Pleistocene Overkill and North American Mammalian Extinctions

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Keywords

Clovis, megafauna, hunting, extinction, climate change, ancient DNA

Abstract

Clovis groups in Late Pleistocene North America occasionally hunted several
now extinct large mammals. But whether their hunting drove 37 genera of
animals to extinction has been disputed, largely for want of kill sites. Overkill
proponents argue that there is more archaeological evidence than we ought
to expect, that humans had the wherewithal to decimate what may have been
millions of animals, and that the appearance of humans and the disappearance
of the fauna is too striking to be a mere coincidence. Yet, there is less to these
claims than meets the eye. Moreover, extinctions took place amid sweeping
climatic and environmental changes as the Pleistocene came to an end. It
has long been difficult to link those changes to mammalian extinctions, but
the advent of ancient DNA, coupled with high-resolution paleoecological,
radiocarbon, and archeological records, should help disentangle the relative
role of changing climates and people in mammalian extinctions.

INTRODUCTION

Paleontologist Alfred Romer was perplexed. His just completed (it was 1933) chronological analysis had shown that 26 genera of North America's large mammals had survived the Pleistocene, only to vanish in a geological instant at its end. But why? He saw no evidence of climate or vegetation changes that might have triggered their extinction, and the only change in the fauna was the "late arrival [of] man himself." Yet, Romer thought it "improbable" that hunters drove the animals to extinction, given how few kill sites there were. Perhaps, he hesitantly suggested, extinctions were set in motion by the arrival of humans throwing "out of balance a fauna in delicate adjustment" (Romer 1933, pp. 76–77).

Today, we still seek to explain the cause of Romer's "late and wholesale extinction." Much has been learned since, of course: The tally of Late Pleistocene losses is now at 37 genera in North America and 52 in South America (Barnosky & Lindsey 2010; Grayson 2015). More is known of the fossil and archaeological records, the criteria for evaluating the role of humans in the accumulation of a fauna, and the chronology of the appearance of people and the disappearance of the large mammals. It was especially the latter that fueled Paul Martin's widely influential idea of Pleistocene overkill: the idea that fast-moving Clovis hunters who entered North America at the end of the Pleistocene were responsible for extinctions there and indeed throughout the hemisphere (Martin 1967, 1973, 1984, 2005).

Initially formulated for the Americas, the overkill hypothesis was soon exported by Martin and others to other places and times, especially where the sudden appearance of humans seemed too closely timed to the extinction of the local fauna to be a mere coincidence (e.g., Barnosky et al. 2004, Martin 1984, Martin & Steadman 1999, Steadman et al. 2005, Surovell et al. 2005, cf. Ugan & Byers 2008). These extinctions occurred in different epochs—during the Pleistocene (in Australia), at its end (in the Americas), and in the Holocene (across the Pacific)—and involved a range of mammals and birds; yet in all cases they seemingly had human arrival as a common denominator. This suggested that hunting (and, for Martin, hunting alone) was responsible for all of these extinction episodes (Alroy 2001a, Gillespie 2008, Martin 2005).

Perhaps. But overkill has long been a flashpoint of debate in archaeology and paleoecology. In North America and elsewhere, it has spawned a rich and at times quarrelsome literature. Dispute occurs because the question of a human role in the extinctions cuts to the core of our attempt to understand the adaptation and behavior of hunter-gatherers, particularly those on an unfamiliar landscape. It also speaks to issues of biodiversity, sustainability, and the impact of humans on their environment; to the consequences of environmental and climate change for animals (and people); and, for some, to the ethical responsibility we might bear for reconstituting those now vanished biotic communities (Braje & Erlandson 2013, Donlan et al. 2006, Grayson 2001, Hames 2007, Martin 2005, Meltzer 2009, Surovell & Waguespack 2009). Dispute also occurs because we have long lacked the analytical tools to resolve it; fortunately, those are now at hand.

Although overkill has been globally applied, my focus is on Pleistocene North America south of the ice sheets.[1] This was Martin's iconic case, for here there is evidence that Clovis people hunted large mammals, as well as a chronological correlation between the arrival of humans

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[1] Relatively recent overviews of extinctions are available for other areas of the Americas (Barnosky & Lindsey 2010, Borrero 2009, Mann et al. 2013), Africa (Faith 2014b), Australia and Tasmania (Cosgrove et al. 2010, Field et al. 2013, Gillespie et al. 2012, Miller et al. 2005, Wroe et al. 2013), Europe and Eurasia (Nikolskiy et al. 2011, Stuart 2005, Stuart & Lister 2012, Stuart et al. 2004), the Pacific Islands including New Zealand (Duncan et al. 2013, Martin & Steadman 1999, McWethy et al. 2009), and other island settings (Dewar 1997, MacPhee et al. 2007).

and the disappearance of the fauna.[2] However, the devil is in the details: Given that extinctions coincided with the end of the Pleistocene, to make the case that overkill was the primary cause of extinctions, one has to isolate a human signal amid the noise of climatic and ecological changes that also occurred as the planet shifted from a glacial to an interglacial mode.

Two other possible causes can be taken off the table at the outset. One is habitat alteration by people: This played a key role in Pacific Island extinctions (Grayson 2001), but newly arrived Clovis groups did not have a similarly destructive impact on their landscape (Marlon et al. 2009, cf. Pinter et al. 2011). The other is that the cause came from outer space in the form of an exploding mass (Firestone et al. 2007, Wittke et al. 2013) or radiant energy (LaViolette 2011), but these claims have neither conceptual merit nor empirical support (Meltzer et al. 2014, van der Plicht & Jull 2011, van Hoesel et al. 2014).

WHAT'S IN A WORD?

By Martin's definition, overkill is "human destruction of a native fauna either by gradual attrition over many thousands of years or suddenly in as little as a few hundred years or less," whereas blitzkrieg indicates the "sudden extinction following initial colonization of a land mass inhabited by animals especially vulnerable to the new human predator" (Martin 1984, p. 357). "Sudden" is taken to mean <1,000 years (Brook & Bowman 2004, Martin 1984, Waguespack 2013). The blitzkrieg idea, Koch & Barnosky (2006, p. 240) observe, "irks many critics" of overkill. Proponents are irked too, but for a different reason. Haynes (2013, p. 94) believes that "the most important logical mistake made by the anti-Overkillers is to equate all possible variants of Overkill with the blitzkrieg model." The idea of humans as the cause of extinctions, he asserts, is not exclusively tied to the blitzkrieg model.[3] It is in North America, however.

