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## Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

## Overkill and the North American archaeological record—not guilty by association? A comment on Wolfe and Broughton (2020)

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## ARTICLE INFO

## Keywords:

Pleistocene extinctions  
North America  
Overkill  
Clovis  
Foraging theory  
Bison  
Mammoth

## ABSTRACT

The “associational critique” holds that there are too few archaeological kill/scavenging sites to support the hypothesis that human hunting caused the late Pleistocene extinction of 38 genera of primarily large mammals. Wolfe and Broughton (2020) assessed this critique on both theoretical and empirical grounds and found it wanting, with a focus on the arguments presented in Grayson and Meltzer (2015). We welcome their evaluation, including their effort to improve on our prior analyses. However, we are unconvinced by their assertion that hunters will always pursue large ungulates on encounter. We also reject their conclusion there is no systematic difference in the abundance of extant and extinct taxa in terminal Pleistocene archaeological contexts since they made two errors that undermine their analysis. First, they confounded calibrated and uncalibrated radiocarbon years. Second, they failed to note the parameters of the Cannon and Meltzer (2004) study on which their tally of archaeological kill/scavenging sites of extant taxa is based. With these mistakes corrected, the results confirm what we showed previously: extant large mammals occur in kill/scavenging sites far more often than extinct forms. This result also supports our previous suggestion that the now-extinct fauna had either already disappeared or was much reduced in abundance by the time people arrived on the landscape.

## 1. Introduction

The “associational critique” (Grayson, 1984a, 1984b) holds there are far too few archaeological kill/scavenging sites to support the hypothesis that human hunting—overkill—caused the late Pleistocene extinction of 38 genera of primarily large mammals. This is a longstanding critique of the overkill model, first raised by Guilday (1967) and Jelinek (1967). Paul Martin responded to this argument with the assertion that human hunters radiated so rapidly throughout the Americas that kill/scavenging sites would not be expected to be found (Martin, 1967, 1973; Mosimann and Martin, 1975; see the discussion in Grayson and Meltzer, 2003).

We have not been swayed by Martin’s counter to the associational critique for several reasons. First, we have long been skeptical that all the genera that became extinct did so synchronously at the very end of the Pleistocene, as opposed to their disappearance having been staggered across space and through time (Grayson, 1987, 1989, 1991, 2001, 2007, 2016; Grayson and Meltzer, 2003, 2004, 2015; Meltzer, 2004b,

2009, 2015; see also Boulanger and Lyman, 2014; Stuart, 2015).

Second, we question whether early peoples in North America always focused on the pursuit of big-game, given both the risks of such a subsistence strategy (Bird and O’Connell, 2006; Bird et al., 2013; Lupo and Schmitt, 2016; Meltzer, 2004a, 2009, 2015; see also Hawkes et al., 1991), and the evidence that these groups had broad-based diets that incorporated a variety of resources, dependent in part on the structure of the environment they inhabited (e.g. Cannon and Meltzer, 2004, 2008; Grayson, 2011, 2016; Meltzer, 1993, 2004a, 2009).

Finally, we have shown that there are only 16 occurrences (at 15 sites) documenting that people were responsible for the death or dismemberment of a now-extinct mammal (Grayson and Meltzer, 2015:178). Those extinct mammals are limited to five genera: camel (*Camelops*), horse (*Equus*), gomphothere (*Cuvieronius*), mastodon (*Mammut*), and mammoth (*Mammuthus*).<sup>1</sup>

As a part of that demonstration, we compiled data from FAUNMAP (Graham and Lundelius, 2010) on the abundance of these taxa in the Late Wisconsin (35,000–10,000 radiocarbon years before present [<sup>14</sup>C

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E-mail address: [dmeltzer@mail.smu.edu](mailto:dmeltzer@mail.smu.edu) (D.J. Meltzer).<sup>1</sup> Were we updating the list presented in Grayson and Meltzer (2015), we would add the newly-published La Prele (WY) site as a mammoth kill/scavenging occurrence (Mackie et al., 2020).<https://doi.org/10.1016/j.jas.2020.105312>

Received 20 July 2020; Received in revised form 31 August 2020; Accepted 14 December 2020

Available online 15 March 2021

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yr BP]) fossil record. We showed that the extinct fauna are under-represented archaeologically relative to their abundance in the fossil record, particularly in comparison to the number of kill/scavenging sites of the genera of large mammals that survived the end of the Pleistocene—the extant fauna (Grayson and Meltzer, 2015; see also Grayson, 1984b, 2001, 2007; Meltzer, 1986, 2015; Meltzer and Mead, 1985). We concluded that the rarity of kill/scavenging sites of now-extinct mammals is not a consequence of the speed with which Clovis hunters radiated across the landscape, as Martin (1973, 2005) proposed. Instead, this scarcity is to be expected given the likelihood that many of the extinct genera had vanished before humans arrived, while others had declined in number as they approached extinction (as is now becoming visible in analyses of ancient DNA [e.g. Chang et al., 2017; Cooper et al., 2015; Enk et al., 2016; Lorenzen et al., 2011; Orlando and Cooper, 2014]). These animals would thus have only rarely been available to human hunters (Grayson and Meltzer, 2003), whose own relative numbers were beginning to expand rapidly (as shown by emerging ancient DNA evidence, e.g. Bergström et al., 2020; Llamas et al., 2016) but on an absolute scale were still few and scattered widely across a vast landscape (Meltzer, 2009).

Wolfe and Broughton (2020:3) have recently questioned the validity of the associational critique on both theoretical and empirical grounds. Specifically, they identify two hypotheses they believe explain the “apparent low proportional abundance of kill/scavenging sites for extinct taxa” that we previously documented. They first challenge the idea, not suggested by us, that “early hunters selectively avoided would-be extinct large mammal genera and pursued them upon encounter less frequently relative to extant taxa.” In their view, since large mammal prey are high-ranked, the logic of foraging theory implies that they “should *always* be pursued upon encounter” (Wolfe and Broughton, 2020:3–4, emphasis in original).

