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Chronology and ecology of late Pleistocene megafauna in the northern Willamette Valley, Oregon

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ABSTRACT

Since the mid-19th century, western Oregon's Willamette Valley has been a source of remains from a wide variety of extinct megafauna. Few of these have been previously described or dated, but new chronologic and isotopic analyses in conjunction with updated evaluations of stratigraphic context provide substantial new information on the species present, timing of losses, and paleoenvironmental conditions. Using subfossil material from the northern valley, we use AMS radiocarbon dating, stable isotope (δ^{13}C and δ^{15}N) analyses, and taxonomic dietary specialization and habitat preferences to reconstruct environments and to develop a local chronology of events that we then compare with continental and regional archaeological and paleoenvironmental data. Analysis of twelve bone specimens demonstrates the presence of bison, mammoth, horse, sloth, and mastodon from ~15,000–13,000 cal yr BP. The latest ages coincide with changing regional climate corresponding to the onset of the Younger Dryas. It is suggested that cooling conditions led to increased forest cover, and, along with river aggradation, reduced the area of preferred habitat for the larger bodied herbivores, which contributed to the demise of local megafauna. Archaeological evidence for megafauna–human interactions in the Pacific Northwest is scarce, limiting our ability to address the human role in causing extinction.

Introduction

The Pleistocene/Holocene transition in North America is marked by the earliest unequivocal evidence for humans as well as the demise of ~35 genera of mostly large mammals. For decades, discussion has continued as to whether these two events were related or coincidental, essentially asking if climate change, human "overkill", or some combination were responsible for megafaunal extinction. The matter remains unresolved (Barnosky et al., 2004; Koch and Barnosky, 2006; Grayson, 2007; Lorenzen et al., 2011; Grund et al., 2012; Boulanger and Lyman, 2014). Grayson (2007) suggests that the lack of resolution in the debate over both the timing and the causes of the extinctions in North America results from a deficiency in understanding local histories of individual taxa, coupled with close analysis of paleoenvironmental and archaeological findings.

To develop such a history for one region, we studied Pleistocene megafauna from paleontological contexts in the Willamette Valley, Oregon. We synthesized available information on fossil remains including species present, conducted radiocarbon and stable isotopic analyses for twelve latest Pleistocene specimens post-dating about 15,000 cal yr BP, and evaluated geologic context and regional paleoenvironmental and archaeological records. Robust estimates for the timing of local extinctions will require larger sample sizes. Nonetheless, our analyses suggest that extinction timing and trends in species type and isotopic composition correspond to regional paleoenvironmental changes leading up to the cold Younger Dryas stadial of 12,900–11,600 cal yr BP (Grootes et al., 1993; Alley, 2000; Stuiver and Grootes, 2000). Extinction also post-dates first known occupation of the Pacific Northwest at about 14,000 cal yr BP (Jenkins et al., 2012), indicating that humans and megafauna co-existed. Archaeological evidence for megafauna–human interactions in the Pacific Northwest and the Willamette Valley in

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particular is scarce, however, thereby limiting conclusions for the human role in megafaunal extinctions.

Setting and Willamette Valley Quaternary history

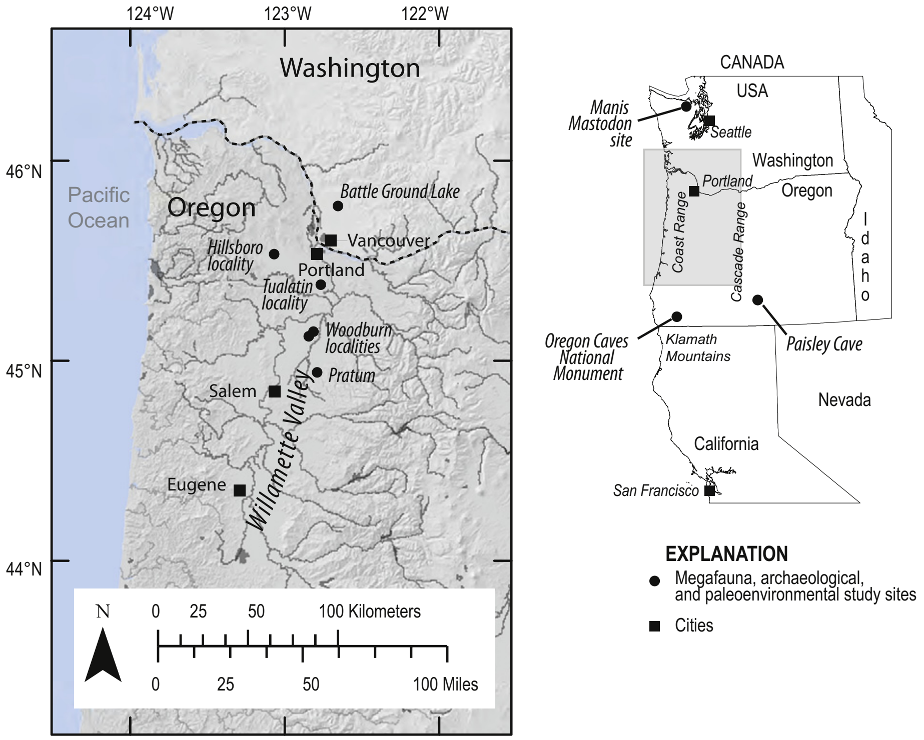
The specific setting of the Willamette Valley of northwestern Oregon is ideal for investigating terminal Pleistocene megafauna. The wide flat-bottomed valley (Fig. 1) occupies a broad structural depression between the volcanic arc of the Cascade Range to the east and the uplifted marine sedimentary and volcanic rocks of the Coast Range to the west (Gannett and Caldwell, 1998). The valley bottom extends 190 km south to north, from Eugene to Portland, averages about 40 km wide, and is chiefly underlain by Pleistocene and Holocene alluvium deposited by the Willamette River and its major tributaries (O'Connor et al., 2001).