If, as is widely agreed, Clovis groups were the continent's first big game hunters and arrived just before 11,000 years ago, and if, as is again widely agreed, the large mammals had vanished by 10,000 years ago, there was blitzkrieg. (All ages are in radiocarbon years.) Martin deemed blitzkrieg necessary to explain the hunters' success as well as the dearth of archaeological evidence of that success. The hunters were targeting animals previously unexposed to human predation, and their naiveté made these animals "a bonanza of easily utilized nutrition" (Alroy 1999, p. 126). But even naïve prey can "process information about predators swiftly," perhaps within a generation (Berger et al. 2001, p. 1,039). Because their advantage would not last long, hunters would have had to move on quickly, thus reducing, according to Martin, the odds that their activities would be preserved (Martin 1973, p. 974).

DRAMATIS FAUNA

To understand overkill's strong allure to some and the deep skepticism it elicits in others, it is useful to begin with the apparent victims. There were 37 genera of large mammals that went extinct

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[2]There is scattered evidence of a pre-Clovis presence in the Americas, not all of which is compelling and which has been subject to long-standing controversy (Meltzer 2009). In principle, that dispute does not intersect the overkill debate because it is generally agreed that regardless of when the first Americans arrived, Clovis groups were the first big-game hunters in the New World (Grayson & Meltzer 2003). Martin nonetheless is sharply critical of pre-Clovis claims, given that prior exposure to humans would have made the Pleistocene fauna less naïve by the time Clovis hunters arrived on the scene, their naiveté being a key assumption of the overkill model (Martin 2005).

[3]Haynes himself seems to equate blitzkrieg with overkill when he asserts: "First-contact extinctions [indicate] that when modern *H. sapiens* first arrived in continents and islands, most of the largest animals disappeared soon thereafter" (Haynes 2013, p. 94). As he uses the term "soon," it indicates "as little as perhaps decades to centuries" (Haynes 2013, p. 95).

in North America by the end of the Pleistocene. How many species that number represents is unknown, because such finer-scale taxonomic distinctions are often difficult to make with fossils. Estimates of the number of horse species, for example, range from 2 to 20 (Grayson 2015). Studies of ancient DNA are starting to clear this clutter (Orlando et al. 2009), often showing less taxonomic diversity than indicated by macrofossils (Orlando & Cooper 2014). But for now, discussion is in terms of genera, although researchers acknowledge that this may mask physical and behavioral characteristics of individual species that are potentially important to understanding their extinction (Boulanger & Lyman 2014, Grayson 2015).

The great majority of the 37 extinct genera were herbivores ($n = 30$), and the remainder were carnivores ($n = 7$) (see **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Many of these were quite large, megafauna even, including several multi-ton proboscideans (mammoth, mastodon, and gomphothere). Most scholars follow Martin (1967) in defining megafauna as animals weighing ≥44 kg (Koch & Barnosky 2006, cf. Brook & Bowman 2004). On that scale, 32 of the 37 genera qualify. From the perspective of rodent-sized animals that cutoff appears reasonable, but by this gauge humans are also megafauna, which seems at odds with the vision conjured of massive beasts (or, conversely, of megafauna smaller than humans). Moreover, not all animals ≥44 kg on the Late Pleistocene landscape went extinct: Nine genera survived (**Figure 1**). Still, there can be little doubt that a disproportionate number of large mammals that inhabited Pleistocene North America had disappeared by its end.

Beyond their size, these animals shared few other obvious attributes. In broad strokes, some primarily occupied the colder northern portions of unglaciated North America (e.g., the stag-moose *Cervalces* and the musk ox *Bootherium*), whereas others were seemingly restricted to more southern climes (e.g., the pampathere *Holmesina* and *Paleolama*). A number inhabited only the open grassland of western North America (e.g., horses, camels, and the pronghorns *Capromeryx* and *Tetrameryx*); others appear to have solely dwelled in the eastern North American forests (e.g., tapir and the peccaries *Mylohyus* and *Platygonus*); still others ranged across a variety of habitats (e.g., the ground sloth *Megalonyx*, the llama *Hemiauchenia*, mammoth, and mastodon). There were denizens of semiarid settings and ones that lived near water and possibly were semiaquatic (e.g., the glyptodont, giant beaver, and the capybara *Hydrochoerus*). Some were grazers, others browsers, others mixed feeders. Some were likely herd animals (e.g., horses, the pronghorn *Stockoceros*), though others probably lived in smaller, more solitary social units (e.g., *Platygonus* and the mastodon). Among the carnivores, a few were highly specialized, with teeth and jaws adapted to killing large animals (e.g., *Smilodon fatalis*, the sabertooth cat), whereas others were omnivores (e.g., the giant short-faced bear *Arctodus*) (see Anderson 1984, Grayson 2015).

If so diverse a set of animals went extinct simultaneously across North America, it is fair to ask, as Martin has asked, what "single climate switch" could have been thrown at the end of the Pleistocene that was so abrupt, severe, and widespread as to have a geologically instantaneous, devastating impact on animals with such a wide range of habits and habitats (Martin 2005, p. 174). It is difficult to imagine one.

