A premature burial: comments on Grayson and Meltzer’s
“Requiem for overkill”

Stuart Fiedel, Gary Haynes

Louis Berger Group, 2300 N St., NW, Washington, DC 20037, USA
Anthropology Department, University of Nevada, Reno, Reno, NV 89557, USA

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In a recent JAS article (“A requiem for North American overkill”), Donald Grayson and David Meltzer [39] attack Paul Martin’s “overkill” hypothesis that humans caused America’s Terminal Pleistocene megafaunal extinctions. This is one of three similar recent articles by these authors [37–39] in which, by scrupulous evaluation of the archaeological record, they have reduced the list of unambiguous instances of human interactions with now-extinct mammals in North America to 14 proboscidean kill sites. We applaud their informed skepticism about the evidence, especially since one of us (Haynes) wrote a set of strict standards that Grayson and Meltzer used in their analyses. Regrettably, they did not exercise the same critical scrutiny and caution when they evaluated purported evidence of pre-Clovis occupation in South America [24,76].

Although their critical assessment of the Late Pleistocene archaeological record is laudable, Grayson and Meltzer unfortunately make numerous mistakes, indulge in unwarranted ad hominem rhetoric, and thus grossly misrepresent the overkill debate. In this comment, we first briefly address those aspects of their papers that represent mere theatrical posturing, and then we turn our attention to their more serious errors of fact and interpretation.

First, the theater. A phrase repeated or paraphrased in each of the articles is that overkill is “a faith-based policy statement rather than a scientific statement about the past, an overkill credo rather than an overkill hypothesis” ([39], p. 591). By thus denying the very scientific legitimacy of the overkill hypothesis, Grayson and Meltzer seek to preclude any further serious engagement with its advocates. Science is not advanced by such dogmatic dismissal of competing hypotheses. Also theatrical but unfounded are three points Grayson and Meltzer [39] chose to emphasize in their article summary: (1) overkill has been rejected for western Europe (it has decidedly not been rejected by knowledgeable experts, such as A.J. Stuart [100] and colleagues [101]), (2) Paul Martin is the only reason overkill is still discussed for North America and Australia (also wrong—see, for example, the recent work of Alroy [6,7], Flannery [27–29], and O’ Connell [85]), and (3) “there is virtually no evidence” to support overkill, which, as we show in this reply, is absolutely wrong. In fact, we think there is far more support for overkill than for climate change as the principal cause of the extinctions.

1. Is there no evidence of overkill?

It seems as though it should be simple enough to test the overkill hypothesis. If, as hypothesized, Paleoindian hunters killed thousands of giant mammals, there ought to be lots of kill sites with unambiguous evidence of hunting and butchering (e.g., broken, cut, and burned bones, semi-disarticulated skeletons at hearth areas, associated stone tools). But in reality, such sites are very rare. Martin has responded to archaeologists’ disappointment over the scarcity of megafaunal kill sites by stating that,

Sufficiently rapid rates of killing could terminate a prey population before appreciable evidence could be buried. Poor paleontological visibility would be inevitable. In these terms the scarcity of known kill sites on a landmass which suffered severe megafaunal losses ceases to be paradoxical and becomes a predictable consequence of the special circumstances which distinguish invasion from cultural development within a continent. Perhaps what is remarkable in America is
not that so few, but that any kill sites of extinct mammals have been found ([66], p. 670).

In short, the absence of kill sites is just as expectable as their presence. Thus, the overkill hypothesis seems immune from any simple and conclusive archaeological testing. For this reason, Grayson and Meltzer condemn Martin’s theory as unscientific, driven by ideology not evidence. They also contend that the circumstantial evidence used by Martin to support a global overkill model is weak or nonexistent.

Grayson and Meltzer present their opinions ex cathedra; trust us, they advise the reader, because we are experts on Pleistocene North America, whereas overkill advocates such as Martin, John Alroy, and Tim Flannery are not. To the extent that they attempt to substantiate their opinions with actual evidence, they provide outmoded data and interpretations and ignore or deliberately omit the most recent chronological, archaeological and climatic data.