An important interruption in the Quaternary record of Willamette Valley aggradation was deposition of locally thick accumulations of fine-grained sediment of Columbia River provenance (Glenn, 1965; O'Connor et al., 2001). This sediment, deposited in rhythmically bedded sequences totaling as much as 35 m thick, was deposited between 20,000 and 15,000 cal yr BP by dozens of Missoula floods (Glenn, 1965; Waitt, 1980, 1985; O'Connor et al., 2001; O'Connor and Benito, 2009). These massive floods, derived from failure of ice-dammed Glacial Lake Missoula in northwestern Montana, coursed down the Columbia and backflooded 200 km up the Willamette River, reaching as far south as Eugene and elevations as high as 120 m above sea level (O'Connor et al., 2001; Minervini et al., 2003). Each of at least 40 sediment charged floods left a layer of slackwater sand, silt and clay, forming the rhythmically bedded deposits that underlie most of the valley bottom outside of the latest Pleistocene and Holocene floodplains (Glenn, 1965; O'Connor et al., 2001). These deposits, left near the end of the Pleistocene, provide a distinctive stratigraphic unit allowing identification of post-flood, therefore post-15 ka, megafauna.

Fossil megafaunal sites and material

The Willamette Valley contains a long-known but little-studied record of Pleistocene-aged megafauna. Early accounts date to the 1840s (Perkins, 1842; Wilkes, 1844: 385; Simpson, 1942), and by the early 20th century reported taxa included mammoth (*Mammuthus*), mastodon (*Mammut*), ground sloth (*Paramylodon*, *Megalonyx*), bison (*Bison*), horse (*Equus*), and camel (*Camelops*) (McCornack, 1914, 1920; Hay, 1927). Finds have continued, chiefly by archaeologists searching for Pleistocene-aged cultural sites (Cressman and Laughlin, 1941; Cressman, 1947; Reese and Fagan, 1997; Lysek, 1999; Stenger, 2002; Connolly, 2003a,b) and by amateurs and community groups (Stenger, 2002; Addington, 2006; Yamhill River Pleistocene Project, 2010). Despite the lengthy history of finds, few of these remains have been closely analyzed.

Our analysis of latest Pleistocene megafauna in the Willamette Valley began with collecting all known records of remains of extinct mammalian herbivores reported for the valley. We reviewed published and unpublished reports and catalogs at the University of Oregon Museum of Natural and Cultural History (UO MNCH) and solicited knowledge from professional and amateur researchers and community groups known to have worked on Pleistocene-aged faunas over the past 40 years. Our search identified 87 fossil finds of various types, including single skeletal elements, parts or almost complete skeletons, or multiple individuals (Supplementary Table 1). The actual skeletal materials from over half of these finds could not be located; for example, we found none of the specimens first reported by McCornack (1914) and Hay (1927). But we did locate fossil remains from 33 of the reported finds, including multiple examples from amateur collections that are in the process of being cataloged and brought into the UO MNCH curation system. Judging from available records and the stratigraphic context as determined from site visits, many of these remains pre-date the Missoula floods (Supplementary Table 1) and are not further considered in this report.



Base map modified from U.S. Geological Survey digital data, various resolutions.
Projection: NAD83 UTM, Zone 10N.

Figure 1. Map of Willamette Valley and larger regional context, showing locations of paleontological, archaeological and paleoenvironmental sites noted in study.

Many specimens, however, were in stratigraphic settings that indicate emplacement after the Missoula floods. These were mostly bogs, swales, or alluvium above or inset into Missoula flood deposits. None of the specimens we examined show sign of cultural modification such as cut marks, impact fracture, or burning. Nor do they show any sign of battering, impacts, or rounding. Consequently we infer that they were sampled near their death position and were not transported by the Missoula floods or other processes. Overall, the specimens were in good condition based on visual criteria, and high collagen content (see isotopic analysis below) supports the conclusion that the specimens did not suffer from much post-depositional exposure and reworking. In short, the Willamette Valley megafaunal remains we studied do not reflect “kill sites” or other types of archaeological sites, but are in-situ remains of natural death and deposition of animals that once lived in the valley (Gilmour, 2011).

Of the specimens we re-located, we selected 11 that would allow for confident taxonomic identification and that were most suitable for direct accelerator mass spectrometer (AMS) ^{14}C dating and stable isotope analyses (Table 1). A twelfth specimen (Mammoth 2) included in our study was previously analyzed and dated by Barton and Cearley (2008) and Cearley (2008). Remains were identified using comparative reference materials and published guides, with assistance by H. Gregory McDonald (National Park Service), Eric Scott (San Bernardino County Museum), Chris Shaw, Aisling Farrell and Meena Madan (George C. Page Museum). The 12 samples represent five bison (*Bison* sp./*Bison antiquus*), two mammoth (*Mammuthus* sp./*Mammuthus columbi*), two horse (*Equus* sp.), two sloth (*Paramylodon harlani*), and a single mastodon (*Mammut americanum*) (Table 1; Fig. 2).

The specimens are from six Willamette Valley localities (Table 1; Fig. 1): three in the Tualatin Valley, a subbasin of the northwest

Table 1
Results of isotope and radiocarbon analysis, by locality.