THE BROADER CONTEXT

Yet, it is important to see this episode in its broader context, for large mammal losses were not the only significant changes that took place on the Late Pleistocene landscape. Some 20 genera of birds, multiple genera of reptiles, and even a spruce tree, *Picea critchfieldii*, also went extinct at the end of the Pleistocene (Faith 2014a, Grayson 2007, Jackson & Weng 1999). Nor did the nine large mammal survivors emerge unscathed: Several, such as bighorn sheep and elk, decreased in
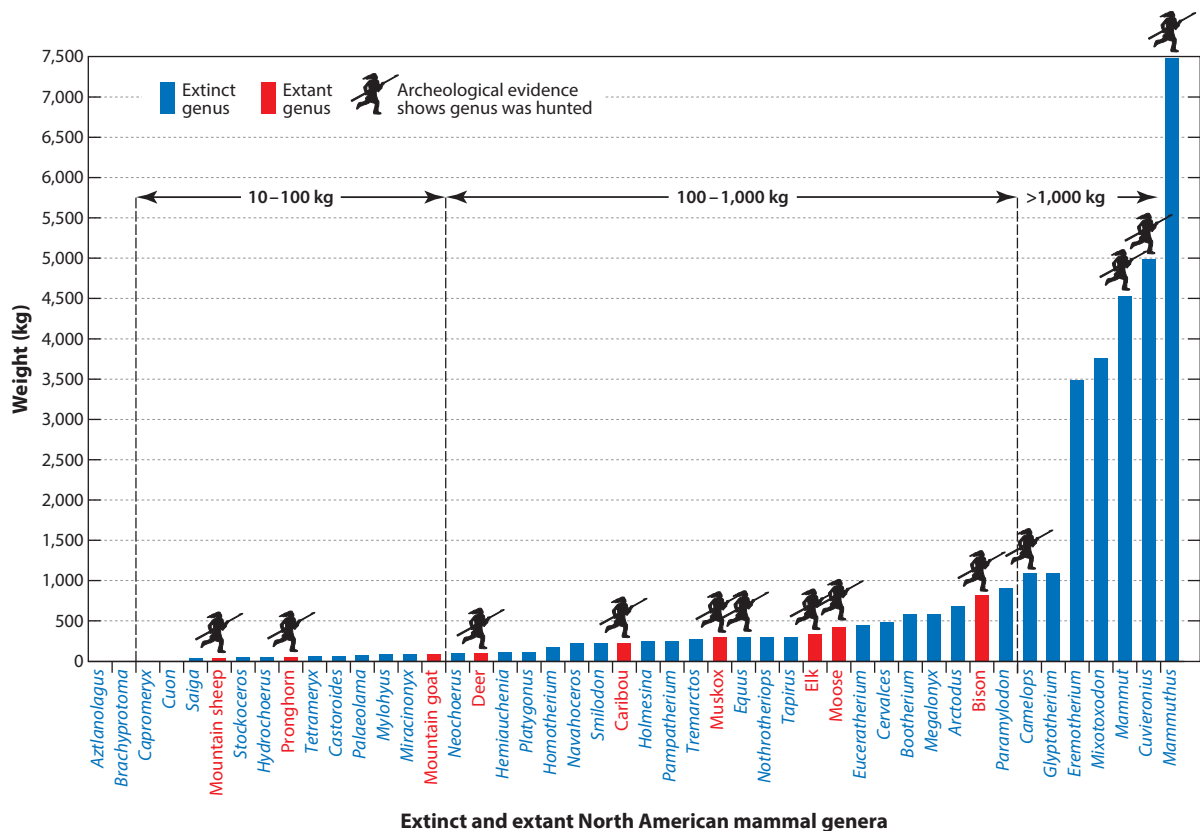
Figure 1

Histogram of extinct and extant species ordered by estimated body weight and indicating genera for which there is evidence of human predation between 12,000 and 10,000 radiocarbon years BP [when Faith & Surovell (2009) suggest extinctions occurred]. Columns in blue are extinct genera, and columns in red are extant genera. Body weight estimates are from Grayson (2015) and Smith et al. (2003); evidence of extinct fauna exploited by Late Pleistocene groups is from Cannon & Meltzer (2004, 2008), Grayson & Meltzer (2015), and Hill (2008).

size through the Late Pleistocene; a new species of bison arose; and there was substantial loss of genetic diversity, much of which began well before the first appearance of humans and testifies to strong selective pressures in the environment (Boulanger & Lyman 2014, Hofreiter & Barnes 2010, Orlando & Cooper 2014).[4]

In addition, other plants and animals were undergoing sometimes extensive range shifts and local extirpation. These were not lockstep shifts of entire biotic communities but rather, as evident at the macrofossil and molecular levels, a biogeographic free-for-all in which individual plants and animals moved in varied directions and at various speeds in response to climatic signals at different times in the Late Pleistocene (not just at its end), dependent on individual tolerance limits, dispersal abilities, competition, full glacial location, the opening of suitable habitats, and a host of other factors (Cannon 2004, Grayson 2007, Grimm & Jacobson 2004, Lorenzen et al. 2011, Meltzer 2009, Orlando & Cooper 2014, Scott 2010, Webb et al. 2004).

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[4]It has been suggested that the evolutionary shift in bison could be explained by targeted hunting (Brook & Bowman 2005; Koch & Barnosky 2006, p. 227), but the archaeological record gives no support to this hypothesis (Hill et al. 2008).

Grund et al. (2012) claim there were no significant changes in range size among Late Pleistocene large animals. However, the ranges in their analysis are derived by drawing circles and polygons around fossil occurrences that accumulated over a 25,000-year span; therefore, these are not "ranges" in any ecologically meaningful sense and would not detect changes in range size or over time that had occurred. In fact, there can be no question that some large mammal ranges changed: Caribou no longer live in Mississippi nor muskox in Tennessee, as each had during the Pleistocene (Grayson 2007).

That all these changes were occurring during a period of significant climatic and ecological flux begs the question of whether the explanation of megafaunal extinction should be viewed in isolation and requires a sui generis cause, or it is better understood as one end of a spectrum of changes, including the arrival of people, that all have the same underlying cause: the end of the Pleistocene. It is a fair question, which takes on more weight if extinctions were not simultaneous across all 37 genera, and if we consider that larger animals are more likely than smaller ones to respond to climate change and have a higher extinction risk (McCain & King 2014). I will come back to that question, but for now I wish to focus on overkill as the supposed primary explanation for their disappearance.

DANGEROUS PREDATOR/VULNERABLE PREY

Martin & Steadman (1999, p. 34) think the megafauna disappeared "not because they lost their food supply but because they became one," which they attribute to the animals' naiveté and size (see also Grund et al. 2012, Lyons et al. 2004). They were "large, slow moving and eminently huntable animals" whose innocence of human predators made them attractive prey (Martin 2005, p. 136). Even those that tasted "foul" would not have escaped, Martin supposes, because "their unusual vulnerability would have tempted younger hunters or their preteen followers to use the luckless animals for target practice" (Martin 2005, p. 139).

If it is true that "size made all the difference in terms of which animals went extinct" (Martin 2005, p. 166), size fails to explain the loss of the Aztlan rabbit (cottontail-sized) or the diminutive pronghorn *Capromeryx* (which barely tipped the scales over 10 kg). But for Martin they were large enough to be attractive to hunters. Yet, this hypothesis in turn fails to explain why bighorn sheep, pronghorn, mountain goat, deer, caribou, muskox, elk, moose, and bison survived. Martin supposes bison made it because they were "wilier at avoiding hunters," and the other genera survived because they were accustomed to people, having "originated in or [being] closely related to species found in the Old World" (Martin 2005, pp. 141, 155). Alternatively, perhaps they were better able to tolerate hunting or had other behavioral or ecological advantages (Alroy 2001a, Brook & Bowman 2002, Johnson 2002); or, as some suggest, extinction may not have been entirely size selective (Brook & Bowman 2004, 2005; Zuo et al. 2013).

The quandary of large mammal survivors and small mammal losses aside, overkill is said to have begun when the Pleistocene came to an end and the Cordilleran and Laurentide continental ice sheets melted back, opening an ice-free corridor that allowed big-game hunters, possibly no more than 100, to emerge onto the northern Great Plains. The new predators came upon a target-rich landscape of naïve prey, and they "persisted in killing animals as long as they were available" (Martin 1973, p. 972). Their hunting success triggered a rapid increase in population size and resource demands, and, spurred by the abundance of prey, they spread across the continent.