While Grayson and Meltzer mostly restrict their “requiem” to North America, which is the region of their self-proclaimed exclusive authority, they also deign to pronounce upon evidence from other parts of the world and in so doing reveal deficiencies in their knowledge. We are glad to provide a less biased overview of the recent literature, which tends to contradict their case. Regarding the European record, in which extinctions cluster at 40–20,000 and 14–10,000 rcbp, they write that “Human hunting had nothing to do with the Eurasian losses” of several megafaunal species, extinctions which were “scattered in time and space” ([39], pp. 588–589). Although they cite A.J. Stuart’s recent informed assessment of the European record in support of their assertion that overkill is today rejected by European scientists, in fact, Stuart ([100], p. 266) concludes that “the staggered pattern probably results from the interplay of climatic change and overkill by human hunters.”

Grayson and Meltzer ([39], p. 588) specifically cite the cases of Rangifer (reindeer) extirpation and Megaceros (“Irish elk”) extinction in western Europe as too early for humans to have played any role. They provide terminal radiocarbon dates from the British Isles of 10,610 rcbp for Megaceros (in Ireland) and 10,250 rcbp for reindeer (in Britain). In so doing, they appear unaware of younger Megaceros dates of 9430 ± 65 rcbp from Scotland and 9225 ± 85 rcbp from the Isle of Man [32] and a date for reindeer of 9930 ± 90 rcbp from King Arthur’s Cave, Britain [90]. The dates indicate that both of these species survived beyond the end of the Younger Dryas. In fact, the terminal dates for Megaceros overlap with the earliest dates for Mesolithic occupation in the British Isles (Star Carr, Yorkshire, ca. 9600 rcbp, 10,920 cal BP [18]). “Survival of M. giganteus in the temperate, forested environment of northwestern Europe in the early Holocene allows the possibility that Mesolithic hunters could have been responsible for the giant deer’s final demise” ([32], p. 754).

Grayson and Meltzer correctly observe that there is a cluster of Late-glacial extinctions and extirpations of megafauna in Europe very roughly contemporaneous with the North American extinctions. As human predation on these mammals is well attested even before the advent of Upper Paleolithic industries and presumably modern humans in Europe around 40–35,000 rcbp, it is appropriate to ask why, if hunting was a causative factor as overkill proponents suspect, these faunal demises took so long, and why they should cluster around 13,000–10,000 rcbp. As a tentative answer, we suggest two explanations: (1) The long history of predation by pre-sapiens hominins in Europe had created selective pressures for prey wariness and defensive behavior (the 400,000 year old wooden javelins and butchered horses at Schöningen [102] indicate a long history of big-game hunting); (2) Human populations clearly abandoned large areas of northern and western Europe in the coldest millennia of the Last Glacial Maximum, and re-colonized after milder climates returned at the end of the Pleistocene. Magdalenian sites in many areas represent an explosive re-colonization after the abrupt Bølling warming ca. 12,500 rcbp (14,700 cal BP). Indeed, this process was comparable to Clovis expansion [56], and it should not be surprising that the indigenous megafauna—locally naïve after millennia of isolation—should have suffered similar dire consequences from a sudden upsurge in human predation coincident with radical climate change and vegetation shifts.

Grayson and Meltzer shrewdly avoid detailed discussion of the Australian evidence, which appears to contradict their position. The picture of extinction emerging there is best interpreted as a case of human overkill with minor climatic assistance. New dates now indicate that humans arrived and rapidly expanded throughout Australia about 45,000 ± 3000 BP, and megafauna (giant marsupials, reptiles, and birds) became extinct about 46,000 ± 4000 BP. “According to the most recent TL, OSL, and U/Th results, many species of megafauna from all climatic zones became extinct at about the same time as people spread across the continent … which could be interpreted as supporting the global ‘blitzkrieg hypothesis’ for megafaunal extinction proposed by Martin (1984)” ([31], p. 469; [67]). It is generally accepted that the Australian extinctions did not coincide with a major climate change episode [28,77,91], and thus Australia may be a better case than America in which to attempt to disentangle human vs. environmental impacts. However, some indication does exist of fluctuating arid and humid conditions at the time of human arrival in the Lake Mungo region [17], so the Australian extinctions may be
yet another instance of the combined effect of human first-contact and climate changes.

