal group; Grand Canyon ecology and paleoecology as an overkill test case; the global correlation between human arrival and extinctions; the question of when humans arrived in the Americas; the interpretation of archeological sites; and the particulars of competing extinction hypotheses. All of this sets the stage for a pair of concluding—and controversial—chapters on species restoration. Several short, free-standing essays are interspersed throughout the book. Most relate tangentially to the study's main subjects, but one offers an exceptionally clear and very useful overview of carbon dating techniques. Although Martin recounts several key research experiences, *Twilight of the Mammoths* is only secondarily a memoir. The book's main concerns are Late Pleistocene extinctions and ecological restoration. Accordingly, this review will also focus on those topics.

The section on extinctions is the stronger of the two. Martin provides a thorough overview of the species lost, although the book deals mainly with North American faunas. Debate about the cause(s) of the extinctions generally centers on the relative explanatory merits of climate shifts and human activities, including hunting, the introduction of destructive exotics (e.g., rats, dogs), and landscape alteration (e.g., as from burning), and all these topics are covered. Although not impartial, Martin's assessment of the debate is informed, fair, and civil. He accurately observes that no existing climate change model explains the observed extinction pattern but also remains willing to have his hypothesis tested. He notes that two lines of evidence would cast serious doubt on overkill: first, unique features of Late Pleistocene climate shifts that could explain the loss of large mammals and, second, evidence for long-term coexistence of humans and megafauna in the Americas or Australia.

The few minor problems with Martin's treatment of the extinctions will pose difficulties primarily for those unfamiliar with the subject. A clear, concise definition of overkill would have been helpful. As presented, the term could reasonably be interpreted as referring either to extinctions resulting solely from hunting or those resulting from a combination of human activities including hunting. Similarly, while Martin is careful to cite works that contradict his overall

conclusion, he does not always point out the range of opinion bearing on the specific evidence he presents. For instance, on the subject of prey naiveté, the literature is nowhere near unanimous in accepting that an accurate parallel can be drawn between the North American megafauna that the first Paleoindian hunters encountered and the vulnerable island species that evolved isolated from predators and were easily eradicated by humans as a result.

The final two chapters represent an exchange in a broader dialogue on the rewilding movement, which calls for a significant portion of North America to be restored to a wild condition, with core wilderness areas, corridors, and viable complements of native species. Here, Martin proposes a Pleistocene standard for American restoration efforts. The argument has much to recommend it. The ecosystems that European colonists encountered were shaped both by the first Americans and their sudden decimation by Old World disease. Consequently, it is difficult to differentiate between those aspects of early colonial ecosystems that are atypical and those that represent a “normal” condition toward which restoration should aspire. A Pleistocene restoration standard also involves difficulties—even leaving aside the problem of extinctions. Pleistocene floral and faunal assemblages frequently lack modern analogues, and it is unclear how well they can be approximated under current climatic conditions. Martin proposes a radical plan to address these difficulties.

“Resurrection ecology” would restart the evolution of some megafaunal lineages by reintroducing them to North America. The approach would involve a multi-generational commitment, caution, and considerable research. For these reasons it is important to avoid becoming mired in a premature debate about particulars. Martin’s suggestions to introduce a host of species—from zebra and elephant to gemsbok and rhino—are tentative and should be read as such. The justifications for such a major enterprise, however, should be both clear and fully articulated, and in this respect the study falters. In addition to the presumed main justification of preserving evolutionary potential, Martin briefly offers a variety of arguments for the plan, but none are fully developed. Those rooted in ethics are the most fragmentary. For instance, it is difficult to determine in what context taxa could be considered to have an inherent right to evolve free of human interference. Martin also briefly offers a series of additional arguments: that resurrection ecology could save endangered Old World species, provide the conservation movement with much-needed optimism, and allow humans to develop deeper ecological understanding by creating a host of real-world experiments. Details are scarce, however. By predicating so ambitious a restoration plan on so fragmentary a series of arguments, *Twilight of the Mammoths* falls short of persuasiveness.

Martin explicitly states that his support of resurrection ecology is independent of his views on overkill. But he acknowledges that, if the hypothesis were validated, one controversial argument supporting his restoration plan would be that humans bear a moral responsibility to repair the ecological damage they have inflicted. Although Martin expresses reluctance to advance that argument, it

nonetheless remains in the rhetorical background, as does a linkage between overkill and resurrection ecology. Martin writes that extinct megafauna are America's evolutionary legacy, commenting: "They are what is natural" (p. 201). But if megafaunal extinction proves not to have been a consequence of overkill or other human activities, the opposite argument—that megafaunal extinction is "natural"—would be more compelling. Certainly, there are many lineages whose evolutionary fortunes we might wish to reverse. The main unanswered question here is this: Absent compelling proof for overkill, why should these lineages receive so much attention? The lack of a clear answer to that question leads to the book's major rhetorical shortcoming – i.e., the appearance it gives that proponents might favor resurrection ecology simply because they think it would be a fine and pleasing thing to do. An esthetic hunch about how to work toward an attractive, newly configured American landscape is far too shaky a foundation for so large and uncertain an enterprise. In addition, some who might support the plan if its underlying logic were clearer might end up opposing it by misreading potential clues the book offers. For instance, Martin writes of the importance of a long-term perspective on Cenozoic mammal evolution, noting that it is vital in conceiving of how we might "design with nature" (p. 186). In context, comments like this one raise the possibility that a call for resurrection ecology might actually be a call for novel ecosystem design and construction—something many supporters of restoration would oppose.

In the absence of details, it is difficult to either accept or reject Martin's perspective. Individuals must decide for themselves whether or not it has a firm basis in ethics or science, a far shakier one in aesthetics or whim, or, perhaps, something in between. Nonetheless, a long-term perspective on conservation biology and restoration is long overdue, as is a bolder, more proactive approach. Whatever the particulars of a more ambitious conservation agenda might turn out to be, the vast majority of conservation biologists would probably agree that while we go about formulating that plan, additional research and larger reserves with greater connectivity would be worthy medium-term goals. Long-term goals can come later. Martin offers his own views on the subject and invites us to consider them—and to formulate our own. Although occasionally incompletely argued, the broad messages presented in *Twilight of the Mammoths* merit consideration—and in that regard Martin's study is a noteworthy success.