Specimen	Museum no.[a]	Laboratory no.[b]	% collagen	%N	%C	δ^{15}N	δ^{13}C	C:N	Conventional age (^{14}C yr BP)[c]	Error (± ^{14} C yr)	2 SD calibrated age range[d] (cal yr BP)
Hillsboro											
Bison 1	F-29240	UCIAMS78124 X	12.8	10.9	29.6	4.7	−20.5	3.17	12,500	40	15,058–14,359
Bison antiquus		AA87427 U							12,670	130	15,495–14,342
		AA87427 S							12,700	130	15,590–14,449
Sloth 1	F-29242	UCIAMS78125 X	9.0	9.7	26.5	7.4	−20.8	3.18	12,315	35	14,550–14,081
Paramylodon harlani		AA87426 U							12,490	120	15,135–14,171
		AA87426 S							12,530	130	15,203–14,189
Mammoth 1	F-29247	UCIAMS78126 X	3.5	10.4	28.3	7.9	−21.6	3.18	12,430	35	14,852–14,220
Mammuthus sp.		AA87425 U							10,810	100	12,945–12,560
		AA87425 S							12,610	100	15,323–14,255
Tualatin											
Mastodon 1	F-30282	UCIAMS78127 X	7.9	10.4	28.3	6.4	−20.1	3.18	11,480	35	13,425–13,255
Mammut americanum		AA87428 U							11,570	120	13,706–13,143
		AA87428 S							11,490	110	13,545–13,114
Tualatin River–Fanno Creek											
Sloth 2	THS-2	UCIAMS78123 X	8.9	10.9	29.8	6.6	−21.0	3.17	12,340	35	14,632–14,113
Paramylodon harlani		AA87429 U							12,600	130	15,307–14,250
		AA87429 S							12,700	130	15,590–14,449
Woodburn-Legion Park											
Horse 1	F-37000	UCIAMS78128 X	10.7	11.1	30.4	5.6	−21.7	3.19	11,240	40	13,187–13,040
Equus sp.		AA87436 U							11,850	110	13,965–13,457
		AA87436 S							11,880	120	14,014–13,463
Horse 2	F-38518	UCIAMS78129 X	5.1	10.2	28.3	5.7	−21.8	3.24	11,520	35	13,444–13,283
Equus sp.		AA87433 U							11,960	230	14,685–13,314
		AA87433 S							11,740	100	13,770–13,381
Bison 2	F-38522	UCIAMS78130 X	9.7	9.8	27.2	5.4	−20.8	3.23	11,035	40	13,035–12,773
Bison sp.		AA87432 U							11,222	95	13,278–12,843
		AA87432 S							11,334	98	13,400–13,038
Bison 3	F-40523	UCIAMS78131 X	8.1	9.0	25.3	6.7	−20.7	3.28	12,175	35	14,185–13,946
Bison sp.		A87434 U							12,380	110	15,002–14,075
		A87434 S							12,480	120	15,125–14,164
Bison 4	F-40527	UCIAMS78132 X	7.6	10.3	28.4	6.6	−20.9	3.21	12,295	35	14,473–14,062
Bison sp.		AA87435 U							12,520	120	15,171–14,199
		AA87435 S							12,550	120	15,215–14,231
Woodburn High School											
Bison 5	F-42801	UCIAMS78133 X	18.5	10.3	28.2	6.6	−21.0	3.18	11,300	40	13,251–13,070
Bison antiquus		AA87430 U1							11,320	120	13,443–12,955
		AA87430 S1							11,310	110	13,420–12,974
		AA87431 U2[e]							11,470	100	13,480–13,104
		AA87431 S2[e]							11,460	120	13,539–13,080
Pratum											
Mammoth 2	F-55633	Wk-21807	~15.0	17.0	46.6	8.4	−21.3	3.20	12,023	77	14,103–13,721
Mammuthus columbi		(ultrafiltration)									

[a] Specimen numbers with “F” curated at the UO MNCH. Specimen numbers with “THS” curated at the Tualatin Heritage Center, Tualatin, Oregon.
[b] Processing method: X — XAD (University of California Irvine); U — Ultrafiltration, S — Standard (both University of Arizona).
[c] Corrected for isotopic fractionation using the δ^{13}C following the conventions of Stuiver and Polach (1977).
[d] Calibrated using the OxCal 4.2.3 radiocarbon calibration program (Bronk Ramsey, 2010), using the IntCal13 atmospheric data from Reimer et al. (2013).
[e] Replicability test: two samples from same bone processed by University of Arizona.

Willamette Valley (Hillsboro, Tualatin, and Tualatin River–Fanno Creek); two distinct localities in the Woodburn area (Woodburn-Legion Park and Woodburn High School) and a site near Pratum in the central Willamette Valley.

Based on find location, stratigraphic context, body-part representation, and radiocarbon content, the 12 specimens represent 12 individual animals (Table 1). In particular, the number of individuals represented at the Woodburn-Legion Park locality was initially ambiguous because of incomplete contextual information. Judging from stratigraphic context alone, specimens from Legion Park that we designate Horse 1 and Horse 2 could be from the same animal; and Bison 2, Bison 3 and Bison 4 could also be from one individual. But as described below, the chronometric data indicate that the three bison specimens from Woodburn-Legion Park are three distinct individuals, and the two horse specimens are also from different animals. Bison 5 from the Woodburn High School locality, located 0.5 km from Legion Park, represents a single, well-preserved individual distinct from the Legion Park bison specimens. In sum, our samples represent 12 individual organisms.