It has often been noted that the lithic toolkit of the earliest Australians did not include finely crafted killing implements on a par with the magnificent Clovis spearpoints. However, even the mid-Pleistocene Schöningen spears demonstrate the potential predatory effectiveness of sharpened sticks, which almost never survive in the archaeological record. Perhaps because of the perceived inadequacy of earliest aboriginal weaponry, several authors (e.g., [77]) suggest that in Australia, human impact upon megafauna was mainly indirect, hastening extinction by intentional burning of vegetation. In contrast, Flannery [27] has argued that ubiquitous fires were a post-overkill phenomenon, resulting from the accumulation of vegetation which megafauna would formerly have consumed. Meltzer and Grayson state that, to date, no widespread support has been found for such dramatic landscape alteration by fire in North America, but recently Robinson et al. [92] have suggested that burning in southern New York might be a sign of human arrival there in the late Allerød (pre-Younger Dryas) interval [58]. The sequence they propose—initial massive kill of megaherbivores—vegetation accumulation—fire—echoes that suggested by Flannery in Australia. Also, it should be noted that fire frequency, as indicated by accumulation of charcoal in lakebeds, does increase dramatically in Central America [87] and in southern Chile [80] at 11,000 rcbp, coincident with the arrival of Clovis-derived fishtail point-makers. A similar initial burning that may be human-caused occurs at the mouth of the Amazon, ca. 10,800 rcbp, 12,800 cal BP [11]. However, it is difficult to unambiguously distinguish human-set fires from naturally occurring fires that seem to accompany the global aridity of the Younger Dryas [43].

Meltzer [74–76] has not previously been reticent to evaluate the early archaeological record of South America. We think that he and Grayson were injudicious in their validation of the bizarre and confusingly described Monte Verde site [24] as conclusive proof of pre-Clovis human entry into the continent. In spite of major problems with the site’s evidence, they persist in this judgment (e.g., [38], pp. 314, 346). Their newfound pre-Clovis convictions have become integral to their rejection of overkill. Yet, despite their evident recognition of the importance of the South American record, they surprisingly have declined to address megafaunal extinction in South America. They could have added equids and ground sloths (Hippidion saldiasi and Mylodon darwini) to the list of confirmed killed or butchered species, based upon well documented associations with Fell I (fishtail) lithic assemblages at Cueva del Medio [82,83] and Piedra Museo [4]. Solid cases also have been argued for human predation on extinct fauna at several other sites, such as Paso Otero 5 (Equus neogenus, Megatherium americanum, Toxodon sp., Hemiauchenia, Glossotherium, and possibly Glyptodon) [69], Tagua Tagua (Stegomastodon humboldti) [84], Tres Arroyos 1 [16] and Arroyo Seco 2 [78,89].

The South American case is of particular interest because faunal extinctions occurred there several hundred years later than in North America (probably completed by ca. 10,200 rcbp, or about 12,000 cal BP—as one would anticipate if there was a slightly later human entry) and because changes in climate and vegetation were not synchronous with those of the Northern Hemisphere. Southernmost South America warmed gradually, coevally with Antarctic warming, after 18,000 cal BP (15,000 rcbp) [15,73,93]. While the Northern Hemisphere warmed abruptly at 14,700 cal BP, southern South America felt the effects of a relatively minor cooling (Antarctic Cold Reversal) [14]. Younger Dryas-like climate changes occurred at least as far south as Colombia (the El Abra Stadial), and probably in the Amazon basin [59,70] but any effects in the Southern Cone were minor [13] and evidently preceded the northern climate shift by about 500 years [44]. Thus, if warming or cooling with attendant precipitation and vegetation changes were causative forces in extinction, megafauna should have been dying out in South America before the North American extinctions. Obviously, this is not what happened.

Grayson and Meltzer [39] strangely omit from their discussion the ca. 150 radiocarbon dates run on bones of megafauna by Tom Stafford, Russ Graham and Holmes Semken. Although there has been a delay in the formal publication of those dates, oral presentations have been given in several public venues (e.g., [35,36]). A brief summary of the new dates was published in Quaternary Times, the newsletter of AMQUA, in June 1999 [22]. Indeed, Grayson [37] demonstrates an awareness of the new dates for proboscidean extinction. Although they do not cite the new dates, presumably Grayson and Meltzer ([38], p. 346) allude to them when they assert that “to date, of the 35 genera involved, only 15 can be shown to have survived beyond 12,000 years ago. As a result, it is possible, though certainly not demonstrated, that a significant number of the losses predated the Clovis arrival” (see also [39], p. 588). This is misleading sophistry, as it leaves the false impression that the extinctions of the 15 well-dated genera (17, actually) might have occurred sporadically over the millennium between 12,000 rcbp and Clovis expansion at 11,000 rcbp [or were even “scattered across thousands of years, as occurred in Europe” ([39], p. 591)]. In fact, the 17 genera all disappear abruptly and simultaneously at 10,800–11,400 rcbp. Grayson and Meltzer do not acknowledge that these dates fatally undermine their arguments for gradual climate change as the cause of the extinctions. As they have recognized, demonstration that the extinctions were synchronous “requires that we
attribute to the extinction ‘event’ ... speed and taxonomic breadth. ... Once that is done, explanations of the extinctions must be structured to account for these assumed properties, whether those explanations focus on people, climate ... or disease.” ([38], p. 347).