Second, they consider the hypothesis that the “apparent underrepresentation of extinct taxa in archaeological assemblages” is due to the fact that “they had already declined in proportionate abundance by the time Paleoindian hunters appeared on the North American landscape in appreciable numbers” (Wolfe and Broughton, 2020:4). To resolve that question they argue, quite reasonably, that an empirical assessment of the associational critique must be based on data from the period when Paleoindians could have encountered them (Wolfe and Broughton, 2020:4). They correctly note that this was not the case for our Late Wisconsin tally (Grayson and Meltzer, 2015). Based on an analysis of data from the Neotoma Paleoecology Database (<http://www.neotomadb.org>), which incorporates and expands on FAUNMAP, they conclude that there is “no systematic difference in the abundances of extant and extinct taxa in archaeological versus paleontological contexts” (Wolfe and Broughton, 2020:7).

However, in compiling data that purports to show there is no systematic difference in the abundances of extant and extinct taxa in archaeological versus paleontological contexts, they make two significant errors, discussed in detail below. When the data are correctly assembled the results confirm our earlier conclusion: extant large mammals occur in kill/scavenging sites in terminal Pleistocene contexts far more often than do extinct forms. This result also supports our suggestion that the now-extinct fauna had either already disappeared or were much reduced in number by the time humans arrived on the landscape.

We address their hypotheses and analyses, and our reanalyses using the appropriate data, after briefly considering a few other matters in their discussion.

## 2. A few clarifications

Citing Grayson and Meltzer (2015), Wolfe and Broughton (2020:2) report that 37 genera of mammals became extinct in North America during the late Pleistocene. Since we wrote our paper, however, the tally has increased to 38 genera, owing to the addition of the horse

*Haringtonhippus* (Heintzman et al., 2017; Jiménez-Hidalgo et al., 2019; Rook et al., 2019; but see Barrón-Ortiz et al., 2019). Nonetheless, to be consistent with Wolfe and Broughton in our reanalyses, we will use 37 genera.

We agree with Wolfe and Broughton that mammoth and mastodon habitats differ, and that differential patch use by human foragers would map on to such differences (e.g., Cannon and Meltzer, 2008). Nonetheless, their suggestion that the relative dearth of mastodon kill sites compared to those of mammoth is because mastodon habitats were “used less frequently by human foragers” (Wolfe and Broughton, 2020:7) is problematic. As Widga et al. (2017:778) showed, “>90% of dated mastodons overlapped with [the period of] human occupation” in the upper Midwest, a region where they deem conditions “ideal” for preservation of both natural and cultural death sites. The scarcity of kill sites notwithstanding, this is also a region that has some of the highest densities of fluted point occurrences in North America (<https://pidba.org/content/fluted.JPG>). Indeed, many years ago, Martin (1967:101) touted the overlap of fluted points and mastodon occurrences in Michigan as compelling evidence in support of overkill.

Further afield, Wolfe and Broughton (2020:2) assert that “in Australia... Humans and extinct fauna overlap for only 8.8% of the ~50,000 [cal] year archaeological record for the region.” However, the youngest secure date for an extinct Pleistocene vertebrate in Australia is for the diprotodont *Zygomaturus* at the Willandra Lakes in New South Wales, with OSL dates of approximately 33,000 years ago (Westaway et al., 2017). As Westaway et al. (2017) observe, this date indicates an overlap of 17,000 years, or 34%, of a 50,000 year archaeological record. If the 65,000 year OSL date from Madjedbebe site is accepted (Clarkson et al., 2017; but see O’Connell et al., 2018), then the overlap increases to nearly 50%. On a related matter, the extinctions in Australia appear to have been time-transgressive, with the last appearance dates (LADs) for the many of the taxa involved being earlier than any suggested date for the human arrival in Sahul (Wroe et al., 2013). This, however, is an issue that is far from resolved (see, for instance, Saltré [2016], and the detailed chronological assessments in Peters et al., (2019)).

Finally, although Wolfe and Broughton (2020:2) mention New Zealand’s “plethora of [archaeological] associations” with extinct vertebrates, it is important to emphasize that late Holocene extinctions here ranged from lizards, frogs, and tiny flightless acanthistid wrens, to giant moas (e.g. Worthy and Holdaway, 2002; Mitchell et al., 2012; Tennyson and Martinson, 2006; Wood et al., 2020; Worthy, 2016). This sweeping set of extinctions was certainly anthropogenic in origin, but the cause lies in a complex combination of hunting, profound habitat alteration, and the consequences of introduced predators, including the Pacific rat, *Rattus exulans* (see Dussex et al., 2019; McWethy et al., 2010; Tennyson and Shepherd, 2017; Worthy, 2016, among many others).

## 3. Were large extinct taxa always pursued on encounter?

In considering the low proportional abundance of kill/scavenging sites that we reported (Grayson and Meltzer, 2015), Wolfe and Broughton (2020:3) suggest that one explanation might be that “early hunters selectively avoided would-be extinct large mammal genera.” It is unclear if they are attributing that explanation to us, but we take this opportunity to state this is an argument we did not make in Grayson and Meltzer (2015), or in any other discussion of this topic by either of us. Indeed, we would not have explored the incidence of hunting of extinct large mammals (Grayson and Meltzer, 2002, 2003, 2004, 2015) if we thought mammoth, mastodon, or other extinct large genera were avoided or ignored by Clovis hunters. We conducted those analyses precisely because we wanted a clear idea of just how often Clovis hunters did take such animals.

That said, we are not convinced that now-extinct large mammals would “always” be pursued by hunters upon encounter (Wolfe and Broughton, 2020:4). Wolfe and Broughton (2020) reached this conclusion through straightforward logic drawn from behavioral ecology. They

observed that for vertebrate prey, there is “a significant positive relationship between prey body size and post-encounter return rate.” From this, they argued, it follows that the largest prey also have the highest return rates, and thus that “high-ranked prey—prey with the highest post-encounter return rate available in a given resource patch—should *always* be pursued on encounter” (Wolfe and Broughton, 2020:4; emphasis in original). While they note that there are exceptions to these guiding tenets, they also observe that those exceptions apply only to a very narrow range of prey types.