Radiocarbon dating and timing of Willamette Valley megafaunal extinction

One of our primary goals was to improve the chronology of the post-Missoula flood megafaunal assemblage in the Willamette Valley. Dating was by AMS ^{14}C analysis. Replicates of 11 bone samples were each dated at two laboratories, the NSF-Arizona AMS Laboratory (UA) and the University of California Irvine Keck Carbon Cycle AMS Facility (UCI). Additionally, the samples analyzed at UA were assayed twice, once using their standard filtration process and again using an ultrafiltration process (Brown et al., 1988). As a test for replicability, a second bone sample from the Bison 5 specimen was submitted blind to the lab, and also processed using the two filtration methods. UA thus generated a total of 24 AMS measurements.

The UA radiocarbon measurements were corrected for isotope fractionation using δ^{13}C measurements made off line using a dual inlet stable isotope mass spectrometer. Bone sample background was defined by measurements on similarly processed permafrost-preserved Pleistocene cow bone (*Bos* sp., Lemon Mine, >41 ka ^{14}C yr BP). Modern was defined by measurements on Oxalic Acid I and II. A mass-dependent background correction was applied to samples smaller than 0.5 mg.

Samples from the same 11 skeletal elements were prepared at the University of Oregon Archaeometry Facility using XAD-purification (styrene-divinylbenzene; Stafford et al., 1988, 1991) and analyzed at UCI using stable nitrogen and carbon isotopic work as an independent quality control measure (van Klinken, 1999). Radiocarbon ages were δ^{13}C-corrected for mass dependent fractionation with δ^{13}C values measured on the AMS (Stuiver and Polach, 1977) and compared with samples of Pleistocene whale bone (background, >48 ka ^{14}C yr BP), a ~12,400 ^{14}C yr BP horse bone, ~1840 ^{14}C yr BP bison bone, late AD 1800s cow bone, and OX-1 oxalic acid.

In sum, eleven bone samples had three separate radiocarbon assays, each using different pretreatment methods. One of these had the three separate analyses plus the two additional blind test analyses. Additionally we include the single AMS radiocarbon analysis for Mammoth 2 (Wk-21807), reported by Barton and Cearley (2008) and Cearley (2008), processed at the Waikato Radiocarbon Dating Laboratory and extracted using a modified Longin (1971) method with ultrafiltration. Calibrations on all results were based on the IntCal13 curve (Reimer et al., 2013) using OxCal 4.2.3 software (Bronk Ramsey, 2010).

Despite the different laboratories and pretreatments, results from individual samples are generally in agreement, although the XAD dates analyzed at UCI are more precise and generally slightly younger than either of the corresponding assays conducted at UA (Table 1; Fig. 3). Chi-squared tests comparing the radiocarbon ages (Ward and Wilson, 1978) of individual samples show statistically significant outliers ($p < 0.05$) among the three analyses for seven of the 11 bone samples (Supplementary Table 2). For six of the seven cases, the XAD results were significantly younger than the two UA analyses. For Mammoth 1, the UA ultrafiltered sample gave a significantly younger age than both UCI's XAD-purified sample and the UA standard filtration sample (which had similar results). For two samples of three analyses, chi-squared tests indicate all three results are mutually consistent, and this is also the case for five analyses done for Bison 5 (but with the XAD results being slightly younger in two of these three cases). For Mammoth 2, we only have the single analysis, so we could not make a similar assessment of variability.

The differences in these radiocarbon results—all derived from splits of the same material—must owe to laboratory processing and analysis techniques. Because the UCI XAD results are typically more precise, and because the additional elemental and isotopic analyses were done from splits of samples sent to UCI, our discussion of overall chronology relies primarily on the UCI dates. Nonetheless, this unusual circumstance of multiple analyses involving different pretreatment methods shows that the type of laboratory processing may significantly affect final age determination, which complicates close comparison of radiocarbon results from different studies.

Pair-wise chi-squared tests on XAD dates of Bison 2, 3, and 4 from Woodburn-Legion Park indicate that the ^{14}C content of all three is significantly different ($p < 0.05$), supporting the interpretation that they are distinct individuals (Table 1, Supplementary Table 2). Similarly, Horse 1 and Horse 2 have distinct ^{14}C content. In conjunction with the stratigraphic and location information, these results show that the 12 samples represent 12 individuals.

As expected from their post-Missoula flood geological context, the 12 specimens date to the latest Pleistocene (Table 1; Fig. 3). The calibrated two-sigma age ranges of all age analyses for all specimens range between 15,590 and 12,560 cal yr BP. The range is narrower—15,058 to 12,773 cal yr BP—if only the UCI XAD results with stable isotope quality-control measurements are considered. The oldest bone was that of Bison 1 (15,058–14,359 cal yr BP) and the youngest was Bison 2 (13,035–12,773 cal yr BP). These results are consistent with their post-Missoula flood stratigraphic context and the 20–15 cal ka BP age of the floods (O'Connor and Benito, 2009). But these analyses also indicate that megafauna roamed the Willamette Valley for some 1500–2000 years after the last of the large floods and before the death of the youngest individual between 13,000 and 12,800 cal yr BP. This most recent death may closely coincide with local megafaunal extinction but a more robust estimate of extinction time requires additional dated remains, perhaps in conjunction with the simulation modeling approach of Bradshaw et al. (2012).

Stable isotope analyses, megafaunal diet, and paleoenvironmental conditions

Stable isotope analyses provide an assessment of sample quality and support inferences of animal diet and, by extension, paleoenvironmental conditions. Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) were measured on a small split of each XAD-purified sample using a Fisons NA1500NC elemental analyzer and Finnigan Delta Plus isotope ratio mass spectrometer at UCI measured with a precision of <0.1‰. Isotopic ratios are expressed in standard delta notation, where $\delta^{E}X = (R_{sample}/R_{standard}\text{-}1) \times 1000$ and ^{E}X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard is the marine carbonate V-PDB for δ^{13}C and atmospheric N_2 for δ^{15}N.