Slow breeders, as most of the Pleistocene megafauna likely were (Johnson 2002, Lyons et al. 2004), would not have been able to reproduce fast enough to offset even a relatively modest level of predation (Alroy 2001a, Haynes 2007). Carnivores and scavengers boomed with the sudden fortune in freshly killed meat on the landscape, then went bust when the supply on which they

were dependent ran out (Martin 1967).[5] Within 1,000 years, humans had spanned the hemisphere and left behind an impoverished mammalian fauna (Gillespie 2008, Martin 1973).

Estimates of how many animals were killed vary: Martin calculates between 100 and 200 million (Mosimann & Martin 1975, p. 313). Others estimate comparable but mostly lower figures (Alroy 2001a, Haynes 2009). No one knows. However, and on this point proponents and critics agree, there is very little archaeological evidence of megafaunal hunting in North America, and none as yet confirmed in South America (Borrero 2009; Gillespie 2008; Grayson & Meltzer 2002, 2015; Haynes 2009, 2013; Surovell & Grund 2012; Surovell & Waguespack 2009).

Advocates of overkill are untroubled by the absence of evidence, arguing that a scarcity of kill sites is to be expected (Haynes 2013, Martin 1973, Surovell & Grund 2012). Moreover, they point to simulation models of human hunting, which show that extinctions were virtually inevitable, given that large animals were highly ranked prey and especially susceptible to predation pressure (Alroy 2001a, Brook & Bowman 2004, Zuo et al. 2013). They also highlight the seemingly strong coincidence of the appearance of people and the disappearance of those 37 mammal genera (Waguespack 2013). However, each of these justifications, the principal load-bearing elements of the North American Pleistocene overkill hypothesis, warrants scrutiny.

SO MANY MEGAFAUNA, SO LITTLE TIME

I begin with the question of whether there should be archaeological evidence of overkill. Martin, as noted, did not think so. Because the hunters moved so rapidly, they would spend no more than a dozen years in any particular area, and this, compounded by the odds against artifacts and bones being preserved, led Martin to conclude that even a dozen kill sites continent-wide was "a rich, not a poor record of extinction by overkill" (Mosimann & Martin 1975, p. 313; see also Alroy 2001b, Haynes 2007).[6] As Braje & Erlandson (2013) observe, few archaeologists agree with this assertion, especially in light of the ~100 kill sites of moas (flightless birds) in New Zealand that accumulated on the heels of the arrival of people (Grayson 2001).[7]

Surovell & Grund (2012), however, believe they can show that overkill is supported by the presence and absence of evidence. Their argument is based on a model that estimates an expected number of kill sites for the period of human and extinct faunal coexistence, factored by age, taphonomic biases, sampling, and human demography, and compared among Australia, North America, and New Zealand. In broad terms, their model predicts kill sites ought to be rare in Australia where extinctions were earliest and relatively abundant in New Zealand where they were most recent, with North America in between. That proves to be the case (though hardly explains why South America does not have the number of kills of North America, as it should by the model). On that basis, and because other hypotheses are "compatible with a scarcity of [hunting] evidence" (naturally: climate change doesn't hunt), Surovell & Grund (2012, p. 682) conclude

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[5]As to why the carnivores (at least the less specialized ones) did not shift their prey to surviving large mammals, Ripple & Van Valkenburgh (2010) suggest they were outcompeted by human predators who could themselves fall back on other resources when the megafauna went extinct.

[6]Johnson offers a different take on the potential scarcity of archaeological evidence, based on a model suggesting that low fecundity species that were already in decline when human hunters arrived need not have experienced intensive predation to go extinct. A slight increase in mortality rates would have been sufficient, and thus the simultaneous killing of large numbers of prey—and a correspondingly abundant archaeological record of kill sites—need not have occurred (Johnson 2002, p. 2,225).

[7]Ground-nesting flightless birds in New Zealand and on remote Pacific Islands were easy prey to hunting and habitat alteration, and thus susceptible to rapid extinction (Grayson 2001, Martin & Steadman 1999). North America's Channel Islands and the adjacent California mainland had their own flightless bird, the sea duck *Chendytes lawi*, but even though it was preyed upon by people it survived for some 8,000 years after human arrival before going extinct (Jones et al. 2008).

that "the archaeological record of human predation of extinct animals [is] largely irrelevant" to overkill.

One can scarcely doubt that the frequency and likelihood of the discovery of sites varies inversely with antiquity, but one can question the decision to treat as comparable three regions that have very different cultural, environmental, and geological histories and are vastly different in size and ecological scaling (and hence in the impact and archaeological visibility of humans). Nor does this model measure what it purports to measure. The so-called associational critique does not question whether the number of archaeological sites (kills included) is what would be expected; rather, it questions whether the number of archaeological kill sites is higher or lower than would be expected given the record of Pleistocene megafaunal occurrences (Grayson 1984).

There are preservation and sampling biases to contend with in making that assessment (Koch & Barnosky 2006, Meltzer 1986), not least the fact that whether an extinct taxon has been found in a kill site depends in part on its abundance in the fossil record [though not always: Horses are the most common fossil in the Late Wisconsin and gomphothere one of the rarest, but only a single kill is known of each (Grayson & Meltzer 2015)]. Of course, such biases should equally apply to the large mammal survivors (**Figure 1**); indeed, because many of the survivors were smaller bodied and/or inhabited forested settings that might have reduced their interaction with human foragers, they are perhaps even less likely to be well represented (Faith 2014a, Lyman 1994). That proves to be the case: In the fossil record of the Late Wisconsin (35,000–10,000 years ago), extinct genera are much more abundant ($n = 522$) than the large mammal survivors ($n = 187$) (data from Graham & Lundelius 2010).

And yet, despite their greater numbers, extinct taxa occur in only 15 archaeological kills, with only 5 genera—mammoth, mastodon, gomphothere, horse, and camel—represented (Grayson & Meltzer 2002, 2015). In contrast, there is evidence from the same period—between 12,000 and 10,000 radiocarbon years BP [the window of time in which Faith & Surovell (2009) suggest extinctions occurred]—of more than 110 kills of 8 of the 9 large mammal survivors (Cannon & Meltzer 2004, 2008; Grayson & Meltzer 2004; Hill 2008).[8] That the extinct genera occur in fewer kills than would be expected given their fossil abundance, and the survivors in more, is statistically significant (**Table 1**). It must be added that more than 30 other extinct genera do not appear at all in archaeological kill sites, and at least half a dozen of those are more abundant in the fossil record (and much larger bodied) than most of the large mammal survivors.