We are sympathetic to the approach taken by Wolfe and Broughton (2020) and most certainly do not criticize them for it. However, exacting work with modern foragers has documented that the relationship between prey body size and post-encounter return rates is not straightforward. Many years ago, for instance, Broughton (1994; see his Fig. 1C) hypothesized that post-encounter return rates declined for the largest prey types, and many subsequent researchers have also questioned the assumption that post-encounter return rates necessarily scale to body size across the full range of these sizes (e.g. Bird et al., 2009; Bird and O’Connell, 2006; Lupo, 2007; Lupo and Schmitt, 2016; Smith, 1991).

As we have mentioned, Grayson and Meltzer (2015) found secure evidence of human hunting and/or dismemberment of five now-extinct terminal Pleistocene mammals in North America, including mastodon, mammoth, and the gomphothere *Cuvieronius*. With the exception of the Channel Islands pygmy mammoth (*Mammuthus exilis*; see Agenbroad, 2012), these were animals that weighed 4000 kg or more (Grayson, 2016 and references therein).

At those weights, these proboscideans vastly exceed the body masses used by Broughton et al. (2011) in their defense of the use of body sizes to infer prey ranks in archaeological settings. Following Smith (1991:

Table 5.7), they assigned the largest of the animals used in their analysis (beluga whale, *Delphinapterus leucas*) a body mass of about 500 kg. As a result, their paper, as important as it is, does not establish that post-encounter return rates necessarily scale to body size across the full range of these sizes.

Recent work by Lupo and Schmitt (2016) on the energetics of large-game hunting in sub-Saharan Africa is relevant in this regard, showing that elephant (*Loxodonta africana*) hunters in this setting had an 80% post-encounter failure rate. This failure rate is matched only by the rate for giraffe (*Giraffa camelopardalis*) and is far higher than the rate for such animals as buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), and zebra (*Equus quagga*; see Lupo and Schmitt 2016:Table 2). From a nutritional perspective, they conclude, “elephants were low-ranked relative to other medium and large African prey and might have been infrequently targeted irrespective of their encounter rates on the landscape” (Lupo and Schmitt, 2016:194). While noting that African elephants are not the same as American mammoths, they also observe that their data as a whole document that larger prey have higher handling costs and that “high hunting failure rates would always make mammoths an expensive option if the only benefits associated with dispatching these animals are consumptive” (Lupo and Schmitt, 2016:194; see also the important discussion in Lupo et al., 2020).

Since the extinct camel *Camelops hesternus* is also among the taxa accepted by Wolfe and Broughton (2020) as having been preyed upon by human hunters, we point out that contemporary Martu foragers in the Australian Western Desert avoid hunting feral dromedaries (*Camelus dromedarius*) for reasons that are social, not nutritional (Bird et al., 2013). As Bird et al. (2013) discuss in some detail, that fact may have significant implications for our understanding of late Pleistocene human

