

Chapter 5:

Radiocarbon chronology and the response of Late Quaternary Megafauna to Rapid Climate Change

5.1 INTRODUCTION

The Quaternary megafaunal extinction is the most recent of Earth's major extinction events and wiped out nearly all large and slow-breeding mammals. On a global scale, the extinctions followed first appearances of humans or expanding human populations in many regions as well as the end of the last glacial period (1). However due to uncertainties in dating, estimates of the duration of co-existence between humans and megafauna remain imprecise. The megafaunal extinction is also difficult to explain by relying solely on environmental change as megafauna had survived through previous glacial-interglacial cycles, as well as several rapid climate change events. Debate about the possible cause of the extinction has continued for over 150 years, stimulated by new fossil finds, dating techniques, and modes of analysis.

There are several hypotheses for how climate change could have affected the megafauna extinction. They all focus on the ecological effects of climate change that would lead to extinction, for instance, the "habitat loss hypothesis" (HLH), the "mosaic-nutrient hypothesis" (MNH), the "co-evolutionary disequilibrium hypothesis" (CED) and "self-organized instability Hypothesis" (SOI). HLH posits that as climate changed, areas with adequate conditions to maintain megafauna reduced in area, making it difficult to support megafauna populations (2). MNH suggests that climate change reduced the growing season, local plant diversity, and increased plant antiherbivore defenses all of which reduced the ability of the land to support herbivores (3). The CED hypothesizes that the rapid glacial-interglacial transition stressed the flora, causing a reorganization of the ecology. This reorganization essentially starved herbivores, as preferred species became less abundant (4). The SOI hypothesis holds that species in an ecosystem will reach a certain level and will subsequently be maintained through immigration, speciation, or extinction. A slight perturbation (in this case climate change) is amplified into

a catastrophe by dynamics intrinsic to complex ecosystems with multiple subunits (5). To disentangle the processes underlying megafauna response to climate change, we investigated the radiocarbon chronologies of megafauna from the La Brea Tar Pits and other deposits around the world.

The La Brea Tar Pits are located in Downtown Los Angeles and span 23 acres. They are an exceptional fossil deposit in the Miocene-aged Monterey Shale Formation and have preserved over three million fossil skeletons including 3400 large mammals. These deposits provide the type assemblage of the Rancho Land Mammal Age and provide a unique view of terrestrial ecology in the LA Basin during the Pleistocene. The deposits are a series of open asphalt seeps that have acted as animal traps for at least the past 50,000 years (6). Previous studies have been limited by weak chronological control, as stratigraphic position is known to be an unreliable indicator of relative age within the asphalt deposits (7). Dating the megafauna remains in this fossil deposit could help put further constraints on the relationship of terrestrial megafauna in North America with climate change. The preferred method for dating megafauna remains has been radiocarbon dating. However, radiocarbon dating remains from the La Brea Tar Pits has been plagued by difficulties in removing the impregnating asphalt.

Radiocarbon dates on bones are often the most direct method of obtaining chronological information on geological and anthropological events in terrestrial settings. They are also helpful for bypassing problems with stratigraphic correlation or the necessity of finding and dating coeval wood or charcoal. However, radiocarbon dates on bones are particularly problematic, as some dates have yielded ages contrary to stratigraphic or cultural expectations (8, 9). This discrepancy has been attributed to environmental contamination of the bone sample. Preservation of bone is influenced by the depositional environment, including pH, microbial activity, temperature, and water (10). It has been thought that if ^{14}C from the original bone itself could be isolated and analyzed, the correct age of the bone could be determined.

Another difficulty with radiocarbon dating of bones is how to isolate fractions of bones that are not susceptible to environmental contamination. Bone is composed of two carbon-

bearing fractions, hydroxyapatite and organic matter. Hydroxyapatite has an open structure into which precipitates from ground water can easily be deposited, so it is not commonly used for radiocarbon ages. In modern bone, organic matter or proteins make up 30% of the bulk of bone material of which 90–95% is composed of collagen.

There has been much recent development to reduce contamination in radiocarbon dating, including filtering organic components through molecular filters and isolating specific molecular components (11). The most common of these is to isolate amino acids from bones using column chemistry. However it is possible that single amino acids in bone could have several sources besides the animal itself, such as contamination from bacterial degradation products or natural ground water (12).

It was first suggested by Ho et al. in 1969 (13) that isolating hydroxyproline from bones in the La Brea Tar Pits could improve radiocarbon dating of bones because hydroxyproline is a nonessential amino acid that is found almost exclusively in mammalian collagen and elastin. However extracting and suitably purifying hydroxyproline from bone has proved to be a challenging task. The isolation of hydroxyproline has almost exclusively relied on ion-exchange chromatography, XAD resins and derivatization routines, using organic solvents (14). These resins, organic solvents and derivatizing compounds could be a potential source of carbon contamination. Here, I have developed a high-performance liquid chromatography method for separating hydroxyproline from other amino acids in collagen using only Milli Q H₂O.

5.2 METHOD DEVELOPMENT

All analyses for method development were made using a *Smilodon fatalis* femur dated previously to 29,600 years by separating collagen-derived amino acids using a liquid chromatography method (6). Fractions of bones were analyzed using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\Delta^{14}\text{C}$ to determine the proper procedure for extracting organic matter from bones. Once the organic matter was extracted, a high performance liquid chromatography (HPLC) method was developed for separating hydroxyproline from organic matter.

5.2.i Extracting Organic Matter from Bones

Several grams of bone was cut from the femur using a Dremel tool and powdered finely to pass through a ~ 200 μm sieve. This powder was divided into three portions. One portion was acidified in 1N HCl for 8 hours and washed with water. An aliquot was removed for %C and $\delta^{13}\text{C}$ analysis, and the process was repeated eight times to determine the amount of HCl needed to remove carbonates from powdered bone. A second portion was processed through a microwave assisted solvent removal system (MARS). The MARS allows organic matter (asphalt, humic acids) to be leached from bones at a much faster rate than typical reaction times on bench tops because the MARS elevates the temperature of the sample. The bone sample was dissolved in 20 ml of 9:1 Dichloromethane/acetone and heated to 100°C in the MARS. Afterwards an aliquot was removed for %C and $\delta^{13}\text{C}$ analysis and the process was repeated eight times. The third portion was decalcified, processed through the MARS, again decalcified and again processed through the MARS. Aliquots were removed at each step for %C and $\delta^{13}\text{C}$ analysis. The aliquots were analyzed for %C and $\delta^{13}\text{C}$ and the results are shown on Figure 5.1.