Of the survivors, bison are especially relevant: They were first hunted in Clovis times, and among the ∼1,000 bison kills that occurred since then are sites where hundreds to tens of thousands of bison were slain (Haynes & Huckell 2007, Reher & Frison 1980, Wheat 1972). They were obviously not that wily at avoiding hunters. Yet, after 11,000 years of hunting by Native Americans, followed by their relentless slaughter by nineteenth-century Euro-American commercial hide hunters, bison survive. It is odd, then, that the supposed killing of 37 genera of megafauna, possibly representing millions of animals hunted to extinction in fewer than 1,000 years, hardly left an archaeological trace.

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[8]As the Clovis occupation does not span the entire period that Faith & Surovell (2009) identify, overkill could not have been due solely to Clovis groups, but must also be due to other Paleoindians as well. That provides the warrant to look at hunting of all genera, extinct and extant, in Paleoindian sites within that time frame. I note that the number of archaeological kills of surviving taxa in **Table 1** was not derived from a comprehensive investigation of all taxa in all Paleoindian sites from this period. Nonetheless, this preliminary tally, based on a limited number of sources, is sufficient to make the point. Were one to systematically examine all possible kills of all extant taxa in all Paleoindian sites continent-wide and vet them to insure subsistence use (the procedure in Grayson & Meltzer 2002, 2015), I anticipate the final tally will still support the end result seen here.

Table 1 Contingency table of kill sites versus fossil occurrences of the extinct and surviving large mammal genera of North America in archaeological kills between 12,000 and 10,000 radiocarbon years BP [the extinction time period as per Faith & Surovell (2009)]

	Extinct genera	Surviving genera	Total
Number of fossil occurrences	322 (3.14)	170 (−3.82)	492
Number of archaeological kills	15 (−8.74)	111 (5.95)	126
Total	337	281	618

The five extinct genera are camel, horse, gomphothere, mastodon, and mammoth. Two of those, camel and horse, occur in the Wally's Beach site. The surviving eight genera are bison, caribou, deer, elk, moose, pronghorn, mountain sheep, and musk ox.

$G = 125.34, df = 1, p = 0.000$. Numbers in parentheses are Freeman-Tukey deviates; all values are significant at the $p = 0.05$ level (± 0.980).

All of this makes it difficult to accept the accusation that overkill is being held "hostage" by an insistence on rare evidence for which we will "be waiting a long time" (Surovell & Grund 2012, p. 683). Because the evidence of overkill fails to measure up to that of the hunting of the large mammal survivors, which are even rarer in the fossil record, the answer seems to be already at hand, no hostage-taking necessary.

TARGETING BIG GAME

The intensive hunting of bison over many thousands of years raises the question of whether Clovis hunters could have wiped out a continent's megafauna in a matter of centuries. Alroy (2001b, p. 1,460) proclaims that "all reasonable [simulation] models predict rapid extinctions." That claim is incorrect (e.g., Johnson 2002), but in any case "reasonable" simulation models are not necessarily realistic ones, nor should these models be confused with evidence that people did kill off the megafauna (cf. Gillespie 2008).

The simulations (e.g., Alroy 2001a, Brook & Bowman 2004, Bulte et al. 2006, Mosimann & Martin 1975, Zuo et al. 2013) are built around a core set of variables, notably prey population density and growth rates, human population density, and prey harvest rate (Yule et al. 2014). The challenge is assigning values to those variables and determining the weight of factors such as prey naiveté, competitive relationships, initial human population size, growth rates, and hunting skill. The goal is to determine whether or when (after initial contact) prey populations drop below a sustainable threshold.

Yet, as Yule et al. (2014, p. 103) observe, in virtually all models the parameters are "either unconstrained or poorly constrained," the results cannot be replicated for want of transparency in their construction, and some of the underlying assumptions may never be amenable to validation (see also Brook & Bowman 2002). Thus, some treat prey as a single target, assume constant success across taxa (but ignore the costs or consequences of switching prey), or ignore predator-prey dynamics.

Perhaps not surprisingly, the results vary as to which genera go extinct and which survive and what variables (e.g., body size, life history traits) are more relevant in driving the outcome (Yule et al. 2014). Moreover, "simulation studies will conceal regional and local responses to various parameters, as well as subtle interplay at fine spatial and temporal scales" (Roberts 2014, p. 143;

see also Bliege Bird 2015). It is thus difficult to accept these models even as testimony to overkill's plausibility.

It is perhaps an exaggeration to declare that these simulations view "humans as 'super predators' who spend their time either hunting or procreating" (Bulte et al. 2006, p. 299). However, it is fair to say they are mostly unencumbered by what has been learned about human foraging strategies, and particularly the role of large-game hunting in subsistence (or other purposes such as status), hunting success rates, risk factors, and resource rank, and the role of landscape learning (e.g., Bird & O'Connell 2006, Bird et al. 2013, Bliege Bird 2015, Hawkes & Bliege Bird 2002, Marlowe 2010, Silberbauer 1981, Speth et al. 2013).

Martin deemed "absurd" the possibility that hunters would "neglect to hunt desirable and vulnerable large prey" (Martin 2005, pp. 138–39). The issue is more complicated. Foraging theory and empirical evidence indicate that large animals are often high-ranked prey, though that is not necessarily true of all large animals when risk is factored in (Bliege Bird & Bird 2008, Byers & Ugan 2005, Silberbauer 1981). Bird et al. (2013) suggest slow and nonaggressive megafauna (ground sloths?) may have been highly ranked, but such attributes may have applied only to some of the Pleistocene megafauna.[9] Further, hunters would have had to be appropriately organized in the size and structure of their kin group, mobility strategy, and ability to buffer risks, in order to realize returns from megafaunal hunting. If these groups were highly mobile, dispersed, and relatively small and targeted high-return resource patches, the argument that megafauna would have been "more than an occasional provisioning resource seems tenuous at best" (Bird et al. 2013, p. 165).

Moreover, it is unlikely hunters could quickly convert tactics successful against one prey for use against another, especially if the prey was an unfamiliar animal in an unfamiliar habitat (Silberbauer 1981). To "successfully match wits with wild animals with the intent to kill them," Frison (2004, p. 226) notes, "requires a thorough knowledge of the hunting territory and the behavioral patterns of the species residing within it." Finally, on game-rich landscapes devoid of other people, as Late Pleistocene North America was, patch choice models and the Marginal Value Theorem (Charnov et al. 1976) suggest foragers would abandon a patch well before the extinction of the local fauna and not "after hunting it out" (Martin 2005, p. 145). Winterhalder & Lu (1997) identify circumstances in which patch depletion and extinctions are plausible, but it is doubtful those characterized Late Pleistocene North America (Meltzer 2009).