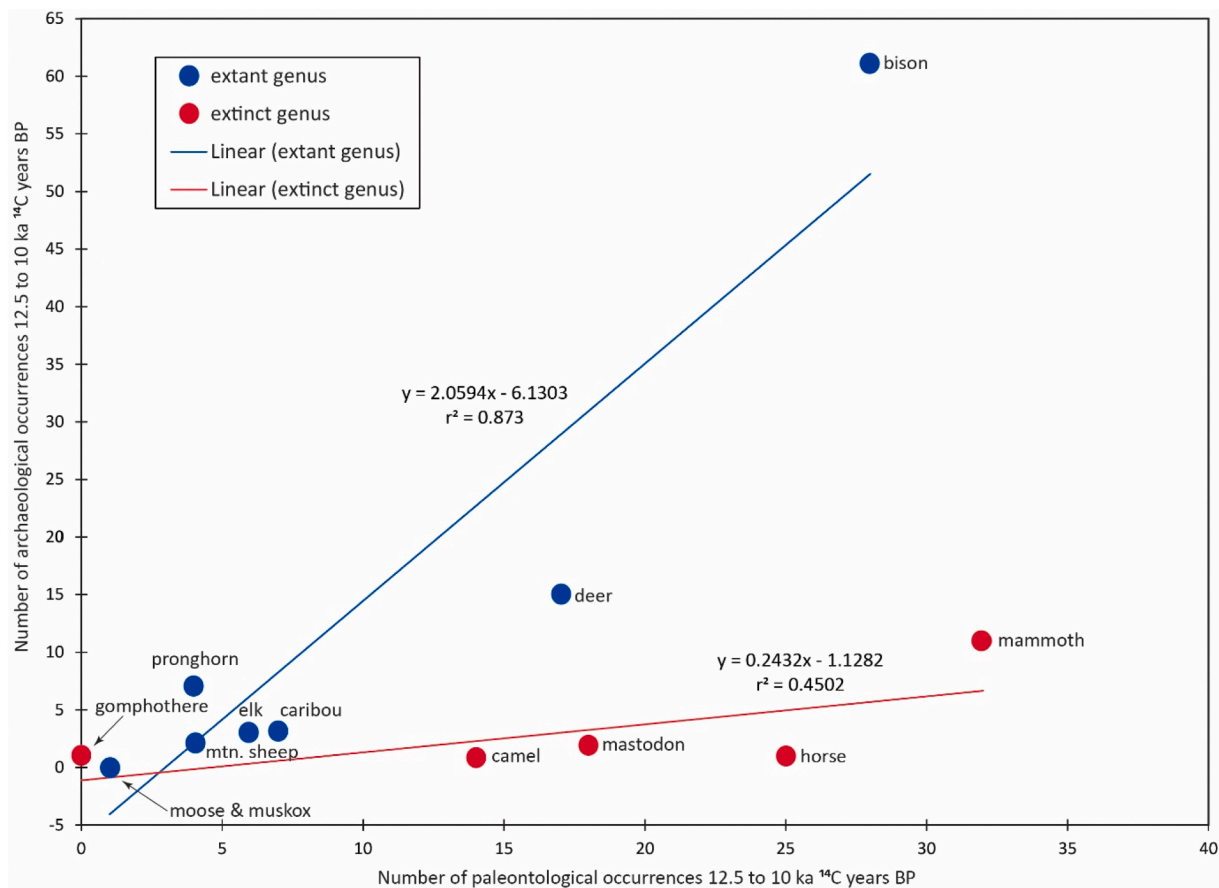


Fig. 1. Plot of the number of paleontological occurrences against the number of archaeological kill/scavenging sites for the 5 extinct and 8 extant genera of large North American mammals for the period 12,500–10,000  $^{14}\text{C}$  years BP. Data from Table 1, Columns D and E. The regression slopes and intercepts for the respective faunas differ significantly ( $F = 21.177$ ,  $p = 0.0013$ ).

adaptations in North America, especially since these two genera of camels were closely related (Heintzman et al., 2015).

Again, we are sympathetic with the approach that Wolfe and Broughton (2020) have taken to these issues, an approach that has been extraordinarily productive in many archaeological settings. Our comments are simply meant to stress the complexities of the issues involved here, and to observe that there is no compelling reason to think either that such huge animals as mastodon, mammoth, and gomphotheres were always pursued on encounter, or that the late Pleistocene peoples of the Americas purposefully avoided large mammals.

#### 4. Were extinct and extant taxa being taken in the same proportion by early Americans?

We previously explored the question of the predation by hunters of extinct versus extant genera proportional to their relative abundance on the landscape (Grayson and Meltzer, 2015; Meltzer, 2015). As a proxy measure of how abundant these taxa were, we compiled data on their fossil occurrences using the FAUNMAP database (Graham and Lundelius, 2010).

We used the Late Wisconsin period (as noted, 35,000–10,000 <sup>14</sup>C yr BP) in our search of localities in FAUNMAP (Graham and Lundelius, 2010). Doing so returned both radiocarbon dated specimens and those for which there was sufficient geological evidence to place the fossils in that time window. An alternative approach might have been to compile only individual radiocarbon-dated specimens for the period closer to when hunters were on the landscape, but these are relatively few and, as we noted then, subject to “sampling and preservation biases” that reduce the representativeness of the resulting samples (Grayson and Meltzer, 2015:189; Meltzer, 2015:40; see also Widga et al., 2017). Accordingly, we opted for the aggregate approach to generate a larger and relatively less-biased sample, though obviously in doing so we sacrificed temporal precision.

In our analyses of those data, we observed that sites containing the remains of extinct genera were more numerous during the Late Wisconsin than those containing the remains of extant ones, but that the extant genera appeared more often in kill/scavenging sites, a difference that was statistically significant (Meltzer, 2015: Table 1). A plot of archaeological occurrences against paleontological occurrences for both extinct and extant fauna (Grayson and Meltzer, 2015: Fig. 2) showed a far steeper regression line for the latter, indicating that the extant taxa occur at proportionately greater frequencies in archaeological kill/scavenging sites than the extinct taxa, whose absolute scarcity in kill/scavenging sites is matched by their relative scarcity (Grayson and Meltzer, 2015:189–190).

Wolfe and Broughton correctly suggest that a better procedure to assess whether there was differential predation on extinct versus extant fauna would be “to assess the abundances of these animals in North America in relation to the frequencies that they were hunted, not during the Late Wisconsin in general but during the period when Paleoindians could have encountered them” (Wolfe and Broughton, 2020:4, emphasis in original). They identify that period as “15.0–10.0 ka” (Wolfe and Broughton, 2020:5).

We completely agree with them in principle. However, the span of time when humans and now-extinct genera are known to have been on the landscape simultaneously is not the period from which Wolfe and Broughton (2020) paleontological and archaeological occurrence data are derived. This is because in compiling their data, they made two significant errors that undermine their analyses, and thus their conclusions.

First, they confounded radiocarbon and calibrated radiocarbon ages. They assert that humans arrived south of glacial ice in North America “sometime shortly after 15.0 ka” and “that megafaunal extinctions had run their course by approximately 10.0 ka” (hence their “15.0–10.0 ka”). However, they evidently did not realize that the “15.0 ka” date they use, for which they cite Grayson (2011), Halligan et al. (2016), and

Jenkins et al. (2014), is a calibrated age derived from radiocarbon dates that cluster around 12,500 <sup>14</sup>C years BP. The “10.0 ka” age, on the other hand, which marks the LADs of a number of the extinct genera (e.g. Faith and Surovell, 2009; Grayson, 2016), is 10,000 <sup>14</sup>C years BP, an uncalibrated radiocarbon age.

In building their sample of paleontological abundances for the 15.0–10.0 ka period, Wolfe and Broughton (2020) used the Neotoma database, which provides ages in radiocarbon years. Their 15.0–10.0 ka period, therefore, is not just the period when Paleoindians could have encountered extinct animals: using Neotoma, that would have been ~12,500–10,000 <sup>14</sup>C yr BP. Instead, their sample includes an additional ~2500 radiocarbon years (15,000–12,500 <sup>14</sup>C yr BP) for which there is scant evidence people were on the landscape (the span is actually longer in calibrated years, owing to vagaries in atmospheric <sup>14</sup>C during that time [Adolphi et al., 2017; Hajdas et al., 2006]). It should be added that because of the long history of debate over extinctions, which well pre-dates calibration, it is customary to frame the extinctions window in radiocarbon years, as do Faith and Surovell (2009), for example, who put that span from 12,000–10,000 <sup>14</sup>C yr BP.<sup>2</sup>

The second error, which compounds the first, is that Wolfe and Broughton (2020:6) relied entirely on the Cannon and Meltzer (2004) study of taxa exploited by early Americans. However, they apparently failed to realize that this study only includes archaeological kill/scavenging sites from the “Early Paleoindian” period, explicitly defined as the period comprising “the earliest secure evidence of a human presence in the regions in which they occur” (Cannon and Meltzer, 2004:1956). That includes classic Clovis sites, and where Clovis *sensu stricto* does not occur, the earliest sites in that region, the timing of which varies. The Cannon and Meltzer sample of archaeological occurrences therefore did not include all Paleoindian sites up to 10,000 <sup>14</sup>C yr BP. Not tallied by them, and thus omitted by Wolfe and Broughton (2020), were all instances of kill/scavenging of large mammals in Folsom sites, Goshen sites, Agate Basin sites, and Hell Gap sites on the Great Plains, Dalton and temporally related sites in the southeast, and so on.