For successive steps of decalcification, the %C in the sample increases from 12% (predominantly carbonate) to $\sim 40\%$ (predominantly organic matter) over the course of four steps of carbonate removal using implying that only four steps of decalcification are necessary. After four steps, the %C begins to decrease to 25%. The $\delta^{13}\text{C}$ of these samples also drops from -18‰ to -19.5‰ until the fourth decalcification step. Afterwards, the $\delta^{13}\text{C}$ begins declining. There are two possibilities to explain the decrease in %C and $\delta^{13}\text{C}$ after Step 4. One is that the reaction with HCl is removing acid volatile organic matter (carbohydrates and proteins), leaving only lipids in the sample. Lipids are $\sim 4\text{‰}$ depleted relative to carbohydrates, therefore this scenario would also explain the decrease in $\delta^{13}\text{C}$. A second possibility is that the continued reaction with HCl is dissolving the organic matter and leaving behind the asphalt. The asphalt has been characterized to have a $\delta^{13}\text{C}$ of -25‰ (15), so could explain the decline in $\delta^{13}\text{C}$ after four steps of decalcification. For successive steps of MARS reaction, the $\delta^{13}\text{C}$ of the bone immediately rises to -16‰ from -18‰ , and further MARS reaction steps do not alter this value, implying that only

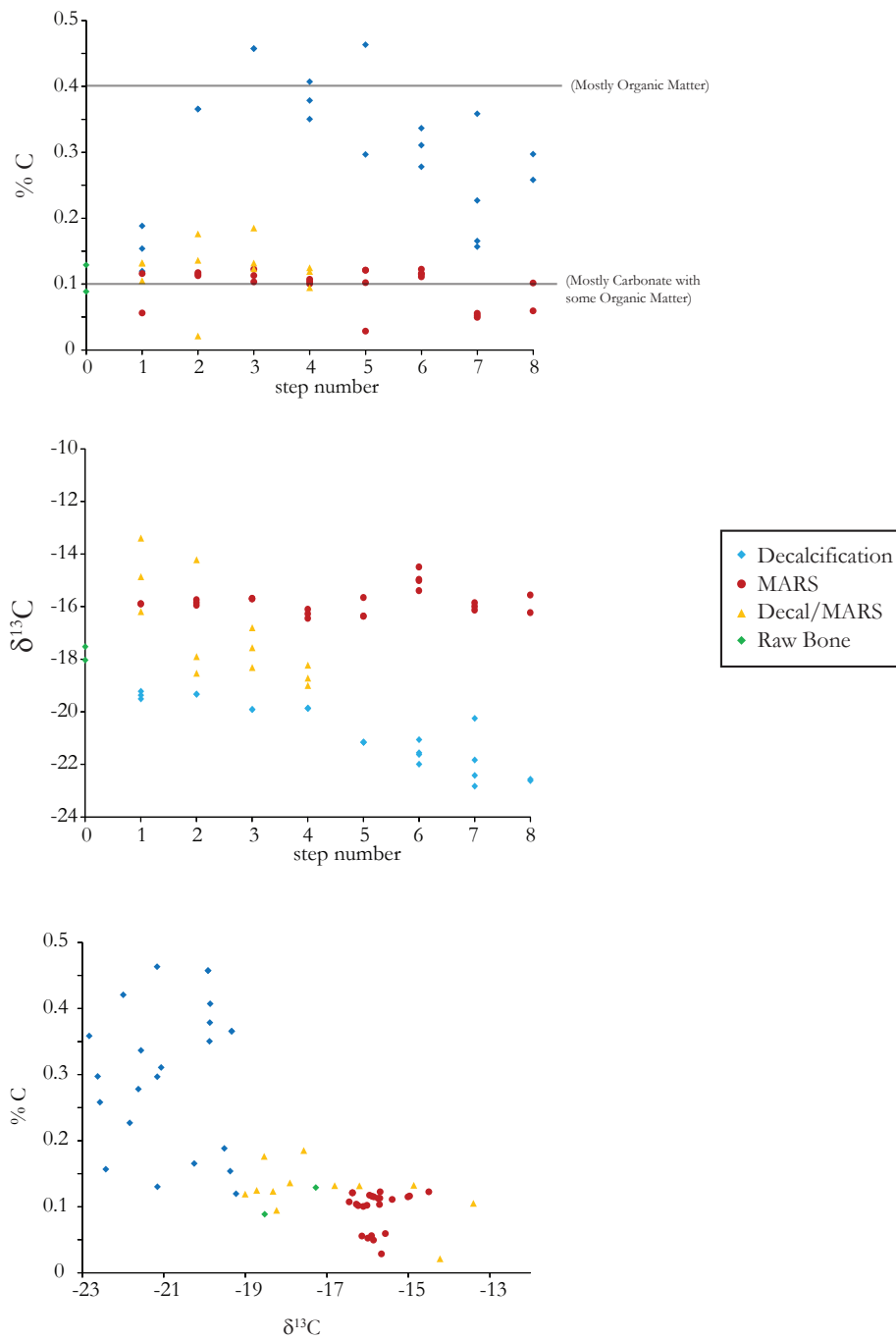


Figure 5.1: %C and $\delta^{13}\text{C}$ results of three different cleaning procedures. Decal: 8 sequential decalcification steps. MARS: 8 sequential MARS steps. Decal/MARS: a sample of bone that was Step 1: decalcified, Step 2: processed through MARS, Step 3: decalcified, and Step 4: processed through MARS

one MARS reaction step is needed. For the alternate decalcification and MARS steps, never rises about 0.2%, and the $\delta^{13}\text{C}$ begins to decline to -20‰, though does not plateau.

Further method development was done using ^{14}C . A bone sample was reacted with 1N HCl, and then processed through the MARS twice. Aliquots of the bone were removed at each step, and the solvents extracted from the bone were also saved. Both the solid and liquid fractions were sent to KECK-UCIAMS for ^{14}C analysis and the results are shown on Figure 5.2. The first step of 1N HCl acidification resulted in the bone increasing in age by 1300 years, implying that young carbonate was removed. The first MARS step lowered the age by 800 years, implying that older asphalt was removed. The second MARS step did not change the age, further confirming that only one MARS step is needed for asphalt removal. The asphalt removed at both steps had a Fm of 0.006, close to the detection limit of the AMS, consistent with the source of the asphalt being derived from the Miocene aged Monterrey Shale Formation.

From these results we conclude that the proper cleaning procedure for these bones is four sequential steps of 1N HCl for 8 hours each and one step of asphalt removal through the MARS.