All that notwithstanding, Clovis hunters occasionally brought down large mammals, they could have been adept at switching targets, and they might have pursued animals beyond the time when foraging theory suggests they should have abandoned patch and prey. Highly mobile, low-density, nonstoring hunter-gatherers on a vast, unfamiliar and unknown land teeming with large game might have behaved unlike any hunter-gatherers known (Meltzer 2009). Yet, if that were true, it is reasonable to expect evidence of their hunting. Thus far, as noted, very little of that has come to light.

Accordingly, support for overkill is often sought elsewhere, with "the strongest evidence for overkill [coming] from the timing of megafaunal extinctions and human colonization" (Braje & Erlandson 2013, p. 17). This idea is based on two interlocking premises: that the "period of extinction in North America occurred approximately 11,500–10,000 years BP" (Sandom et al. 2014)

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[9]Modern elephants show aggressive behaviors toward humans, which Surovell et al. (2005) attribute to their long coevolution with humans in both Africa and India. Whether their distant Pleistocene proboscidean relations would behave similarly is unknown. But given that these animals lived on a landscape with large cats and lions, it is fair to assume they had evolutionarily well-tuned defenses. Surovell et al. (2005, p. 6,235) likewise suggest elephants in Africa and Asia survived by virtue of living in biomes where humans never achieved high population densities. It is fair to point out that population densities in North America at the end of the Pleistocene were likely no higher.

and that megafaunal extinctions were "an abrupt and largely simultaneous event" (Waguespack 2013, p. 214).

DOES THE END REVEAL THE BEGINNING?

Those premises, however, have not been demonstrated. Only 17 genera are directly dated to <12,000 years ago [the El Fin del Mundo gomphothere is undated (Sanchez et al. 2014), but given its association with Clovis it is included in this tally]. Of the other 20 genera, 8 postdate the Last Glacial Maximum but are still >12,000 years old; 7 predate the Last Glacial Maximum; and the other 5 are undated (Faith & Surovell 2009; Grayson & Meltzer 2003, 2004). Hence, it is not known whether 20 out of 37 genera of extinct fauna survived into Clovis times, let alone whether they disappeared simultaneously.

This chronological pattern could be a result of sampling and preservation, and future finds might increase the number of genera dated to Clovis times, as has happened (albeit slowly) over the decades (Grayson 1989). But then it is also possible that the pattern accurately represents the extinction chronology: The reason some genera are not securely dated to <12,000 years ago is that they disappeared before then (Grayson 2007). Extinctions are staggered over time in other regions of the world (e.g., Stuart & Lister 2012, Stuart et al. 2004), and there is neither reason nor evidence to preclude the possibility this occurred in North America (Grayson & Meltzer 2003).

On the basis of a statistical extrapolation, Faith & Surovell (2009) suggest the current sample is "consistent with the synchronous extinction of all taxa between 12,000 and 10,000 radiocarbon years" ago (Faith & Surovell 2009, pp. 20,643–44). Leaving aside the validity of the extrapolation, the timing of extinctions is being determined primarily by Last Appearance Dates (LADs), the youngest age available for a genus. But knowing that an animal was extinct by the end of the Pleistocene is not evidence that it went extinct at the end of the Pleistocene, as is routinely assumed (e.g., Fiedel 2009, Gillespie 2008, Grund et al. 2012, Sandom et al. 2014), nor does it necessarily aid in understanding why a genus went extinct.

This is so for several reasons. First, LADs are just a Last Date, not a Last Appearance. Given the vagaries of preservation and sampling, and the proposition that rare animals disappear from the fossil record before they go extinct (the Signor-Lipps Effect), the last mammoth dated was almost certainly not the last mammoth standing (Meltzer 2009; see also Boulanger & Lyman 2014, Haynes 2013, Waguespack 2013). In fact, the DNA of Pleistocene megafauna has been recovered from Holocene-age sediments in Alaska, revealing that some genera survived well after their last dated appearance as macrofossils (Haile et al. 2009).

More importantly, knowing when the extinction process ended is largely irrelevant: To understand what caused the process we need to know when and why it began (Meltzer 2009; see also Meltzer & Mead 1985). By way of analogy, on Saturday, November 18, 1995, the last Bethlehem Steel plant ceased operations and the company, billions of dollars in debt, went bankrupt. An explanation for why that happened is not the trading price of domestic steel the Friday before, but instead the commercial, economic, political, technological, and other forces that buffeted the company over more than a century. Likewise, to understand what caused mammalian extinctions it is vital to understand the processes that might have led to this outcome (Meltzer 2009; see also Boulanger & Lyman 2014, Bradshaw et al. 2012). An important step toward that goal will be tracking megafaunal population changes through time to identify when the population of an extinct genus began to trend downward. In effect, more will be gained by determining (for lack of a better phrase) the "Initial Decline Date" (IDD) of a genus than its LAD.

Martin believed megafaunal populations were robust up to the moment humans arrived, seeing "no reduction in the deposition of ground sloth dung or other common fossils of extinct species"
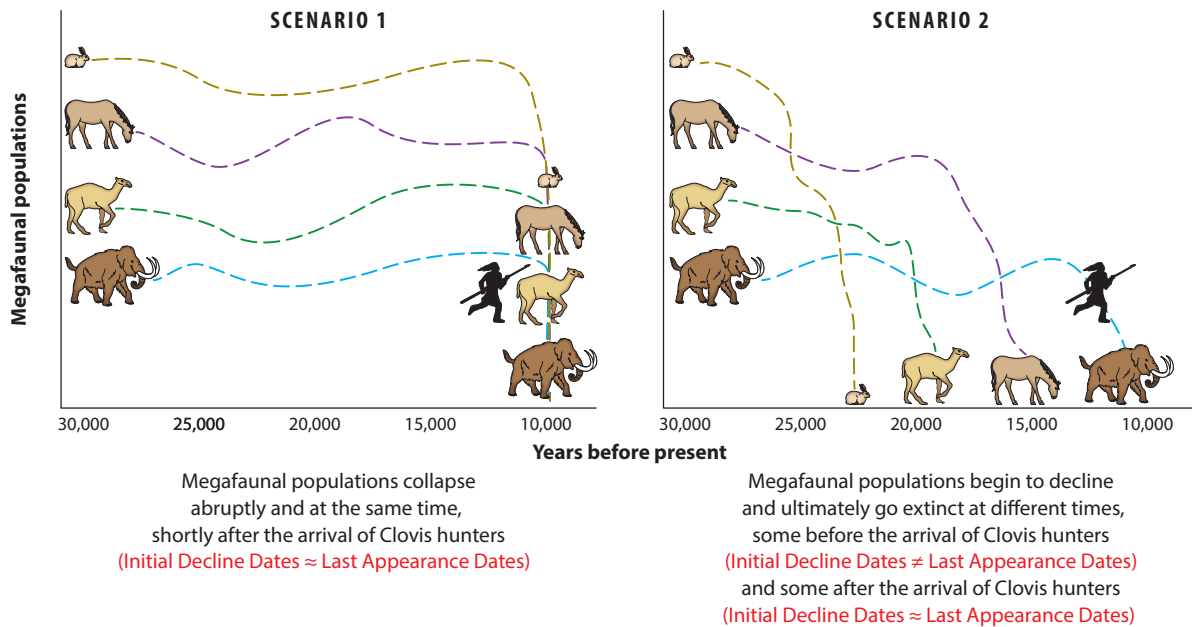
Figure 2