If Wolfe and Broughton (2020) accept that hunters were free to prey upon mammoth, mastodon and the other extinct genera up to 10,000 <sup>14</sup>C yr BP—and some of those genera, including camel, horse, mastodon, and mammoth have LADs almost to that radiocarbon moment (Grayson, 2016)—then hunters must have been equally free to prey on bison (*Bison*), deer (*Odocoileus*), elk (*Cervus*), pronghorn (*Antilocapra*), and so on, during that same time. Thus, Folsom and other later Paleoindian sites that predate 10,000 <sup>14</sup>C yr BP (Holliday et al., 2017; Surovell et al., 2016) should have been included in their analysis.

Because Wolfe and Broughton (2020) confounded radiocarbon and calibrated dates, their sample inflates the number of such occurrences of extinct genera following human arrival. At the same time, it excludes almost a millennium of potential archaeological kill/scavenging occurrences.

To illustrate the consequences of these mistakes, we have redone Wolfe and Broughton’s analyses, but using paleontological occurrences for the 12,500–10,000 <sup>14</sup>C yr BP period, and using an appropriately expanded list of archaeological occurrences from the same time interval (see Supplementary Data, Tables 1 and 2).

Following Wolfe and Broughton (2020), we compiled paleontological abundances from the Neotoma database, searching for all occurrences of the five extinct taxa (camel, horse, mastodon, mammoth, and gomphotheres), and eight extant taxa (moose, muskox, elk, caribou, pronghorn, mountain sheep, deer, and bison) used in their (and our

<sup>2</sup> Faith and Surovell (2009) put human hunting and the extinction of all taxa in the period from 12,000 to 10,000 <sup>14</sup>C yr BP. That window excludes a pre-Clovis presence, but is in agreement with Martin (2005), who long dismissed all claims of a pre-Clovis presence. He also suggested that since Clovis groups were the first big-game hunters in North America, a pre-Clovis presence is irrelevant to the overkill model.

**Table 1**

The number of paleontological and archaeological occurrences for extant and extinct† large mammals; (A) paleontological occurrences for the period from 15,000–10,000<sup>14</sup>C years BP (hereafter, 15.0–10.0 ka), from [Wolfe and Broughton \(2020\)](#); (B) archaeological occurrences for the period from 15.0 to 10.0 ka, from [Wolfe and Broughton \(2020\)](#); (C) paleontological occurrences for the period from 15.0 to 10.0 ka, *this study*; (D) paleontological occurrences for the period from 12,500–10,000<sup>14</sup>C years BP (hereafter, 12.5–10.0 ka), *this study*; (E) archaeological occurrences for the period from 12.5 to 10.0 ka, *this study*. W&B = [Wolfe and Broughton \(2020\)](#). All paleontological occurrences from Neotoma (<http://www.neotomadb.org>); Wolfe and Broughton archaeological occurrences (Column B) from [Cannon and Meltzer \(2004\)](#); archaeological occurrences for *this study* (Column E) from [Cannon and Meltzer \(2004\)](#), and additional sources (Supplementary Data, [Table 2](#)).

Taxon	(A) Number of paleontological occurrences 15–10 ka, W&B	(B) Number of archaeological occurrences, 15–10 ka, W&B	(C) Number of paleontological occurrences 15–10 ka, <i>this study</i>	(D) Number of paleontological occurrences 12.5–10 ka, <i>this study</i>	(E) Number of archaeological occurrences 12.5–10 ka, <i>this study</i>
Bison ( <i>Bison</i> )	38	6	50	28	61
Caribou ( <i>Rangifer</i> )	15	3	16	7	3
Deer ( <i>Odocoileus</i> )	48	3	42	17	15
Elk ( <i>Cervus</i> )	8	0	9	6	3
Moose ( <i>Alces</i> )	1	0	1	1	0
Mountain sheep ( <i>Ovis</i> )	10	0	10	4	2
Muskox ( <i>Ovibos</i> )	0	0	1	1	0
Pronghorn ( <i>Antilocapra</i> )	13	0	11	4	7
Camel ( <i>Camelops</i> )†	36	1	30	14	1
Gomphothere ( <i>Cuvieronius</i> )†	0	1	0	0	1
Horse ( <i>Equus</i> )†	55	1	58	25	1
Mammoth ( <i>Mammuthus</i> )†	80	11	75	32	11
Mastodon ( <i>Mammot</i> )†	89	2	92	18	2
<b>Total</b>	<b>393</b>	<b>28</b>	<b>395</b>	<b>157</b>	<b>107</b>

previous) analysis. However, the data from the Neotoma database cannot be used for this purpose without careful vetting to remove duplicate entries, archaeological sites, and occurrences that fall outside the target time range.<sup>3</sup> As a check to insure consistency with [Wolfe and Broughton \(2020\)](#) data, we first tallied occurrences from the 15,000–10,000<sup>14</sup>C yr BP interval. From those occurrences, we then selected those occurrences within the 12,500–10,000<sup>14</sup>C yr BP span ([Table 1](#)).