5.2.ii Extracting Hydroxyproline from the Organic Matter

The remaining organic matter is composed of proteins, carbohydrates, and lipids. We developed a HPLC protocol for separating hydroxyproline from this organic matter. The organic matter was reacted with 30 ml of 6 M HCl for 24 hours at 105°C under a nitrogen atmosphere following standard laboratory procedures (16). After the reaction was complete, the aqueous acid was lyophilized and then redissolved in MILLI Q H₂O for HPLC separation and analysis. Chromatography was performed on a Agilent 1100 series HPLC system consisting of two isocratic pumps all controlled by HPCORE Chemstation PC software. The autosampler was fitted with a 900 uL sample loop and a 1 mL syringe and a Supelco Primesep A column. Primsep A is a mixed mode column with reversed phase and hydrophilic interaction chromatography making it especially suited for separating amino acids and other weak acids and bases. The column was washed with 2L of 75:25:0.1 'ACN:H₂O:acetic acid'. Up to 900 uL of sample (hydrolyzed collagen or a reference sample) was injected with a flow rate of 4.7 ml/min into the

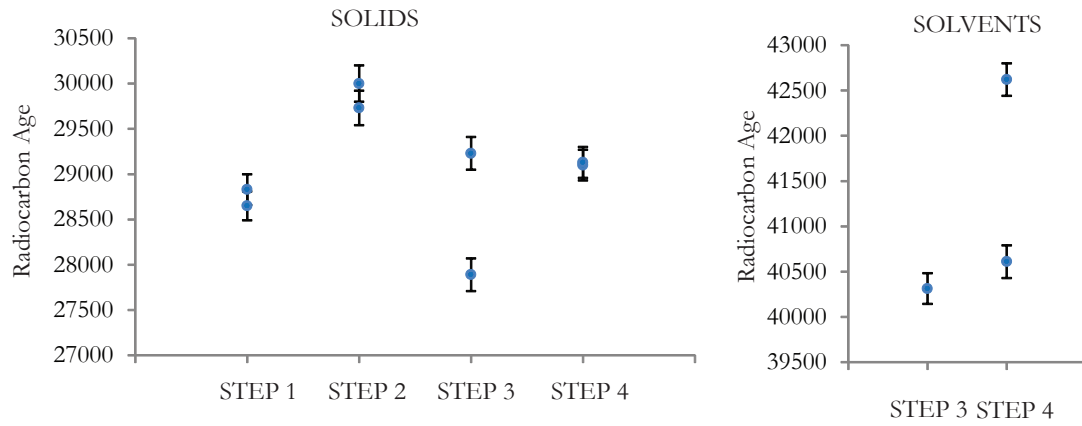


Figure 5.2: $\Delta^{14}\text{C}$ results of a cleaning procedure on one bone sample taken through four cleaning procedures. Step 1: raw bone, Step 2: bone after decalcification, Step 3: bone (or extracted solvents) after the first MARS procedure, and Step 4: bone (or extracted solvents) after the second MARS procedure

guard column with MILLI Q H₂O titrated to pH 4 with concentrated SeaStar HCl. At 2 min, the guard column was then backflushed to remove most of the more nonpolar amino acids, and the polar amino acids (which included hydroxyproline) were allowed to separate for 22.5 min in pH 4 MILLI Q H₂O. This procedure allowed for the separation of aspartic acid, hydroxyproline, glutamic acid, glycine, and proline in MILLI Q H₂O. Amino acids were detected using an APCI quadrupole mass spectrometer. After 22.5 min the mobile phase was changed to 0.5% TFA to flush out any remaining compounds from the column. The column was then re-equilibrated for 20 min with pH 4 MILLI Q H₂O. Complete time from sample injection, separation and column cleaning and re-equilibration was 1 hr. Sample HPLC traces are shown on Figure 5.3. Fractions of hydroxyproline were collected and lyophilized to remove water. Yields were quantified by two methods. The amount of sample injected was compared to peak area calibration curves made for the day (Figure 5.4) or fractions of amino acids were collected and lyophilized to remove water and weighed. Yields ranged from 95–100%. After lyophilization, the hydroxyproline was sealed in quartz vial with baked CuO and Ag and heated to 850°C for 5 hours to generate CO₂ for ease of analysis by Gas Source-AMS. A modern hydroxyproline was analyzed for $\Delta^{14}\text{C}$ before and after processing through the HPLC and no fractionation was observed within error (Figure 5.5). The error bars are larger than traditional hydrolysis ¹⁴C measurements. However, this is a feature of the gas source-AMS. Since these measurements were made, errors made using this technique have declined.

Future work entails measuring the hydroxyproline for $\Delta^{14}\text{C}$ to determine whether hydroxyproline extracted from fossilized bone has a different $\Delta^{14}\text{C}$ signature than radiocarbon dates made on collagen or carbonates in bone, before analyzing bones from the La Brea Tar Pits.

5.3 DISCUSSION

Although bones from the La Brea Tar Pits have not been radiocarbon dated using extracted hydroxyproline, 152 ¹⁴C dates have been made using a variety of different methods (Figure 5.6). The dates were made with two different methods (scintillation counter and AMS) and made on a variety of different carbon extracts, (apatite, carbonate, collagen and amino acids).

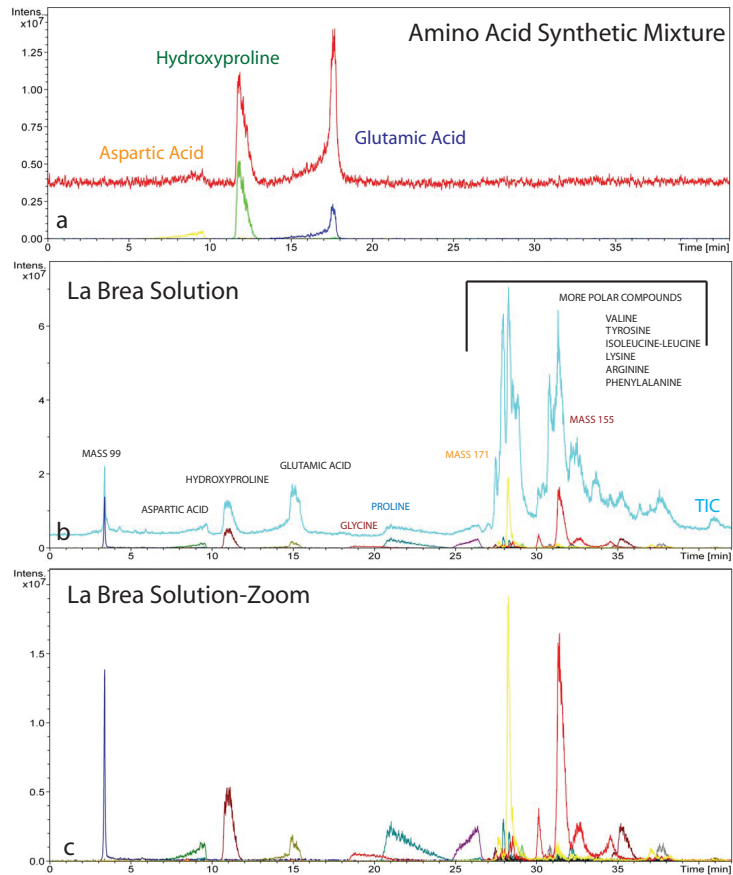


Figure 5.3: HPLC traces of a) an amino acid synthetic mixture of aspartic acid, hydroxyproline, and glutamic acid, and b) a La Brea Solution. Both solutions baseline separate hydroxyproline from all other amino acids.