Two scenarios of the tempo and mode of extinctions. (*Left*) Scenario 1 depicts extinctions as abrupt and synchronous across all taxa and coincident with the arrival of Clovis hunters. (*Right*) Scenario 2 illustrates the possibility that extinctions were neither abrupt nor synchronous across taxa, with only some of them coincident with (although not necessarily caused by) the arrival of Clovis hunters.

(Martin 2005, p. 177). But fossils are not a direct indicator of past population sizes. Others have tallied the herbivore dung-dwelling fungal spore *Sporormiella* in sediment cores as a proxy of herbivore abundance (e.g., Gill et al. 2009). However, *Sporormiella* spores are not specific to particular genera, so which population is being tracked is not known, nor is there an unambiguous way "to translate the number of spores in sediments into past herbivore densities" (Woods & Wilmshurst 2013, p. 3).

We do not know when extinctions began and whether that process was synchronous or staggered across taxa (**Figure 2**). Until these facts are known, it is premature to claim that the current chronology can "constrain the time dimension of the debate and rule out many nonanthropogenic mechanisms" (Gillespie 2008, p. 2,527). Ultimately, if the IDDs of all genera align and if the LADs follow soon thereafter, it is reasonable to conclude that extinctions were broadly catastrophic and the result of a single cause. If the IDDs coincide with the arrival of Clovis hunters, a compelling case can be made for humans being that cause. However, there would still remain the question of how the hunters managed to leave so little archaeological evidence behind. If, on the other hand, IDDs and LADs are staggered across genera (and some predate the Clovis arrival), that points to the possibility of multiple causes and redirects discussion to the complexities of Late Pleistocene climate change, but without the burden of having to identify a "single climate switch" (Grayson 2007, Lima-Ribeiro & Diniz-Filho 2013, Waguespack 2013).

THE CLIMATE CHALLENGE

Driving the end of the Pleistocene was an increase in incoming solar radiation in the Northern Hemisphere that began ~20,000 years ago and ultimately peaked 10,000 years ago at levels not seen in 70,000 years (Berger & Loutre 1991). This factor, coupled with rising levels of greenhouse

gases (CO_2, CH_4) propelled global warming and, starting ~16,500 years ago, the melting of North America's ice sheets. As these diminished their climate-modifying influence declined, which, along with other processes plus a host of amplifying and feedback effects between land, air, and ocean, led to complex changes in temperature and precipitation over space, time, and season (Clark et al. 2012); this resulted in major reorganizations of biota—that biogeographic free-for-all mentioned above. For that matter, if one is to argue that climate cannot be a cause of extinction because these animals did not disappear during prior glacial-interglacial cycles, it is necessary to show that the climate changes then were the same in severity and scale as occurred during the Pleistocene–Holocene transition (Faith 2014a). That has yet to be done.

Among the hypotheses put forward to link large mammal extinctions to Late Pleistocene climate changes are ones that attribute extinction to habitat loss or fragmentation [the latter intensifying the impact of a shrinking range (Brook et al. 2008, McCain & King 2014)], to a reduction in carrying capacity from changes in growing season, or from shifts in vegetation or because of declines in nutrient availability (Faith 2011), to changes in competitive relationships (Scott 2010), or to the dissolution of communities in which fauna had coevolved in carefully partitioned niches (Graham & Lundelius 1984). In some cases, though not in others, these hypotheses are partially supported by data; overall, however, they have not been fully tested, because they demand high-resolution paleoecological evidence that is not yet available (Koch & Barnosky 2006).

A number of simulation models have been built to retrodict the impact of changing climates on fauna (e.g., Lima-Ribeiro et al. 2013; Martínez-Meyer et al. 2004; Nogués-Bravo et al. 2008, 2010; Prescott et al. 2012; Sandom et al. 2014). However, as with the simulations of human hunting, here too details are inevitably sacrificed for the sake of the models. And because these models do not specify mechanism(s) that link large-scale "average" changes in climate or habitat with the extinction of 37 different genera, their explanatory power is limited and in some cases contradictory. One model, for example, deemed climate change in North America "severe" and in South America "relatively stable"; yet in both cases climate was dismissed as a cause because extinctions are "consistent with the arrival of modern humans" (Sandom et al. 2014, p. 6).

Koch & Barnosky (2006, p. 227) doubt it is "possible to explain many aspects of [extinctions] solely by existing environmental hypotheses." At the moment, that is assuredly correct, but the problem now is less about the inadequacies of the hypotheses (or those of the climate simulation models) and more about the manner in which the problem has been approached.

GETTING PAST THE IMPASSE

Much of the effort to explain Late Pleistocene extinctions has been structured as if explaining the extinction of one taxon would explain the extinction of all (Grayson 2007, pp. 193–94; see also Faith 2014a, Grayson & Meltzer 2015). And yet, as studies in historic biogeography have shown, "understanding the structure of assemblages of species requires that the history of each species in that assemblage be studied on its own" (Grayson 2007, p. 194). That means developing high-resolution records of the "biogeographic histories of individual species in relation to paleoclimatic, paleoecological, and archaeological data" (Faith 2014a, p. 5,434) that lead up to the times of extinctions so as to show how changes on the landscape—possibly including the arrival of humans—might have affected them (Grayson & Meltzer 2015, Lorenzen et al. 2011, Meltzer 2009, Metcalfe & Longstaffe 2014, Orlando & Cooper 2014).

Achieving those records has been a challenge because there are large gaps in our knowledge of the physiologies, adaptations, ecological and climatic tolerances, competitive interactions, and life histories of these extinct genera. But those gaps may soon be filled, given that it is now possible to recover and sequence DNA from fossils and ancient sediments; the latter include DNA of a

range of organisms that can help create a picture of the environment that surrounded these extinct animals (Willerslev et al. 2003, 2014).