The [Wolfe and Broughton \(2020\)](#) paleontological data and ours for the 15,000–10,000<sup>14</sup>C yr BP period are quite similar, with tallies of n = 393, and n = 395, respectively (compare [Table 1](#), Column A and [Table 1](#),

<sup>3</sup> In compiling the data from Neotoma, we searched for all occurrences of each genus, including by species name if identified, and entries listed as ‘sp.’ and ‘cf.’ We eliminated duplicate entries (as identified by redundant Site IDs) so as not to inflate counts, except in cases where the entries were from different components at the same site (non-redundant site IDs). When a taxon listed in the Neotoma database occurred at an archaeological site, but was not considered prey, it was counted by us as a paleontological, not an archaeological, occurrence (e.g. deer at the Folsom site, and bison occurrences at the Colby and Lucy sites). Similarly, in our study, if a specimen was tallied as an archaeological occurrence, it was not counted as a paleontological occurrence. Sites identified in the Neotoma database as falling within the 12,500–10,000<sup>14</sup>C yr BP period but which actually postdate that time (e.g. the Claypool and Scottsbluff sites) were removed from the occurrence lists. We note that [Wolfe and Broughton \(2020: Supplementary Data Table 1\)](#) did not eliminate duplicates: *Odocoileus* is counted three times from Aubrey, which is a single component Clovis site, nor did they eliminate archaeological sites from their paleontological tally, or archaeological sites postdating 10,000<sup>14</sup>C yr BP. as discussed below. We counted taxa found in the Canadian ice-free corridor, since, by including the Wally’s Beach site (Alberta, Canada; [Kooyman et al., 2006, 2012; McNeil et al., 2004, 2005, 2007](#)) in their analysis, otherwise said to be “confined to the contiguous US,” [Wolfe and Broughton \(2020\)](#) did the same. We also follow them in including the El Fin del Mundo (Sonora, Mexico) gomphothere ([Sanchez et al., 2014](#)). As [Wolfe and Broughton \(2020: Supplementary Data Table 1\)](#) relied entirely on the Neotoma database for paleontological occurrences, we did as well; we recognize there are paleontological occurrences not listed in that database. Our vetted list is provided in Supplementary Data [Table 1](#).

Column C). It is unclear what accounts for the slight differences in our counts for specific taxa, but overall such differences are minor.

However, there is one significant exception: our respective bison tallies. The [Wolfe and Broughton \(2020\)](#) count for bison for the 15,000–10,000<sup>14</sup>C yr BP period is 38 ([Table 1](#), Column A); our initial search returned 73 records. However, the Neotoma database includes both paleontological and archaeological occurrences. To derive a tally of strictly paleontological records requires removing the archaeological occurrences, including 5 of 23 bison occurrences that postdate 10,000<sup>14</sup>C yr BP (Claypool, Heron Eden, Olsen-Chubbuck, San Jon, and Scottsbluff) We subtracted those occurrences to arrive at our paleontological count of 50 bison for the 15,000–10,000<sup>14</sup>C yr BP span ([Table 1](#), Column C).

It is not clear why Wolfe and Broughton’s tally for bison for that same period is lower than ours, especially since they did not eliminate the archaeological occurrences of bison from their Neotoma-derived list. In fact, their tally of paleontological occurrences ([Wolfe and Broughton, 2020: Supplementary Data Table 1](#)) includes a dozen or so Folsom period and later Paleoindian archaeological bison kill and/or processing sites, including Allen, Aubrey, Blackwater Locality 1, Cattle Guard, Claypool, Cooper, Folsom, Hanson, Hell Gap, Linger, and Olsen-Chubbuck. Some of these postdate 10,000<sup>14</sup>C years BP (e.g. Claypool, Olsen-Chubbuck), while one is counted twice (Aubrey). Even more problematic is why, if Wolfe and Broughton had eliminated these bison kill and processing sites from their paleontological tally because they are archaeological, as would have been appropriate, the sites were not then included in their count of archaeological occurrences, which lists only 3 such occurrences ([Wolfe and Broughton, 2020: Table 1](#); see also [Table 1](#), Column B, here). Human predation is the only or the prime reason bison occur in those particular sites.

More significant is that the 15,000–10,000<sup>14</sup>C yr BP paleontological sample has ~400 occurrences, while the chronologically-correct span of 12,500–10,000<sup>14</sup>C yr BP has only 157 occurrences ([Table 1](#), Column D). It is not surprising, of course, that the number of records for extinct taxa dropped by almost two-thirds (65%), from 255 to 89, once the paleontological occurrences from the 2500 radiocarbon years prior to

12,500–10,000  $^{14}\text{C}$  yr BP were removed from the sample. The paleontological occurrences of the extant fauna declined as well, by ~51%. That the decline was greater in the extinct taxa is likely due in part to the fact these taxa were on their way to extinction.

Wolfe and Broughton (2020) tally 28 archaeological occurrences in the 15,000–10,000  $^{14}\text{C}$  yr BP time range (Table 1, Column B). Of these, 16 are of extinct taxa (data from Grayson and Meltzer 2015: Table 7), and 12 of extant genera (Cannon and Meltzer, 2004). In their plot of the paleontological and archaeological occurrences of both the extinct and extant taxa, Wolfe and Broughton found—*contra* Grayson and Meltzer (2015: Fig. 2)—that the slopes and intercepts were “nearly identical,” indicating that “for any given paleontological abundance, extant and extinct genera are roughly equally represented in the archaeological record” (Wolfe and Broughton, 2020:6–7).

On that basis, they combined the extinct and extant data and fit a generalized linear model (GLM) to the aggregated data, which they then used to predict the likelihood that the 32 genera that currently lack archaeological occurrences might be predicted to occur in that context (Wolfe and Broughton 2020: Table 2). Those results indicate an “expected number of archaeological associations of less than 1.0 for 28 of the 32 genera, and slightly [sic] more than 1.0 (1.04–1.21) for the remaining four” (Wolfe and Broughton, 2020:7). We return to their GLM below.