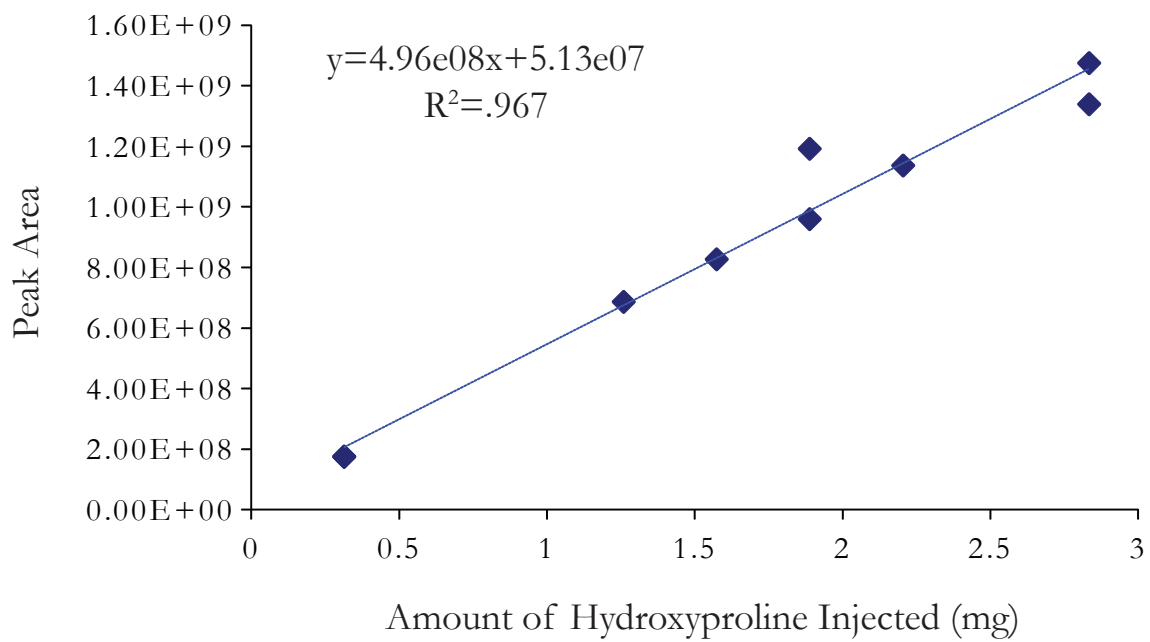


Figure 5.4: An example of a peak area calibration used to quantify yield. Individual points were determined by running a hydroxyproline standard through the HPLC.

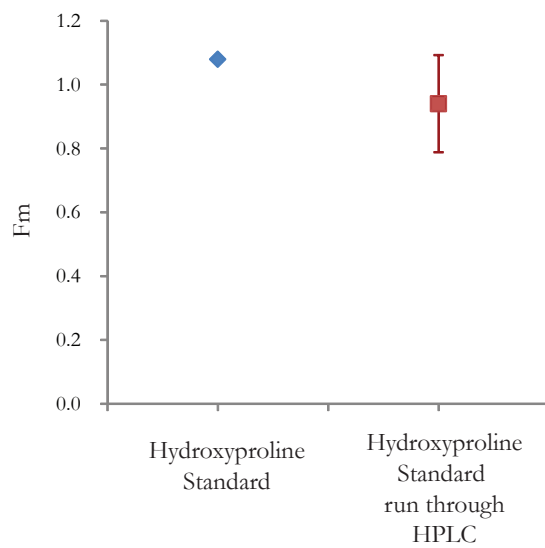


Figure 5.5: Hydroxyproline standard before and after running through HPLC. The hydroxyproline before HPLC was run on a conventional graphite source-AMS. The hydroxyproline after running through the HPLC was run on a gas source-AMS, hence the larger error bars.