The new dates show that at least 17 genera of North and South American megafauna went extinct either at 11,400 or 10,800 rcbp. Graham et al. [22,35,36] have indicated that terminal dates for proboscideans (mammoth and mastodon) cluster at the late end of this period, while those for the “lesser” megafauna such as Equus and Camelops are generally earlier. Graham and colleagues have interpreted this as clear evidence against the “keystone species” version of the overkill model [86], in which removal of the central species leads to a cascading collapse of the entire ecosystem.

We caution against their interpretation of a two-step extinction process, because it reflects a facile approach to the complicated Late-glacial radiocarbon record. At the onset of the Younger Dryas (about 12,900 cal BP), radiocarbon dates drop sharply by 500 years (from about 11,200 to 10,700 rcbp) in less than a century of real time. German trees buried or burned by the Laacher See tephr[a, deposited in an eruption 200 years before the onset of the Younger Dryas, have produced radiocarbon dates of 11,300 to 10,800 rcbp, indicating a date inversion and short plateau during the late Allerød [9,61]. Thus, a bone dated to 11,200 rcbp may actually be younger than one dated to 10,900 rcbp. In addition to these radiocarbon plateau and cliff effects, interpretation of the new bone dates must be tempered by recognition of two potentially contradictory factors. On the one hand, bone dates, even those obtained by Stafford’s exemplary XAD-purified amino acid technique [96], often appear to come out too young. For example, the date of 10,240±120 (AA-2978) for the infant buried with Clovis artifacts at the Anzick site in Montana is certainly too young, and does not overlap, even at two sigma, with the more credible date of 10,940±90 rcbp (AA-2981) for the same specimen [96]. On the other hand, it is statistically improbable that the most recent dated specimen of any particular species is really the very last individual of that taxon. The youngest date obtained on relatively sparse megafaunal taxa should always be taken as only a terminus post quem for actual extinction. Paleontologists know this as the Signor–Lipps effect.

For all these reasons, the radiocarbon dates for the last of the American megafauna, despite their ostensible precision, retain a certain irresolvable ambiguity. However, the abruptness and synchronicity of the extinction event are also clearly manifest in stratigraphic sequences on both site-specific and regional scales. As Vance Haynes [46,47] has emphasized in the Southwest, mega-fauna (mammoth, horse, camel) fossils are found below the ubiquitous “black mats” (spring-laid organic layers), and never above them. These layers demarcate the Terminal Pleistocene extinction event as clearly as the K-T boundary marks the dinosaur extinction. The mats typically date to ca. 10,700 rcbp, early in the Younger Dryas chron. It should also be noted that, at locations frequented by megafauna throughout the late Pleistocene, their dung disappears at 11,000 rcbp or soon thereafter. This is the case at Rampart Cave in Arizona, where Shasta ground sloth dung was not deposited after that date [62]. A similar abrupt cessation of Mylodon ground sloth dung, capped by later charcoal of apparent human hearths, occurs at Gruta del Indio, Argentina, ca. 10,300 rcbp [63]. One might argue that the ground sloths had merely broken with millennia of habitual behavior and moved off to some suddenly more hospitable area, but this is an unlikely scenario. Another proxy index of megafaunal extinction is the dramatic fall-off in abundance of spores of Sporormiella fungi that had thrived on their dung. Such a fungal decline occurs in Northwestern ponds some time before the Younger Dryas onset [58,92]. Davis [19] similarly reports a dramatic fall-off of Sporormiella frequencies in Western ponds around 10,800 rcbp.

2. Is there evidence for climate change as the cause of extinctions?

Grayson and Meltzer advocate a vague theory of climate change in place of overkill, while candidly admitting that for now, “none (of the climate change hypotheses) connect particular climate variables with particular organisms in powerful ways” ([39], p. 591).