Wolfe and Broughton conclude that “for the period of overlap between early North American hunters and Pleistocene megafauna (~15.0–10.0 ka), the number of archaeological occurrences for a given genus is scaled positively to its living abundance, at least to judge from its representation in the paleontological record. There is thus no systematic difference in the abundances of extant and extinct taxa in archaeological versus paleontological contexts as previous analyses have suggested, and thus no support for the Associational Critique is provided from these data” (Wolfe and Broughton, 2020:7).

That conclusion follows directly from their analysis. However, because of the mistakes they made in compiling their data and conducting that analysis, the conclusion is wrong.

In Table 1, Column D, we compile the number of paleontological occurrences of extinct and extant taxa for the chronologically-correct span of 12,500–10,000  $^{14}\text{C}$  yr BP. In Table 1, Column E, we list the archaeological occurrences of kill/scavenging sites of the extinct and extant taxa for that same period. Wolfe and Broughton (2020:6) correctly observed that some of archaeological occurrences of extant taxa we tallied previously (Grayson and Meltzer, 2015:189; Meltzer, 2015: Table 1) included sites that postdate 10,000  $^{14}\text{C}$  years BP (the original tally was based on Hill [2008] and other sources). We have therefore vetted our list, which reduces the number of archaeological occurrences from 111 to 91 (Supplementary Data Table 2). This total is still substantially larger than the number of occurrences of extant taxa used in Wolfe and Broughton’s analysis ( $n = 12$ ) because we included, as discussed above, archaeological sites with extant taxa that postdate the Early Paleoindian period (*sensu* Cannon and Meltzer, 2004), but that predate 10,000  $^{14}\text{C}$  yr BP.

Not surprisingly, the single largest contribution to the increase in our list of kill/scavenging sites of extant fauna over that used by Wolfe and Broughton (2020) is the 10-fold increase in occurrences of bison predation in pre-10,000  $^{14}\text{C}$  yr BP sites, from the Folsom, Agate Basin, Goshen, Hell Gap, and Plainview complexes on the Plains and in the

Rocky Mountains.<sup>d</sup> Bison in those millennia constituted very large prey that were neither avoided or ignored, although hunters routinely used a variety of strategies and topographic settings to disadvantage the animals and reduce the risks inherent in pursuing them (e.g. Frison, 2004; Meltzer, 2006).

It is also important to stress that the number of archaeological occurrences of the extant taxa must be seen as a minimum number. Large areas of North America, notably the eastern United States, have archaeological complexes that fall within this time period (e.g. Dalton), but because of a dearth of preserved faunas or radiocarbon control, the tally of archaeological occurrences from that half of the continent is surely not representative (Cannon and Meltzer, 2004, 2008). That doubtless helps explain the scarcity of kill/scavenging sites of deer, one of the principal large game animals of eastern North America. A “taphonomic rebuttal” (Wolfe and Broughton, 2020:1) loses much of its force if it fails to account for such taphonomic matters.

When the data from the correct time window and the appropriate archaeological records (Table 1, Columns D and E) are used in the analysis, the result confirms our original conclusion.

A plot of archaeological occurrences against paleontological occurrences for both extinct and extant fauna (Fig. 1) yields statistically distinct regression slopes and intercepts for the respective faunas ( $F = 21.177$ ,  $p = 0.0013$ ). For any given paleontological abundance, the extant taxa are far more likely to be represented archaeologically than are extinct taxa. Residuals analysis indicates that among the extant forms, bison are significantly overrepresented archaeologically and deer significantly underrepresented. The former result reflects the widespread expansion of bison hunting in post-Clovis times, and the latter likely reflects the dearth of preserved kill/scavenging sites in eastern North America (Meltzer, 2009). Of the extinct taxa, only mammoth occur more often archaeologically than might be expected based on their abundance in the fossil record.

Thus, using the correctly-timed paleontological and archaeological occurrences for extinct and extant genera, we obtain results that are very different from those obtained by Wolfe and Broughton (2020), and which fully support the analytical conclusions we reached earlier (Grayson and Meltzer, 2015; Meltzer, 2015).

## 5. Applying a generalized linear model

As we have noted, Wolfe and Broughton (2020) fit a generalized linear model (GLM) to a dataset of paleontological and archaeological occurrences of extant ( $n = 8$ ) and extinct ( $n = 5$ ) taxa. Their goal was to predict, for each of the 32 extinct genera in their analysis that have not been found in kill/scavenging contexts, the number of archaeological occurrences that might be expected per taxon from the number of their paleontological occurrences. That list of 32 taxa includes seven genera of carnivores. It has long been assumed that most of the carnivore extinctions were due not to human hunting, but to the loss of their prey (e.g., Grayson, 2016; Martin, 1967). For the sake of analytic consistency, however, we include those taxa in our examination of Wolfe and Broughton’s GLM.

In the “15.0–10.0 ka” period used by Wolfe and Broughton (2020: Table 2), there are a total of 148 paleontological occurrences across the 32 genera. Not surprisingly, given how few paleontological occurrences there are of each (15 of the 32 have a single or no record), their approach

<sup>d</sup> The estimated age range of Plainview is ~10,300 to ~9900  $^{14}\text{C}$  yr BP (Holliday et al., 2017:98), and thus these sites generally predate 10,000  $^{14}\text{C}$  yr BP. Accordingly, we have retained five undated Plainview sites in our sample, along with the Lubbock Lake Plainview component, which has several radiocarbon ages that overlap 10,000  $^{14}\text{C}$  yr BP (Holliday et al., 2017: Table 3.1). Even when those occurrences are removed from the data set, the difference between the regression lines of the extant and extinct taxa remains significant ( $F = 21.154$ ,  $p < 0.001$ ).

predicts extremely low (~0.7–1.2) numbers of archaeological occurrences for each individual taxon. They conclude from this that these animals “were either already extinct or exceedingly rare by the time human hunters appeared on the landscape, and subsequently would be expected to be hunted or scavenged only in very small numbers, if at all,” a trend they see as “consistent with implications of the prey model” (Wolfe and Broughton, 2020:8).