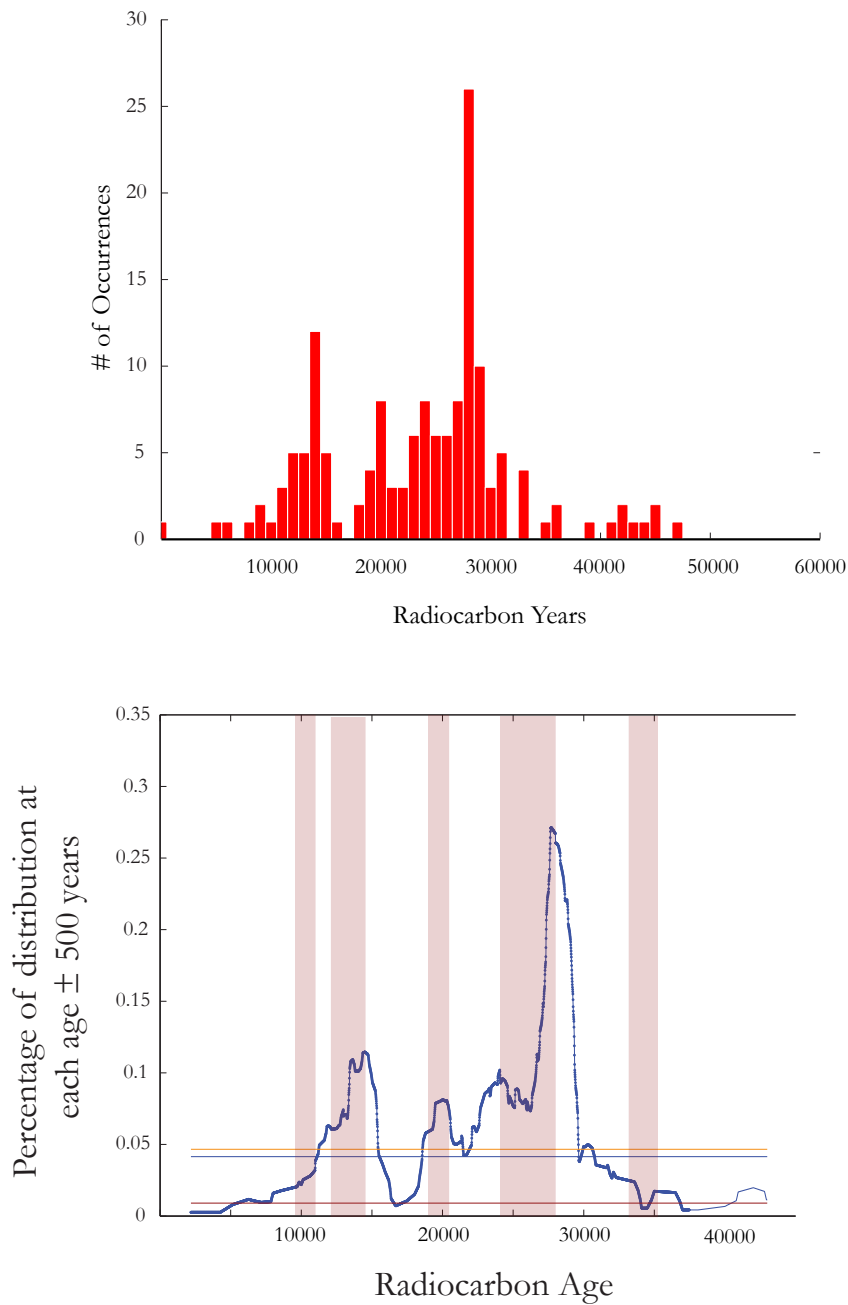


Figure 5.6a: Histogram of all radiocarbon dates made on megafauna from the La Brea Tar Pits.
 Figure 5.6b: Percentage of empirical cumulative distribution at each interval ± 500 years for all distributions studied. The shaded regions are the Younger Dryas and Heinrich Stadial (HS) 1, HS 2, HS 3, and HS 4. Horizontal lines indicate the average percentage of the distribution at Marine Isotope Stage (MIS) 1, MIS 2, and MIS 3, excluding Heinrich Events within those intervals. Note the two graphs are on different axes.

Fossils selected for radiocarbon dating can be assumed to be a random subsample of fossils in the pits as they were not biased by species or to any particular tar pit. Assuming the dates are correct, an interesting pattern unfolds. The abundance of fossils recovered from the La Brea Tar Pits is higher during the Heinrich Events than any other period of time (Figure 5.6).

The Younger Dryas (YD) and the Heinrich (H) Events (17) are seven abrupt climate change events in Earth's history that occurred during the last glacial cycle. H Events are associated with a destabilization of the Laurentide ice sheet during the last glacial period with each of the six events lasting approximately 700–1000 years. The H Events have been characterized in North Atlantic sediment cores, by an increase in abundance of lithic fragments (ice rafted debris), a paucity of polar foraminifera and an increase in detrital carbonate (18). The YD occurred between 12650–11700 years BP (19) and is associated with a temporary readvancement of the Laurentide ice sheet after the last deglaciation. The YD and H Events are frequently assumed to have had the same causes and effects and YD is often called H0. However, there is growing evidence that the YD and H Events were expressed differently in various parts of the world.

H Events are difficult to precisely date. They were first identified in the North Atlantic cores as an increase in ice rafted debris (IRD). However, one characteristic of these cores is that during the peak of the IRD event, there are few foraminifera in the core. Therefore it is difficult to make an age model in these cores using radiocarbon dates of foraminifera. H Events are also subtle features of the Greenland ice cores. The Greenland ice cores display a cold interval (Heinrich Stadial) during which the IRD record occurs, and after which an abrupt warming occurs. H Events have been seen in cave records in China (20) as changes in the precipitation patterns and can be absolutely dated using U-Th systematics. However, it is not clear whether the climate signal that causes an increasing in IRD in the North Atlantic causes a change in precipitation in China at the same time. We have chosen to define the Younger Dryas and Heinrich Stadials as the cold period in Greenland during IRD events.

We examined the empirical cumulative distribution (ECD) function made from dates

made from the La Brea Tar Pits using the dates of Heinrich Events and the YD. We then investigated the percentage of the ECD at the Younger Dryas and H1–H4 (Figure 5.6b). We compared these percentages to the average percentages during the Holocene (Marine Isotope Stage (MIS) 1), the deglaciation (excluding YD and H1) and the last glacial period (excluding H2, H3 and H4). From here onwards, the deglaciation is referred to as MIS 2 while the last glacial period is referred to as MIS 3.

In the La Brea distribution, we find that during H1, H2 and H3 there is a higher percentage of animals than any other time in the distribution. There is also a factor of two more animals at H3 than H1, and a factor two more animals in H1 than H2. Interestingly, the YD and H4 show a notable depletion in fossil abundances implying that a different climate mechanism was at play during the YD and H4 than H1 and H3. There is also a depletion in megafauna abundances at the LGM.

This pattern is remarkable because the effect of rapid climate change has only previously been seen in benthic macrofauna, including ostracods (21), foraminifera (22) deep-sea corals (23) and micromammals (24). Terrestrial megafauna have never before been shown to increase in abundances due to rapid climate change events on the millennial time scale.

It is possible that a climatic variable could be biasing the “trapping efficiency”, thereby artificially increasing the abundance of animals during these time periods. One possibility is temperature. However, temperature is unlikely to control the distribution as studies at the Page Museum have indicated that there is not a preferential trapping of animals in the La Brea Tar Pits during environmentally relevant temperature ranges nor is there a change in the area of asphalt pools (personal communication, John Harris).

The most likely explanation for changes in abundances at this site due to H events is changes in moisture. The Southern California climate is Mediterranean-like and therefore moisture limited. The La Brea Tar Pits are located near the LA river, a major source of water to animals in the region. Therefore, an increase in the number of animals in the tar pits implies that there were more animals in the area, and thus that the region was likely wetter.

Interestingly, there is no “peak” in animal abundances in the tar pits during the YD. The YD is frequently referred to in the literature as similar climatically to the Heinrich Events or even as “H0”. However the lack of a peak in animal abundance suggests that perhaps the Southern California climate responded differently during the YD than during Heinrich Events, perhaps suggesting that different mechanisms were at play for transmitting the climate signal from the North Atlantic to the Southwest US during those time periods. The different climatic signatures between the YD and H1 are not only observed in the La Brea Tar Pits. Other paleoclimate records indicate that the regional signature of the American West during Heinrich events was wet (25, 26) while the YD more resembled a La Niña signal (27–29) with a wet Pacific Northwest and a dry Southwest US.

The global signature of the YD and Heinrich Events suggest that large-scale changes in the ocean-atmosphere system are involved in the transference of the abrupt climate change signal from the North Atlantic to the rest of the globe. However the exact mechanisms are not known. In the modern American Southwest, there are two modes of precipitation patterns seen in the Palmer Drought Severity Index (PDSI) and tree ring records from the US (30, 31). One pattern shows a regional drying or wetting in the western US and another pattern shows a bipolar ENSO like signature with drying (or wetting) in the Pacific NW and wetting (or drying) in the SW US (32). The regional wetting which resembles the H1 signature is associated with high latitude forcing while regional pattern of the YD resembles the ENSO pattern and could be associated with a tropical forcing. The potentially different causes of the YD vs. Heinrich Events could explain the regional patterns seen in North America during those time periods as well as the scarcity of megafauna in the La Brea Tar Pits.