The resulting isotopic values and bone collagen content indicate substantial preservation of original bone material for all analyzed samples (Table 1). The percent nitrogen and carbon in the XAD-treated hydrolysate is lower than published yields for processed gelatin, owing to higher concentrations of salts in the XAD-purified hydrolysate and the addition of water to the amino acids during hydrolysis. Our results are within typical ranges of XAD-treated samples. Nitrogen content was between 9.0 and 17% and averaged 10.8%. Carbon content ranged between 25.3 and 46.6%. The atomic C:N ratios of each specimen ranged from 3.17 to 3.28, within the typical range 2.9 to 3.6 for well-preserved collagen (Ambrose, 1990; DeNiro, 1985). The content of XAD-purified collagen samples ranged from 3.5 to 18.5%, also within the range for unaltered bone specimens in which collagen typically accounts for 1 to 21% of the original bone mass (van Klinken, 1999). Collagen content was not available for Mammoth 2—the sample collected and analyzed by Barton and Cearley (2008) and Cearley (2008)—but isotope values were within ranges expected for well-preserved bone collagen (Petchey, F., Waikato Lab, personal communication, 2011). Consequently, we judge the Mammoth 2 isotope analyses comparable to those resulting from our analyses, but this sample should be reanalyzed in the future with comparable quality-control measures.

Bivariate analysis of both stable isotopes shows clustering by genera (Fig. 4). The two mammoth specimens yielded the highest $\delta^{15}N$ values while bison specimens yielded the lowest values. Horse and mammoth were most depleted in $\delta^{13}C$, while mastodon and bison were most enriched. With five separate samples, bison is the most frequently represented genus in our collection and has the greatest isotopic variation.

Isotopic values indicate organism diet. The stable carbon ($\delta^{13}C$) isotope values range from −20.1‰ to −21.8‰ (Table 1; Fig. 4). Such enrichment levels are consistent with a diet primarily of C_3 plants, chiefly cool weather grasses growing in open environments (Bocherens, 2003: 58). Independent records of Willamette Valley flora for the late Pleistocene are insufficient to reconstruct the proportion of C_3 and C_4 plants, but a C_3 diet would be consistent with the MacFadden et al. (1999) finding that Pleistocene herbivores at latitudes above 45° (which is approximately the southernmost latitude of the sampled Willamette Valley animals) almost exclusively consumed C_3 plants.

A paleoenvironment of open grassland and sparse canopy is consistent with the inferred ecology and dietary preferences of the studied genera. Mammoth was chiefly a grazer (Haynes, 1991; Webb, 1992), whereas bison and horse had variable diets (Koch et al., 1998; MacFadden, 1992; McDonald, 1981; Rivals et al., 2007; Scott, 2006). Sloths were also mixed diet feeders but preferred grassland grazing (McDonald and Pelikan, 2006; McDonald et al., 2004). Of the samples analyzed, only the mastodon is generally associated with more closed environments (Haynes, 1991; Newsom and Mihlbachler, 2006), which should lead to more negative isotope values (Drucker and Bocherens, 2009). Nevertheless, the mastodon, with $\delta^{13}C$ of -20.1‰, was the most enriched of all the samples we analyzed.

Climate change and local megafaunal extinction

Climate research on Greenland ice sheet cores and other records from the North Atlantic show ~1300 years of cold temperatures, the Younger Dryas, which began at about 12,900 cal yr BP and persisted to

Figure 2. A. Posterior view of cranium, Bison 5. B. Anterior view of right femur, Sloth 1. C. Dorsal view of right astragalus, Horse 2. Photographs by D.M. Gilmour.

about 11,600 cal yr BP (Fig. 5; Grootes et al., 1993; Alley, 2000; Stuiver and Grootes, 2000). The age of the most recent Willamette Valley megafaunal sample (Bison 2), between 13,000 and 12,800 cal yr BP, closely corresponds with the 12,900 cal yr BP global onset of the Younger Dryas. Could the timing of local megafaunal losses be related to local climate change associated with the Younger Dryas? Acknowledging recent questions of the severity and global synchronicity of effects linked to the Younger Dryas (Meltzer and Bar-Yosef, 2012; Meltzer and Holliday, 2010), we have investigated the link between Willamette Valley megafaunal losses and the Younger Dryas by reviewing regional paleoenvironmental records that span the Pleistocene–Holocene transition.

Vegetation reconstructions indicate that the period of 15,000 to 12,800 cal yr BP may have been optimal for supporting megafauna that preferred open grassland and sparse canopy, but those conditions changed starting about 13,000 cal yr BP. Barnosky (1985) and Walsh et al. (2008) reconstructed late Quaternary vegetation based on pollen and plant macrofossil records from a core at Battle Ground Lake in Washington State. Although Battle Ground Lake lies approximately 30 km north of the Portland Basin, it is a northern extension of the same structural depression that forms the Willamette Valley lowlands. The lake is at an elevation similar to the floor of the Willamette Valley and within 100 km of all the fossil localities (Fig. 1). Here, the latest Pleistocene portion of the core indicates a succession of three vegetation zones: a period of parkland/tundra transitioning to open forest or parkland at about 14,300 cal yr BP, followed by forest conditions between 13,100 and 10,800 cal yr BP (Walsh et al., 2008; Fig. 5). Aside from Bison 2, all the megafaunal samples come from periods of open-canopy conditions. Bison 2, with a two-sigma age estimate of 13,035 to 12,773 cal yr BP is the only specimen within the post-13,100 cal yr BP time period of more forested conditions near Battle Ground Lake.