Climate change has always been the main theoretical alternative to human predation. Grayson and Meltzer offer no new refinements to the climate model, and seem unaware of recent developments in the study of latest Pleistocene climates. It must be emphasized that a drastic revision of the climatic hypothesis has occurred recently, which they do not acknowledge. Formerly, the demise of megafauna was attributed to dramatic yet rather gradual changes in temperature and vegetation that occurred during the transition from the Pleistocene to the Holocene. But we now understand that the Holocene warming was delayed in the northern hemisphere by the 1100- or 1300-year Younger Dryas [5,40,95,98]. This near-glacial cold interval ended abruptly, in only a few decades, with a sudden warming at 11,570 cal BP (10,000 rcbp) that occurred more than 1000 years after the crash of the megamammals; so, obviously, neither the concomitant temperature, climate, nor vegetation changes can have played an immediate causal role in the extinction. For this reason, Russell Graham, one of the foremost and best-informed proponents of climatic causation, now cites the Younger Dryas onset as the straw that broke the collective backs of the megafauna [33]. This was the last of a series of 24
dramatic climate oscillations over a span of 100,000 years that, by rearranging vegetation zones, had gradually sapped the adaptive strength of all the 35 genera that finally threw in the towel at 12,800 cal BP.

In view of the new paleoclimate data, to make any case for climate as the killer, one would now have to show that the Ice Age (?) megafauna, having survived for 2 million years in climates often much colder than the present, were fatally stressed by rapid cooling, not warming. The Younger Dryas never got as cold, for a sustained period, as the many typical full glacial episodes that preceded it [40]. True, the Younger Dryas caused the congregation of plants into anomalous communities with no precise modern analogues [95], and in some areas of North America, annual temperature extremes during the Younger Dryas were unprecedented in the previous 10,000 years (although conditions during numerous earlier stadial events were probably quite similar [5]). However, except for an insignificant species of southeastern spruce [54]—not demonstrably critical to the diet of any megamammal—no Terminal Pleistocene plant extinctions are recorded. Available dietary evidence (e.g., Columbian mammoth [20] and ground sloth dung [45]) shows that megafauna were not overly picky eaters. They would not have been challenged by a shift in relative percentages of local plant species; and in response to geographic retraction, expansion, or translocation of plant communities on a decadal scale, these big animals were perfectly capable—as are modern proboscideans—of moving hundreds of miles (e.g., see [53] for evidence of mastodon migration between Florida and Georgia).

Younger Dryas effects were muted or absent in much of South America, where even more mammal species died out than in North America. The most recent analysis of DNA in ground sloth dung from the Southern Cone shows that the environment at ca. 13,500 rcbp (more than 1000 years after the start of Antarctic warming) was much like the present, and the animals fed upon various plants that still grow in the locality [51]. Martin long ago noted a similar prevalence of still-extant plants in the dung of Southwestern giant sloths (e.g., [88]). While we hesitate to endorse all of D. Fisher’s [26] claims of human intervention in the demise of proboscideans in the Great Lakes region, his research at least demonstrates that the Terminal Pleistocene mastodons were not suffering stresses attributable to dietary deficiencies. Agenbroad [1,3] has shown that the numbers of mammoths in North America increased dramatically after a bottleneck during the Last Glacial Maximum, and their range expanded northward from 30 degrees to 50 degrees latitude. “Indeed, a significant pattern of the shifts from Glacial to Clovis-age faunas, from the Southern Plains as well as New Mexico, is that diversity INCREASED significantly into the Clovis period. This is hardly the scenario one might expect in a deteriorating post-glacial environment. ALL of the Clovis age taxa survived the LGM, but many were immigrants to this region following the LGM” ([23], p. 210).

Apart from reduction in numbers and migration into hospitable refugia, another way that animal species may react to environmental stresses over time is reduction in body size, presumably the mechanism by which Bison antiquus was transformed into B. bison in the mid-Holocene (although an interesting alternative possibility is that an immigrant bison species from eastern Beringia replaced B. antiquus about 10,000 rcbp ([107], but cf. [94])—in which case we could add giant bison, often hunted by Clovis Paleoindians (e.g., at Murray Springs and Jake Bluff [12] to the list of extinct megafauna). The giant Pleistocene beaver was similarly replaced by its smaller modern relative. Body-size reduction is also evident on Wrangel Island off Siberia, where relatively small mammoths survived until about 3700 rcbp [103] (roughly when people arrived and probably eliminated them). If climate alone wiped out giant mammals, we might expect smaller collateral or descendant forms of those genera to have survived to the present: monkey-sized ground sloths, little ponies, or tapir-sized proboscideans. Sadly, this did not happen on the American mainland. Diminutive ground sloths did evolve on the larger Caribbean islands, only to be wiped out, not when the Holocene began, but when humans arrived after 7000 rcbp [64]. Pygmy mammoths occupied Santa Rosa Island off the coast of southern California in the late Pleistocene. The latest date for this species, recently reported [2], is 11,030 rcbp, statistically indistinguishable from the new date of ca. 10,950 rcbp for Arlington Springs woman [97], who was interred on the same island.