This pattern of increased megafauna abundance during Heinrich Events is not only seen in the La Brea Tar Pits, but also in other megafauna distributions around the world as well as in American micromammals and Siberian humans (Figure 5.7, 5.8 and 5.9). We examine the ECD functions of these different distributions and try to correlate the increased animal abundances during Heinrich Events with changes in the climate in the regional climate.

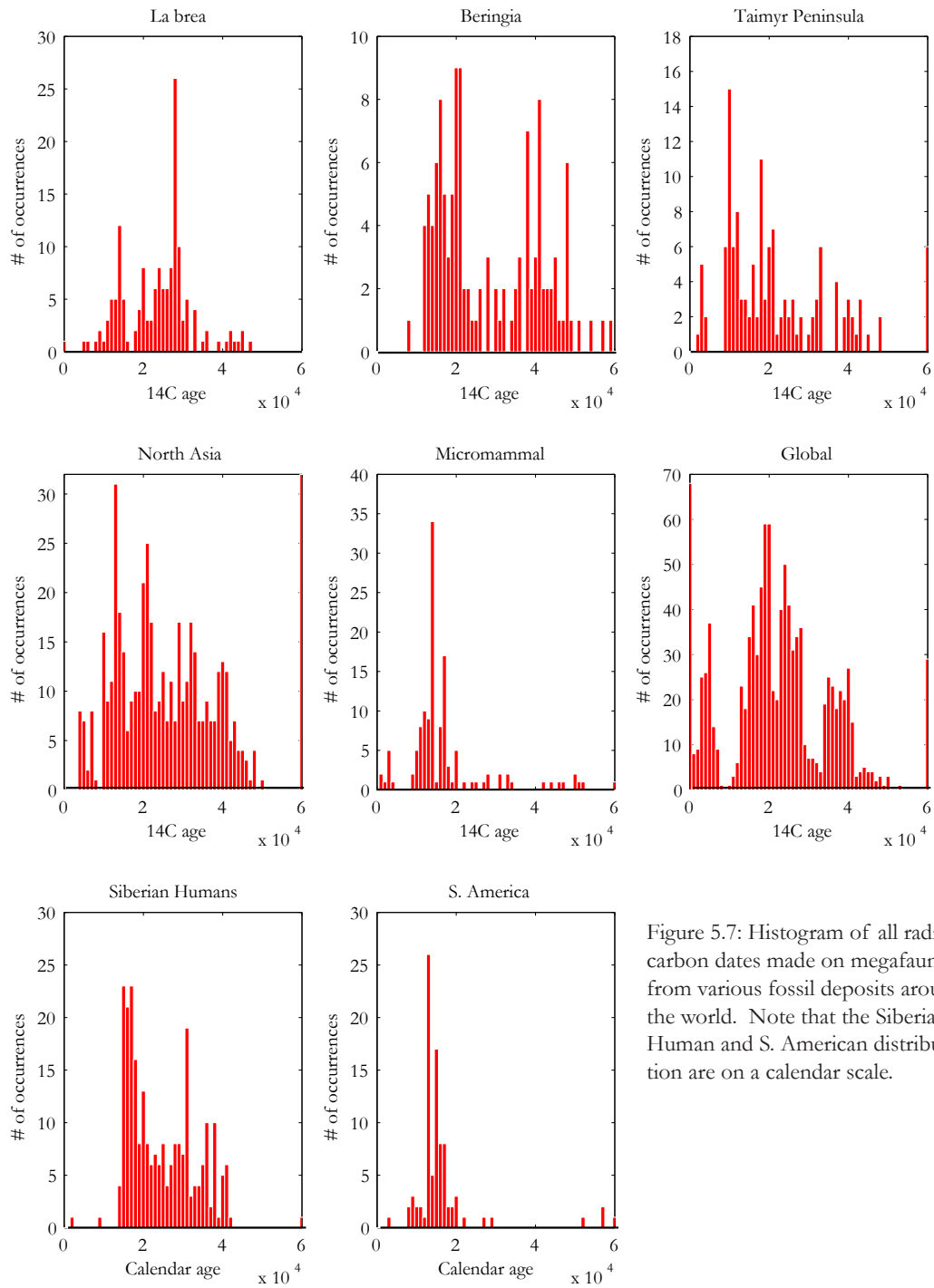


Figure 5.7: Histogram of all radiocarbon dates made on megafauna from various fossil deposits around the world. Note that the Siberian Human and S. American distribution are on a calendar scale.