Studies of ancient DNA (*a*DNA) have the potential to resolve nettlesome taxonomic questions; observe changes in genetic diversity over time in extinct and extant taxa; test hypotheses about climatic and environmental impacts on individual taxa through the analysis of changes in population size and substructure (depending on the subtlety of the changes and the timescale over which they occur); spot phenotypic changes that do not fossilize; and possibly, though such studies are still in their infancy, identify adaptive changes in protein sequences and epigenetic modifications in the genome (Cappellini et al. 2012, Orlando & Cooper 2014, Orlando & Willerslev 2014, Shapiro & Hofreiter 2014).

However, *a*DNA analyses have been brought to bear on North American megafaunal extinctions only in the last dozen years. The majority of these have used mitochondrial DNA (mtDNA), a maternally inherited, selectively neutral trait that occurs outside the nucleus and undergoes mutation at a more-or-less constant and, on a geological timescale, rapid rate. Although relatively plentiful in the geological record, mtDNA reveals only the history of a single locus and is susceptible to genetic drift even though, correspondingly, it can effectively reveal bottlenecks and population changes. Partial or complete nuclear genomes reflect the far broader ancestral pool that contributed to an individual's DNA and can provide a richer and more detailed record of genetic changes over time and other insights into demographic history such as changes in effective population size, genetic diversity, and inbreeding (Nyström et al. 2012, Palkopoulou et al. 2015). Paleogenomic studies, however, are technically and analytically more challenging, and fewer have been conducted on vertebrates other than ancestral humans (Shapiro & Hofreiter 2014). As for whether *a*DNA will allow us to resurrect these extinct taxa, there is less reason for optimism, for a variety of technical reasons and preservation constraints (Orlando & Cooper 2014, p. 590; cf. Shapiro & Hofreiter 2014).

*a*DNA results are available for extinct horses, mammoths, mastodon, mountain goat, muskox, and several of the large cats (e.g., Barnett et al. 2005; Campos et al. 2009, 2010b; Debruyne et al. 2008; Lorenzen et al. 2011; Palkopoulou et al. 2015; Weinstock et al. 2005; Zazula et al. 2014). Additionally, there is ancient and modern DNA coverage of species that survived here or elsewhere, including bison, elk, saiga, bear, wolf, and lion (Barnes et al. 2002, 2009; Campos et al. 2010a, 2014; Hofreiter & Barnes 2010; Lorenzen et al. 2011; Meiri et al. 2013; Metcalf et al. 2014; Shapiro et al. 2004). Because most *a*DNA analyses to date have been on specimens from high-latitude regions (cooler conditions enhance *a*DNA preservation), they do not bear directly on critical questions surrounding extinctions of taxa south of the North American ice sheets.

Even so, the findings to date are significant and hold promise of future insights. They reveal a "clear pattern" of "pronounced dynamicism of genetic population structures over time" (Orlando & Cooper 2014, p. 582). Demographic fluctuations, bottlenecks, and local extirpations occurred in many genera over the Late Pleistocene, though their scale and timing varies across taxa (e.g., Barnes et al. 2002, Campos et al. 2010b, Debruyne et al. 2008, Lorenzen et al. 2011, Mann et al. 2013, Meiri et al. 2014, Shapiro et al. 2004, Zazula et al. 2014). There was also a progressive loss of genetic diversity toward the end of the Pleistocene in both extinct and extant species, with the overall loss being more pronounced in some taxa (bison, lion, muskox, wolf) than others (horse, mammoth, saiga), and again with variation in the timing (e.g., Barnett et al. 2009; Campos et al. 2010a, 2014; Debruyne et al. 2008; Hofreiter & Barnes 2010; Lorenzen et al. 2011; Orlando et al. 2009).

In most cases these changes took place before humans arrived in North America and must be attributed to nonanthropogenic processes (Lorenzen et al. 2011, Orlando & Cooper 2014). But making that attribution still leaves unspecified which changes in, say, climate or vegetation were

taking place, how these affected those individual taxa, and what factors prevented their adaptive response. For that, studies of *a*DNA must be coupled with paleoclimatic and paleoenvironmental records; ecomorphological, isotopic, and osteological analyses of diet and stress; high-resolution chronologies; and continued fine-scale documentation of archaeological sites. All of this will ultimately help construct the individual species' histories that are critical to understanding the role of humans and the extinctions of vertebrates in Late Pleistocene North America (Grayson & Meltzer 2015, Lorenzen et al. 2011, Metcalf et al. 2014).

CONCLUSIONS

Martin's Pleistocene overkill model is important, not because it is correct, but because it sparked vigorous debate and valuable research into questions that are fundamental to understanding the impact of humans and climate change on ecosystems. Almost half a century after it was proposed, overkill is still being debated, and though there are those who wish to declare it victorious and go home (Gillespie 2008), it is too soon for that. There remain too many unanswered questions about whether, why, and how Late Pleistocene changes in climate and environment and the arrival of people affected those 37 genera.

It is fair to suggest humans had a role to play, but the question is one of degree. Clovis groups hunted large mammals (both extinct and extant), but the intensity of their predation and the consequences of their doing so remain unresolved, as does the question of whether they could have been responsible for the loss of those extinct taxa (Byers & Ugan 2005, Cannon & Meltzer 2004, Grayson & Meltzer 2015, Surovell and Waguespack 2009). Moreover, the record so far attests to the hunting of only five of the genera that went extinct, and there is reason to suspect some genera vanished long before humans arrived. This is at best a shaky foundation on which to base the claim that humans "were responsible to some significant degree for Late Pleistocene extinctions in North America" and therefore bear an ethical responsibility to bring about a "Pleistocene re-wilding" of North America by setting aside areas as wilderness and stocking them with Old World large mammals (Donlan et al. 2006, p. 666; cf. Wolverton 2010).

In the absence of compelling testimony blaming humans for the loss of all 37 mammal genera, it has become increasingly common to argue that hunting and climate change are both to blame (Braje & Erlandson 2013, Koch & Barnosky 2006, Lima-Ribeiro et al. 2013). But until it is shown that Clovis groups were not just killing the last lingering members of a few genera already spiraling toward extinction, it is difficult to hold them ultimately responsible for the losses. A coup de grace is not a cause.

The debate over North American Late Pleistocene extinctions has long been complicated by the confluence of climate change and human arrival and the difficulty of disentangling the two, particularly in light of the limited knowledge of the individual histories of these extinct taxa. Now, with the application of *a*DNA in concert with complementary data from paleontological and archaeological sources, there is a clear analytical path toward understanding the cause(s) of their disappearance. Given the stunning success of *a*DNA in resolving a very different, long-standing, and even more vexing dispute, that of the biological relationship of Neanderthals to modern humans, one can be bullish about our prospects for explaining North America's "late and wholesale extinctions" and finally resolving this contentious issue.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

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**Annual Review of
Anthropology**

Volume 44, 2015

Contents

Indexes

Errata

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