For now, as Grayson and Meltzer admit, there is no testable climate change hypothesis. If climate change is to be taken seriously as the sole cause of extinction, its advocates must show that the challenges posed to American fauna by the Bolling–Allerød warming (14,700 cal BP) and Younger Dryas cooling (12,900 cal BP) were unique and more severe than in any past episodes. But the GRIP and GISP2 ice core records of past climates show that the Terminal Pleistocene changes were not unique in either their abruptness or severity. Between the end of the Eemian interglacial, 117,000 BP, and our present Holocene interglacial, global climate oscillated repeatedly and abruptly between cold and warm states (stadials and interstadials) [5,40]. The rapid change at ca. 85,000 BP from cold to warm climate was no less radical than the Bolling warming at 14,700 cal BP. Yet there were no significant megafaunal extinctions at the start of the Eemian (130,000 BP), or at 85,000 BP, or when temperatures plummeted at 70,000 BP [6]. The Younger Dryas episode is unique in its faunal consequences
only because its onset coincided with the arrival of human hunters.

3. Why are there so few killsites if overkill is the better explanation for the extinctions?

To summarize the argument to this point, it is clear that, at the very least, a purely circumstantial case can be made that humans played some role in Terminal Pleistocene extinctions in the Americas. One simply cannot ignore the fact that rapid human expansion is coeval with unprecedented faunal collapse. Plus, the “smoking spear” is there to see for anyone without conceptual blinders. In the very brief interval of Clovis hunting of megamammals, humans left behind at least 14 unambiguous kill and butchery sites in North America, by Grayson and Meltzer’s own conservative estimate, and possibly many more than that according to other authorities. In view of the extremely narrow time interval, this is a phenomenally rich record.

With respect to the scarcity of non-proboscidean killsites, the taphonomic probability is extremely low that natural processes ever would preserve upland sites containing the butchered carcasses of horses, camels, ground sloths, and smaller megafaunal taxa. One of us (Haynes) can speak with authority on this matter, having devoted 25 years to neotaphonomic studies of large-mammal skeletons in Africa, Australia, and North America. Haynes has spent much of his professional career comparing fossil sites with the modern death sites of hundreds of African elephants and other large mammals that died as a result of non-cultural processes such as die-offs or carnivore predation, as well as government-sponsored killing operations. Even in protected situations such as permanent waterholes where burial may be rapid, very (very!) few modern mammal skeletons are preserved whole or meaningfully associated with evidence about the condition of their death, whether it was cultural or non-cultural. In general, modern death sites containing bones are very rarely preserved—in fact, depending on the local conditions, the proportion of large-mammal death sites (cultural or non-cultural) that will be preserved may be as low as 0.01% or less of total numbers being killed or dying naturally.

Grayson and Meltzer ([38], Figure 2, [39], Figure 1) show that 25 of the extinct North American genera are represented by fewer than 50 FAUNMAP occurrences dated to the last millennia of the Pleistocene. Given likely human kill rates and preservation factors, there is an infinitesimal probability that even one of these few cases would be a provable kill site. It is thus remarkable that, for eight of these genera, there should be even ambiguous human involvement.

So there actually is empirical evidence, from analogous modern cases, that overkill would leave few fossil remains behind to indicate the very processes involved in the extinctions. Why then is the osseous evidence of human predation on non-proboscidean taxa so much more abundant in European archaeological sites? One reason is that almost none of these are actual kill sites; the bones occur in camps and settlements, often rockshelters that were occupied for long periods and repeatedly, where occupational debris is thick and abundant. North American Paleoindians, in contrast, rarely occupied rockshelters. Another reason is that hominin predation has a history of some 500,000 years in Europe, as against the few hundred years of Clovis megafauna hunting. The “scores” of bone-bearing archaeological sites in Europe must be only a small remnant of the tens of thousands of original occupational loci, the overwhelming majority of which were not preserved.