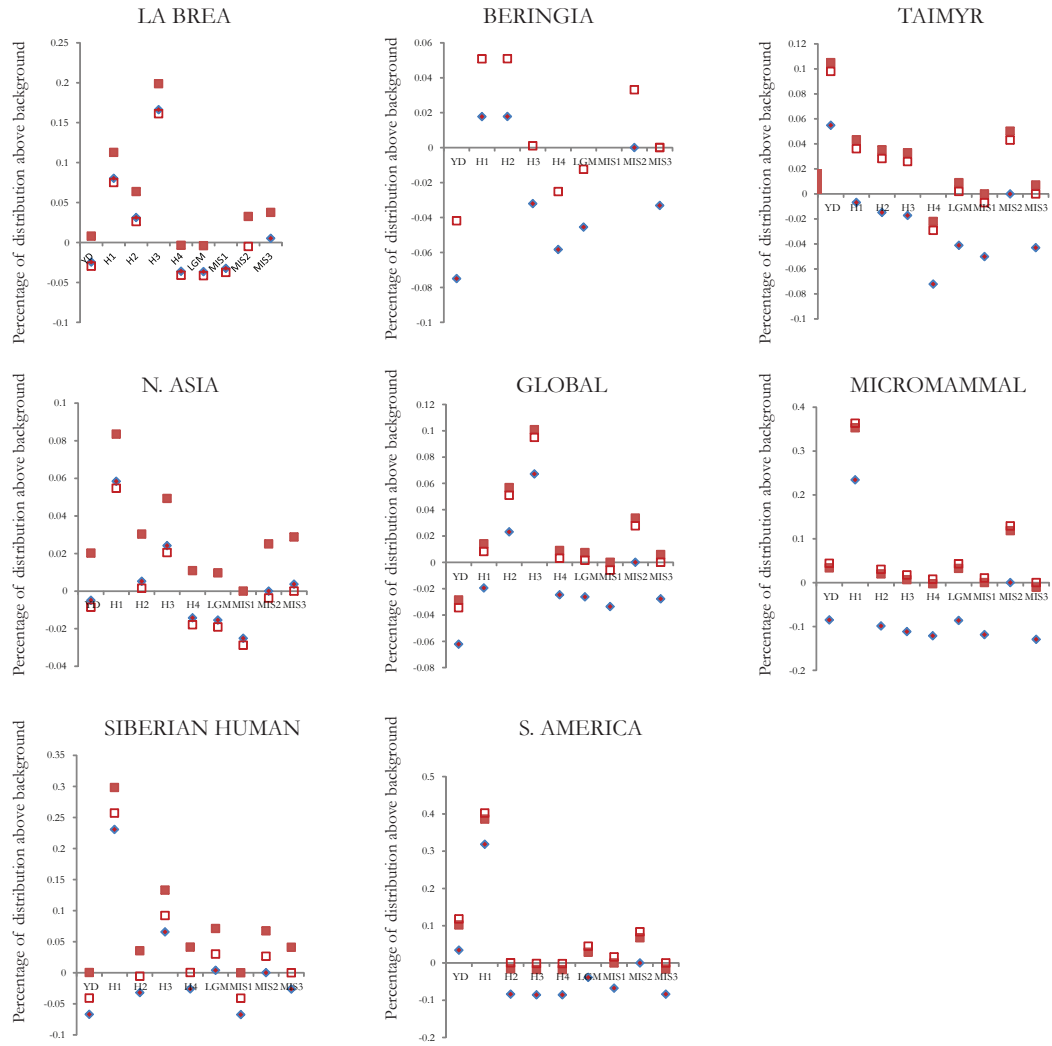


Figure 5.8: The amount of the empirical cumulative distribution (ECD) during each climatic event studied that is above the average amount of ECD during the non YD and Heinrich event times in three background intervals: marine isotope stage (MIS) 1, MIS2, and MIS3.

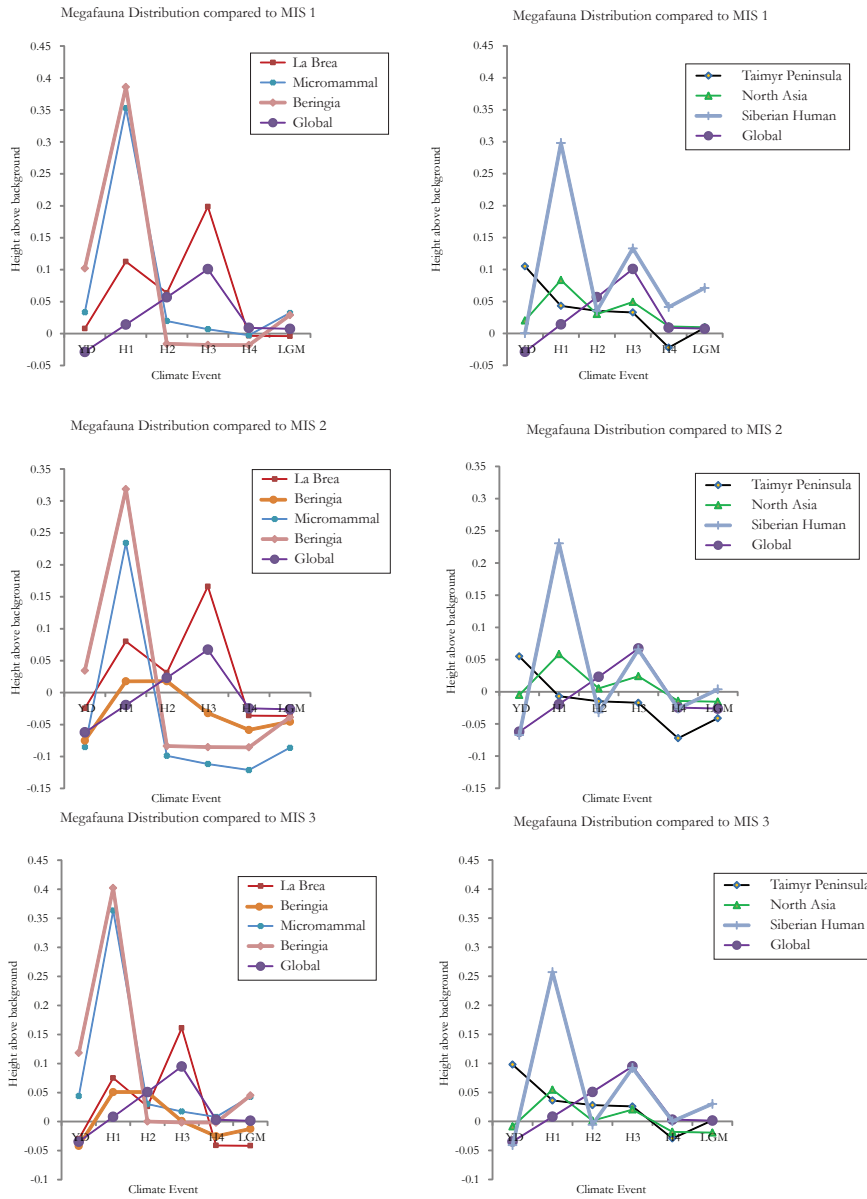


Figure 5.9: The amount of the empirical cumulative distribution function for each climate interval studied about a background. These background periods were marine isotope stage (MIS) 1, MIS 2, and MIS 3, excluding Heinrich Event intervals during these periods.

In Beringia, fossil specimens have been collected from placer mining gravel deposits from around Fairbanks, Alaska. Permafrost fossils are generally exceptionally well preserved morphologically and biogeochemically however they do not have stratigraphic context when found in gravel deposits. Therefore, similarly to the La Brea Tar Pit radiocarbon age distribution, ages made from this gravel deposit can be thought to be random and not biased as no particular age is likely to be collected more than another. Fossil specimens used in this study were compiled from samples curated at the American Museum of Natural History and the Canadian Museum of Natural History. Previous work has been done on measuring these fossil specimens' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to reconstruct diet (33). The Beringian distribution is different from La Brea because there are no megafauna found during MIS 1. However, similarly to La Brea, the megafauna in Beringia respond to Heinrich Events. There is an increase in abundance of megafauna at H1 and H2 compared to the MIS 2 and MIS 3 and not an increase in abundance at H3 or H4. Similarly to the La Brea there is not an increase at the YD and there is a notable decline during the LGM.

Foraminifera-based sea surface temperature estimates in the NW Pacific show that warm phases parallel Greenland cold stadials and vice versa (34, 35). The antiphasing is hypothesized to stem from variations in global thermohaline circulation. The North Pacific upwelling is greatly affected by the meridional overturning circulation, so any slowdown or shutoff of North Atlantic deep water formation could have led to a turnoff or reduction of the upwelling cold Pacific deep water. A reduction in upwelling at the North Pacific would lead to an immediate short-term warming of the surface water. This antiphasing and reduction in upwelling is also consistent with global circulation model runs and simpler models (36, 37). This warming during Heinrich Events could explain the increase in megafauna abundances in the area. However, this warming is also seen during the YD and H3 and H4 when there are no corresponding increases in animal abundances. So other factors must also influence megafauna abundance in Beringia.