The transition to forested conditions near Battle Ground Lake between 13,100 and 10,800 cal yr BP (Walsh et al., 2008; Fig. 5) broadly corresponds to regional geological and paleoclimate records demonstrating significant cooling in western Oregon. Mapping and

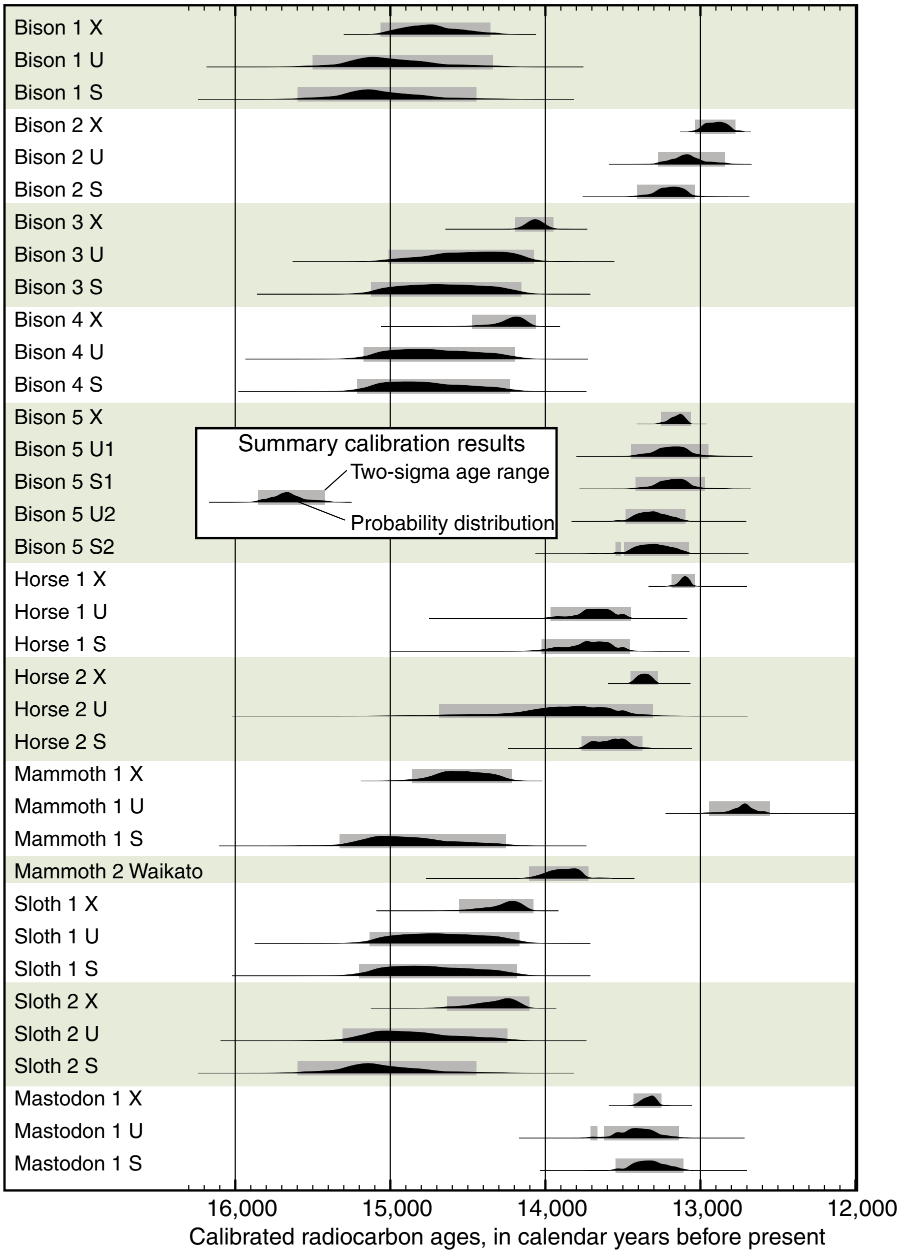


Figure 3. Probability plot of all calibrated AMS measurements obtained for Willamette Valley megafaunal specimens (see Table 1 for specimen context and processing method).

radiocarbon dating of organic detritus within alluvial gravel deposits of the Clackamas and Santiam Rivers indicate regional aggradation of western Cascade Range tributaries to the Willamette Valley began after 15,000 cal yr BP and culminated about 11–12 cal ka BP (O'Connor et al., 2001; Wampler, 2004). This river aggradation is similar to that of the last glacial maximum in the Willamette Valley (O'Connor et al., 2001). In both cases cooling likely enhanced physical weathering, increasing gravel supply and caused channel aggradation (O'Connor et al., 2001; Wampler, 2004). This latter cooling is likely associated with a post-last glacial maximum, but pre-8100 cal yr BP, glacial advance in the central Oregon Cascade Range (Marcott et al., 2009). Similarly in the Oregon Coast Range, south and west of the Willamette Valley, Personius et al. (1993) documented regional aggradation of westward-draining rivers. This aggradation began at about 13,000–12,000 cal yr BP and terminated by about 9000 cal yr BP.

A more precise chronology documenting regional cooling is given by isotopic analysis of a stalagmite in Oregon Caves National Monument (Vacco et al., 2005), about 300 km south of the Willamette Valley megafaunal sites. Here, δ^{18}O records, sampled at 50-yr intervals, shows cooling beginning at 12,840 ± 200 cal yr BP, attaining coolest values at about 12,300 cal yr BP, and abrupt warming at 11,700 ± 260 cal yr BP (ages and uncertainties from a U–Th age model) (Fig. 5).