It is important to observe that, while there are at least two good Terminal Pleistocene kill sites east of the Plains (the Kimmswick mastodon in Missouri [34] and, probably, the Wacissa River bison in Florida [104]), we know of none involving any large mammal from the entire subsequent 12,500-year span of the Holocene. If archaeologists in eastern North America have not yet stumbled upon the remains of any butchered carcasses of elk, deer, bear, or woodland bison of Holocene age—12,500 years with no discoveries—what is the likelihood of finding a butchered Terminal Pleistocene ground sloth, stag-moose, horse, or musk-ox? Should we infer that Clovis hunters never preyed upon those animals? Faunal preservation in the east is generally poor; the common assumption that eastern Paleoindians focused almost exclusively upon caribou hunting is based upon a total of seven minute fragments of cervid bone from three early Paleoindian sites (Udora, Whipple and Bull Brook) [99]. This sparse evidence does not allow confident reconstruction of early Paleoindian hunting behaviors in the east.

Although we contend that human predation was instrumental in the collapse of American megafauna, we are not saying that Martin’s original model was correct on all the particulars of the process. Available archaeological and ecological data suggest that, in several respects, the simulation models of overkill presented by Mosimann and Martin [81] (blitzkrieg at the front of the wave of advance) and more recently by Alroy [7] are rather unrealistic and require modifications of details:

1. Human populations of the Clovis era never approached 500,000–1 million or more; probably, there were no more than 50,000 people in North America at 12,900 cal BP [25,49].
2. Extinction of most species in North America probably was complete within about 400 years after human entry; thus, overkill had to be accomplished
by many fewer people, and over a much shorter time, than Martin or Alroy postulates.

3. Humans probably did not advance in a wavefront across the continent; rather, exploratory stations (marshaling camps, staging areas) [8,21] were established at favorable loci, such as game refugia, lakes and river confluences, and bands “leapfrogged” from one amenable spot to the next. Thus, the dragnet effect that Martin imagined [81], squeezing surviving megafauna into an ever-smaller safe haven ahead of the wavefront, is improbable [10]. Some other circumscription factor—imperative access to potable water under drought conditions, perhaps—would have prevented the animals’ escape from human hunting.

4. Clovis hunters may have either specialized in predation on mammoths, in which case collapse of this keystone species [86] could have set in train a cascading collapse of Late-glacial ecosystems; or Clovis hunting may have been more generalized, in which case low levels of additional predation pressure may have had wider synchronous effects on many genera. A more diverse dietary base would also mean that hunters did not have to curtail hunting in any one region as the numbers of available mammoths dwindled.

5. Various simulations show that a very small increase in predation loss due to humans (less than 5%) can wreak havoc upon animal populations (e.g., [52,79]). This is not the non-stop killing spree that overkill opponents often caricature.

6. We cannot ascertain the precise density of large mammal populations of the Late Pleistocene. We do not think there were vast herds or high-density populations. Some critics of overkill have wondered how Paleoindians armed only with spears ever could have wiped out large numbers of megafauna, when 18–19th century hunters with rifles took so long even to put a dent in American bison populations. The great herds of bison witnessed in the Contact period may have been a brief anomaly, reflecting both Little Ice Age climatic change and the decimation of Native American populations by European diseases after AD 1550 [57]. Was Terminal Pleistocene North America really comparable to the Serengeti? Or to a densely stocked cattle ranch? Or, were there pockets of animals in scattered clearings and river bottoms amid the taiga-like forests covering much of the continent (66), p. 682? Patchy distribution of small prey populations makes overkill more imaginable, given very low-density, mobile human populations.

7. Before arrival of human hunters, the size of mega-herbivore populations may have been limited more stringently by native carnivores rather than by food supply [57]. Several authors [30,55,57,105] have suggested that interactions between humans and indigenous animal predators (dire wolf, short-faced bear, sabertooth cats, lions, cheetahs) may have played some role in rapid megafauna extinction. These could have entailed either human eradication of direct competitors, as argued by Whitney-Smith [105], or disruption and dislocation of longstanding prey-predator relationships. Either way, modeling [57,105] suggests that the consequent collapse of both herbivore and carnivore populations can be dramatic and very rapid.

8. It may never be possible to unambiguously extricate the relative causative roles of abrupt climate oscillations between 14,700 and 11,570 cal BP and of contemporaneous human hunting after 13,400 cal BP in instigating the megamamal collapse. Thus, North America cannot serve as the best laboratory-like example of a pure overkill process. Then again, climate is always changing, so there will probably always be some minor effect that can be temporally associated with any instance of extinction (68), p. 46).