We do not disagree with the conclusion these animals were already extinct or exceedingly rare by the time humans arrived, since, as noted above, we have made exactly the same argument for many years. We might disagree that these results are “consistent with the implications of the prey model” (Wolfe and Broughton, 2020:8), but it could be said that the model does, in fact, predict that prey types that were not available to be hunted were not hunted.

However, the Wolfe and Broughton (2020) model is inconsistent with the record of no known archaeological occurrences for the 32 extinct taxa. Three main issues compromise their conclusions: (1) summing the predicted number of archaeological occurrences in their Table 2 shows that, independent of a particular taxon, their GLM predicts there ought to be an aggregate of about 25 archaeological occurrences across the 32 taxa; (2) their GLM itself may be unreliable due to plotting or programming errors, an issue we could not explore fully because they did not provide the R code they used for this analysis; and, (3) alternative datasets yield fitted GLMs with very different predictions for the archaeological occurrences of the 32 taxa. As discussed in detail in our Supplementary Data, the median predicted number of archaeological occurrences across datasets varies from 12 to 176 for the 32 taxa. None of the GLMs, whether presented by Wolfe and Broughton or discussed here, are consistent with the current record of no observed archaeological occurrences for the 32 taxa.

We refer the reader to our Supplementary Data for further information, including the R code used in our analyses. We note here, however, that our GLM for the 12,500–10,000 <sup>14</sup>C BP data yields a median prediction of 48 archaeological occurrences across the 32 extinct taxa (with a 95% confidence interval of 16–106), roughly twice the number of occurrences predicted by their model (see our Supplementary Data Table 4).

## 6. Discussion and conclusion

Wolfe and Broughton (2020) are correct in observing that the associational critique should be based on data from the period when early Americans could have encountered the now-extinct genera. However, in attempting to conduct such an analysis, their results were undermined by two serious mistakes in compiling their data. First, they conflated calibrated and radiocarbon years, leading them to use an incorrect time period. Second, they undercounted the archaeological occurrences of extant large mammal taxa within the time period they specified.

As we have shown, when the correct temporal parameters are used and the extant archaeological occurrences counted correctly, the results invalidate their assertion that there is “no systematic difference in the abundances of extant and extinct taxa in archaeological versus paleontological contexts,” and does not support their conclusion that their analysis “undermines the longstanding Associational Critique” (Wolfe and Broughton, 2020:7–8). Instead, our reanalysis confirms, as we stated before, “that the surviving [extant] taxa occur at proportionately greater frequency in such sites than the extinct taxa ... and thus the absolute scarcity of kill/scavenging sites of extinct taxa is matched by their relative scarcity as well: this cannot be dismissed as a byproduct of taphonomic bias, given that the survivors are from sites of the same age” (Grayson and Meltzer, 2015:189–190).

On the other hand, the analyses presented here also highlight just how rare kill/scavenging sites involving now-extinct genera are, suggesting in turn that the numbers of these animals decreased dramatically through the final millennia of the Pleistocene. The tally of paleontological occurrences of those genera declined by ~65% in the 2500

radiocarbon years from 15,000 to 12,500 <sup>14</sup>C years BP, a period that predates the onset of the securely-known American archaeological record and that predates the earliest known Clovis sites by about 1000 radiocarbon years. It is perhaps no coincidence that this was also a span of time that saw rapid postglacial climatic and ecological changes that may have impacted the taxa still lingering on the North American landscape (Cooper et al., 2015; Mann et al., 2019).

Of the 37 genera of extinct North American mammals,<sup>5</sup> six have LADs that document their survival into post-Clovis times, between ~10,600 and 10,000 <sup>14</sup>C years ago (Grayson, 2016): Shasta ground sloth (*Nothrotheriops*), giant beaver (*Castoroides*), horse, camel, mastodon, and mammoth. Given the results of the analyses presented here, it is no surprise that there is not a single secure instance of a now-extinct genus in a Folsom or other later Pleistocene Paleoindian site. Nor is it surprising that the genera that are the most abundant in the paleontological record from 12,500 to 10,000 <sup>14</sup>C years BP—horses, camels, mastodons and mammoth—are four of the five taxa represented in Clovis and other Early Paleoindian sites.

Accordingly, there are 32 genera that have yet to be found in an archaeological kill/scavenging context in North America. If we further exclude all seven carnivore genera (as per above), we are left with 25 herbivores. Our GLM results strongly suggest that if people were hunting these extinct large mammals there should be archaeological kill/scavenging for some of them, but such sites do not exist. As we noted at the outset of this paper, we have long suspected that the majority, and perhaps the vast majority, of the genera were gone, or nearly so, by the time people arrived in North America south of glacial ice.

Wolfe and Broughton (2020:8) note that their analyses provide “no direct support for the overkill hypothesis itself.” Were it not for the problems with their work, we would agree and it is certainly true that the analyses we have presented here provide no support for that hypothesis. Wolfe and Broughton (2020) also argue that the causes of late Pleistocene extinctions must be addressed on a taxon-specific basis, through the examination of detailed paleoenvironmental records at smaller geographic and temporal scales, with close attention to the construction of detailed chronologies. We agree with this as well, having made the same suggestion for the North American context long ago (Grayson, 2007; see also Grayson and Meltzer, 2015; Meltzer, 2015). In fact, this approach has been put into play with great success over many years by Anthony Stuart and his colleagues in Eurasia (e.g., Stuart, 2015; Stuart and Lister, 2007; 2011; 2012; Stuart et al., 2004). Given recent advances in our ability to derive demographic, physiological, and adaptational data available from the analysis of ancient DNA, such an approach holds great potential for putting an end to the ancient debate over the causes of North American late Pleistocene extinctions (Grayson and Meltzer, 2015:190).

## Declaration of competing interest

None.

## Acknowledgements

We thank our friend and colleague Karen Lupo for valuable comments on a draft of this manuscript. We also thank our two perceptive anonymous reviewers.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2020.105312>.

<sup>5</sup> Again, we exclude the extinct horse *Haringtonhippus* (Heintzman et al., 2017) from this tally since it was not considered by Wolfe and Broughton (2020).

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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