In sum, the diverse regional evidence for cooler conditions beginning about 13,000 cal yr BP is consistent with the Younger Dryas stadial as known for the North Atlantic. Moreover, all of the high-precision UCI XAD dates with quality control measures from the Willamette Valley megafaunal samples pre-date this cooling: thus, megafauna apparently existed during a time of open parkland or open forest conditions suitable for grassland grazers after the last of the Missoula floods but mostly prior to subsequent cooling and environmental change. The youngest megafaunal sample, Bison 2, approximately coincides with the North Atlantic 12,900 cal yr BP onset of the Younger Dryas, the regional cooling at Oregon Caves, and the transition to more forested conditions at Battle Ground Lake. This coincidence is consistent with cooling and degrading habitat conditions contributing to the local extinction of megafauna in the Willamette Valley. Nevertheless, our sparse sample size combined with the few records of local environmental conditions provides only tentative support for the link between climate change and megafaunal extinction: similar and more records from the Willamette Valley and other locations would provide needed additional support.

What about people and the overkill hypothesis?

The correspondence of Clovis and megafaunal extinction chronologies throughout North America is a key tenant of Paul Martin's "Overkill" Hypothesis, which purports that humans caused or contributed to extinctions. As originally proposed by Martin (1967, 1973), reviewed also by Haynes (2009), Clovis hunters spread into the New World and hunted megafauna to unsustainable numbers. The chronology of Clovis is debated; some suggest a very narrow time span between 13,000 and 12,600 cal yr BP (Rasmussen et al., 2014, see Waters and Stafford, 2007 and Goebel et al., 2008; but see Haynes et al., 2007 for critique), while Meltzer (2004) argued that Clovis culture began 450 years earlier than this narrow span. More recently, strict linkage of overkill to Clovis is challenged by evidence of other cultures, including Western Stemmed Point, overlapping with or pre-dating Clovis (Beck and Jones, 2010; Jenkins et al., 2012).

Aside from the timing of the megafauna in the Willamette Valley, our study cannot directly address the role humans played in local megafaunal extinctions. Well-dated evidence for Pleistocene human occupation of the Willamette Valley is absent, as is evidence for human predation of megafauna. Clovis records for the Willamette Valley include four isolated points (Connolly, 1994). Two Western Stemmed points also have been documented (Connolly, 1994). While both point types are linked to large animal hunting elsewhere, such points are also associated with a wide range of subsistence pursuits including lake and marsh edge plants and small animals (Beck and Jones, 1997; Cannon and Meltzer, 2004; Grayson, 2011; Jones et al., 2003; Lyman, 2013). Consequently, the presence of Clovis or Western Stemmed points in the Willamette Valley is not compelling evidence of significant human predation of megafauna.

Although evidence in the Willamette Valley is sparse, other sites in the Pacific Northwest establish the regional presence of people soon after the Missoula floods and contemporaneous with Pleistocene megafauna. The 13,800 cal yr BP Manis site on the Olympic Peninsula of Washington state includes the remains of a mastodon with a possible embedded bone point (Waters et al., 2011). The Paisley 5 Mile Point Caves site in south central Oregon includes stone tools and human coprolites and was occupied by 14,270–14,000 cal yr BP (Gilbert et al., 2008; Jenkins et al., 2012; but see Goldberg et al., 2009; Poinar et al., 2009). Both of these sites are contemporaneous with several of the Willamette Valley dated megafaunal samples (Fig. 5). These archaeological records show that humans and Pleistocene megafauna coexisted in the Pacific Northwest in the latest Pleistocene period following the Missoula floods (Fig. 5). Consequently, humans could have contributed to local megafaunal extinction, but records available so far do not provide compelling evidence that they were the major factor.

Summary and conclusions

For decades scientists have debated the causes of late Quaternary mammalian megafaunal extinctions in North America. This study addresses this question for the Willamette Valley by establishing a chronology for late Pleistocene megafauna in relation to paleoenvironmental and archaeological records for the region.

Our study of 12 bone specimens supports the following conclusions regarding megafauna in the Willamette Valley during the latest Pleistocene:

- Now-extinct mammalian megafauna ranged within the Willamette Valley after the 20,000 to 15,000 cal yr BP Missoula floods and persisted until about 12,800 cal yr BP. Refinement of extinction time would be enhanced by directly AMS ^{14}C dating additional remains in parallel with appropriate quality-control measures.
- Isotopic analyses and the known ecological preferences of the Willamette Valley species indicate grazing of mainly cool-weather C_3 grasses in grassland, parkland or open-forest settings.

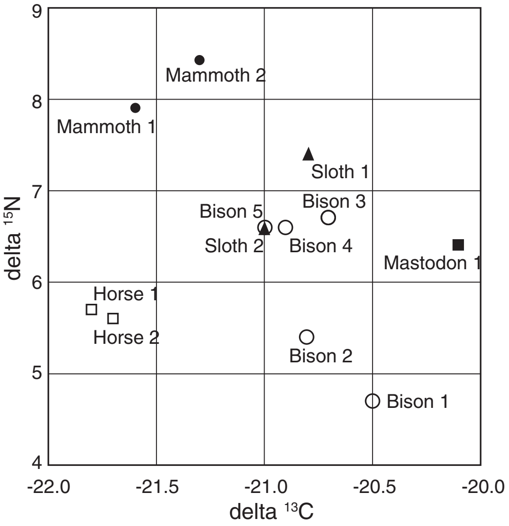


Figure 4. Bivariate plot of stable isotopes (δ^{15}N and δ^{13}C).