It seems that for Grayson and Meltzer, their intellectual problem with overkill may ultimately be an issue of scale. They have no qualms about accepting the central role played by humans in the demise of island faunas (e.g., the extinction of the moas within 150 years after humans arrived on New Zealand [52]). We agree with them that, even in these cases, pure predation need not be the sole human impact. Species that accompany humans (e.g., dogs, rats, pigs) and pathogens played a role in island extinctions, as did anthropogenic transformation of the vegetation by felling and burning (68), p. 27). We are willing to entertain and investigate the possibility that the American case also may have entailed similar factors in addition to hunting per se (e.g., introduction of dogs accompanying the first Paleoindian migrants [60]; possible spread of canine distemper or other zoonotic diseases, perhaps initially to carnivores (along the lines suggested by MacPhee and Marx [64])); landscapes altered by burning in Central and South America and perhaps the Northeast, ca. 11,000 rcbp [80,87,92]. However, for some intuitive reason, which they do not clarify by quantitative modeling, Grayson and Meltzer are incredulous that these processes could have operated at the scale of an entire continent. We wonder if they would classify Australia, at about 7 million km₂, as an island or a continent. As noted above, extinction of megamarsupials, giant reptiles and giant birds appears coincident with the rapid expansion of humans across the entire land mass around 48,000 BP [27,28,31,77,91]. Sure, America is big, but within 500 years or less after their arrival, Paleoindians had explored the whole of America south of the ice sheets, depositing their distinctive and remarkably uniform tools in Washington State, Nova Scotia,
Florida, Sonora, and from Panama to Tierra del Fuego by ca. 12,900 cal BP. Really, a continent is ultimately just a gigantic island. Animals could retreat from human predators for a while, but not indefinitely.

In the end, we do not understand why Meltzer and Grayson have elected to launch their concerted assault upon Martin’s theory just at this moment. Within the last decade, paleoclimate studies, focused on ice cores and lake bed sediments, have achieved an unprecedented decadal precision in chronology, and ingenious use of proxy measurements now allows accurate estimates of temperature and precipitation at a micro-scale. Surely, anyone seriously proposing “climate” as the critical factor in megamammal extinctions should avail themselves of the new data. Yet, Grayson and Meltzer do not. Exciting new Paleoindian sites, some with relevant faunal data, are being reported every year from North and South America. Apart from their dogged defense of the ambiguous Monte Verde site, Grayson and Meltzer do not concern themselves with the rapidly accumulating South American evidence. Their failure to make any use of the new radiocarbon evidence of Sta.

ing South American evidence. Their failure to make any use of the new radiocarbon evidence of Stafford et al. [35,36] has already been noted. Perhaps they are also unaware of several ongoing projects that have generated many new and often surprising radiocarbon dates for Beringian and Eurasian fauna [41,42,65,101]. New technologies for retrieval of ancient DNA [51,88,94,106] and isotopic signatures [71,72] are enabling detailed reconstructions of the diets, behavior, and genetic relationships of extinct fauna. Astonishingly, DNA of extinct species is now reported from permafrost soils in Beringia, as well as moa DNA from cave soils in temperate New Zealand [106]. We have hardly begun to assimilate the mass of new data. Who knows what we may learn in the next few years? Now is not the time to attempt to shut down debate with ill-founded assertions and sophistry. The best explanation for American megafaunal extinctions right now is some form of human predation. As at least one leading archaeologist has recognized, “The right question probably isn’t whether people were involved, but how?” ([85], p. 178). We have begun to outline realistic scenarios entailing human hunting in a time of dramatic climate oscillations [25,48–50]. At the same time, we are eager to employ the latest evidence from many Quaternary subdisciplines to test a plausible competing hypothesis of extinction triggered solely by climate change, but none has been put forward.

If Meltzer and Grayson have a compelling new climate change hypothesis to offer, it behooves them to set it out, in adequate detail, for scientific assessment. Instead, they have published an indefensibly abusive and unsubstantiated ad hominem attack on Paul Martin’s research. If they or anyone else ever does present a climate change hypothesis that purports to fit the rapidly expanding body of evidence, then we can all proceed to do real science. Until then, in the words of Monty Python, “This isn’t an argument—it’s just contradiction.”

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References