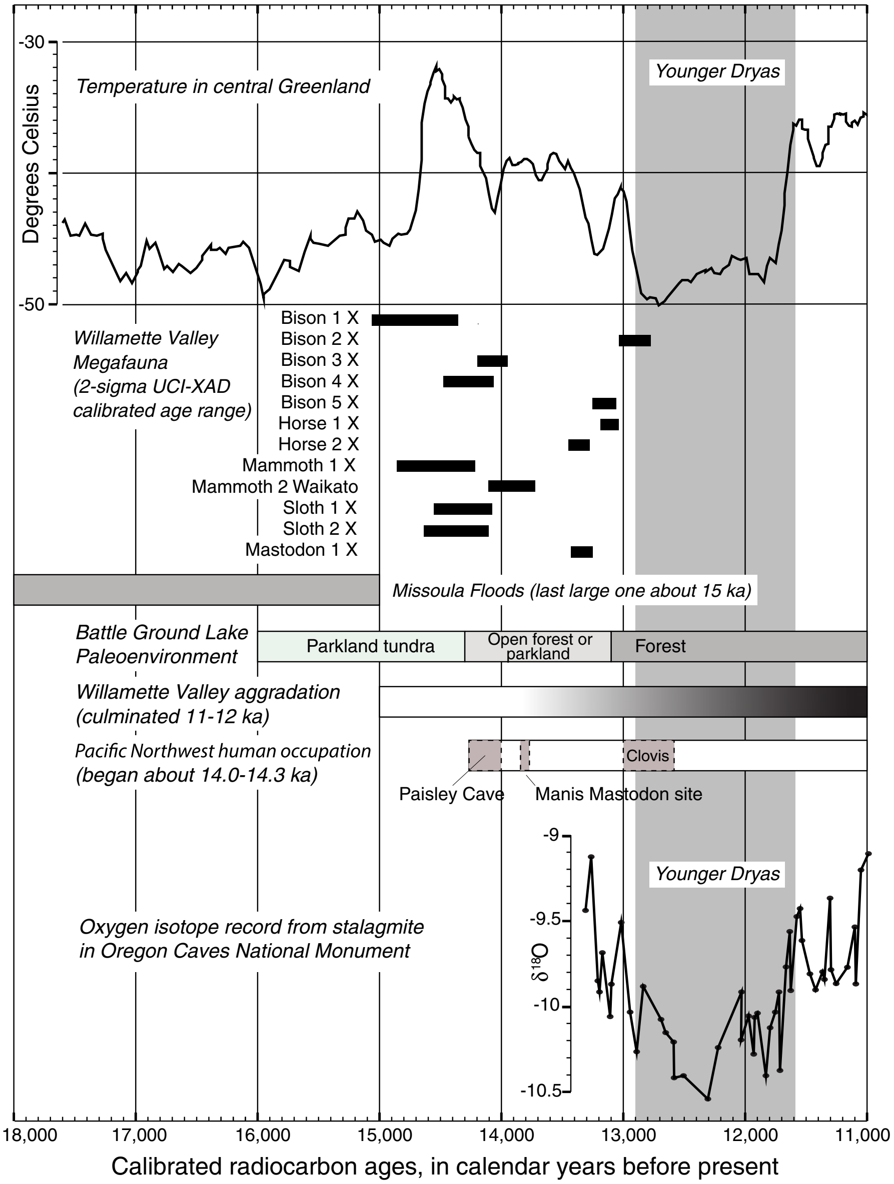


Figure 5. Probability plot of calibrated UCI-XAD AMS measurements of Willamette Valley megafaunal specimens arrayed against natural and cultural events. Upper gray line represents late Pleistocene temperature fluctuation, including Younger Dryas, estimated from the GISP2 ice core (Alley, 2004). Missoula flood chronology from O'Connor and Benito (2009). Battle Ground Lake paleoenvironmental data from Barnosky (1985) and Walsh et al. (2008). Timing of human occupation at Paisley Cave from Gilbert et al. (2008). Age of Clovis from Rasmussen et al. (2014) and Waters and Stafford (2007). Oxygen isotope record from Vacco et al. (2005).

- This period of megafaunal presence overlapped with the earliest known human occupation of the region beginning at about 14,000 cal yr BP.
- The demise of the megafauna corresponds closely with the 12,900 cal yr BP onset of the Younger Dryas stadial period of substantially cooler global and regional temperatures. This cooling coincided with increased forest cover in the Willamette Valley, creating habitat and forage conditions less suitable to the chiefly grassland grazers favored by Willamette Valley megafauna.

From these observations and inferences, we conclude that megafauna did survive the Missoula floods to recolonize the Willamette Valley, but they did not survive several thousand years later within the context of environmental change at the end of the Pleistocene. The demise of these large animals coincides with cooling climate conditions and degrading habitat conditions associated with the Younger Dryas and overlaps with the first human presence in the region. One or both factors may have contributed to local extinction, but the available information more strongly supports cooling and changing habitat conditions as the primary contributing factor. Significant human contribution to the extinction of Willamette Valley megafauna cannot be ruled out but is not compelling, based on the available evidence. Better resolution of specific causes and consequences requires additional studies, including isotopic and chronological studies to better define habitat requirements and extinction timing, geologic and paleoclimate analyses to assess local changes in ecological conditions, and archaeological studies to gain better knowledge of the interaction of the first humans in the region with late Pleistocene megafauna. At least in the Pacific Northwest, we can start addressing these questions with existing collections from museums and historical societies.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2014.09.003.

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