The Siberian arctic is highly sensitive to climate variations and is an important region for understanding climate change. Currently the high Arctic periphery supports only two

species of megafaunal mammals, reindeer and muskox. However several thousand years ago, this same zone supported half a dozen large herbivores. MacPhee et al., (38) has compiled Late Quaternary mammalian megafauna radiocarbon dates from eastern Taimyr Peninsula located in the Siberian arctic. The Taimyr peninsula is intersected by the Byrrangea mountains which form an arc from NE to SW of the peninsula. North of the mountains the landscape is rugged and hilly while southward it merges into the featureless northern Siberian lowland belt. During the last glacial period, the Taimyr Peninsula was largely unglaciated (39). Samples used in MacPhee's compilation were collected from permafrost soils along lake margins and river banks, where fossils are most frequently found. The collecting conditions are considered stochastic as virtually all finds are made at the surface and can be of any age. The frozen ground preserves remains of animals such as woolly mammoth, woolly rhinoceros, steppe bison and reindeers in excellent condition. Sometimes, skin, fur and internal organs are preserved. Dates were made on teeth and long-bone compactum.

The Taimyr Peninsula is anomalous compared to the La Brea and Beringia distribution in that the Younger Dryas has more megafauna than any other time period. However the Taimyr distribution does feel Heinrich Events. There is an increase in animal abundances at H1, H2 and H3 compared to MIS 1 and MIS 3, but not MIS 2. Also, unlike La Brea and Beringia there is a small peak in megafauna relative to MIS 1 and 3 at the LGM.

Several continuous sedimentological records from lakes have been made in the area (40–43). These studies indicate that the Pleistocene climate was generally warmer and wetter than today. Nearby in the Laptev Sea, it has been determined that during Heinrich Events there were a higher abundance of thermophilous xerophytes, meaning the climate was cool and dry. However, the Younger Dryas corresponds to 3–4°C cooler temperatures and 100 mm lower pollen, although there is an increase in abundance of animals. Similarly to Beringia, there is another unidentified variable controlling megafauna abundances during rapid climate change events.

It has been noted that there is an empirical trend towards younger mean date per latitude

interval as one moves northward in Taimyr (38). This observation implies that species managed to persist longer at higher latitudes than lower ones. One possible explanation is that large influxes of meltwater from glaciers left large parts of the northern Siberian lowlands waterlogged for a long period after end of the glaciation, causing megafauna to retreat northwards to the northern part of the Peninsula(38). This explanation could also explain the peak in megafauna abundances at the LGM in Taimyr Peninsula. Heinrich Events correspond to colder and more arid events in Central China and Siberia (44). Perhaps megafauna were retreating northward during these events. Sr isotope analysis of these bones could clarify if any megafauna were retreating northward during these climate change events.

The distributions we analyzed for the remainder of the study are not necessarily a random subsample of the true megafauna distribution like the La Brea, Beringia and Taimyr Peninsula distributions. There are several factors that might create biases and distort this record including problems of preservation or visibility of sites, research priorities, and decomposition of organic material meaning less preserved older sites. However these records show similar patterns of increased animal abundances during Heinrich Events or other rapid climate change events.

A comprehensive review of woolly mammoth ages in Northern Russia has been made recently (45). There are two latitudinal bands with the highest concentrations of radiocarbon dates, the Arctic and southern part of Siberia. In both latitude bands there is an increase in mammoth abundances at H1, H2 and H3 compared to MIS 1. Both latitude bands also have an increase in mammoth abundances at H1 and H3 compared to MIS 2 and MIS 3. This distribution is similar to La Brea in that there is a decrease in animal abundances at the YD and H2 compared to H1 and H3, a feature not seen in Beringia or Taimyr Peninsula.

A notable feature in this record that is also seen in the Taimyr Peninsula record is that during the LGM, there is an increase in mammoths abundances in the northern latitudes without an increase in the southern latitudinal band, implying the mammoths were retreating northwards.

Another megafauna record that was analyzed was a global distribution compiled of six megafauna from Eurasia and North America (46). H2 and H3 show a higher abundance of

animals compared to all other time periods. There is a decline in the abundance of megafauna in the Heinrich Event with decreasing age. This feature is not seen in any other record and could reflect a bias in sample collection.

The effect of rapid climate change events on micromammals can also be seen in a micromammal compilation of radiocarbon dates from 21 cave deposits in southeastern North America (24). The micromammal distribution shows an increase in micromammal abundances at H1 compared to all other time periods. However, there is no increase at the YD or any other Heinrich Event that is substantially above background levels. During Heinrich 1 there is a greater abundance of 'cold intolerant' species (Beautiful Armadillo) and cold-adapted (Taiga Vole) and arid-steppe species (Plains Pocket Gopher) implying that there were reduced temperature extremes and the area resembled a boreal parkland or savanna-like environment. The increase in micromammal abundances at H1 shows that climate change during the Heinrich Events affected several trophic levels in the ecosystem.

A compilation of Siberian human paleolithic occupation sites has also been made (47). There is a higher percentage of Siberian humans in the record at H1 and H3 compared to all other time periods. Similarly to the North Asia megafauna population there is a higher abundance of humans at H1 and H3 compared to the YD and H2. Perhaps human hunters were responding to the availability of prey animals during these time periods.

A final location where radiocarbon dates were compiled is South America (48). South America is the only record examined from the Southern Hemisphere and it shows a higher abundance of megafauna at the Antarctic Cold Reversal (ACR) and H1 compared to all other time periods. The Antarctic Cold Reversal is a rapid climate change event that occurred between YD and H1 and is predominantly seen in the southern hemisphere. Records from Africa or Australia will determine whether the ACR signal in megafauna abundances is specific to South America or the Southern Hemisphere as a whole.

5.4 CONCLUSIONS

In conclusion, we have developed a new HPLC method to separate hydroxyproline from

bones. This method will potentially ameliorate the difficulty of radiocarbon dating bones. We have also investigated the relationship between rapid climate change events and the abundance of megafauna in several radiocarbon chronologies around the world. We find that there is an increase in megafauna abundances during Heinrich Events compared to most other time periods. Taimyr Peninsula is unusual in that there is an increased abundance at the YD. The Taimyr and N. Asian populations also both show an increase in abundance at the LGM, possibly indicating that the megafauna were retreating northwards. The South American megafauna distribution is the only distribution to show an increase during the ACR, which is a feature of Southern Hemisphere ice and marine records. The Siberian human population showed a similar pattern of relative abundances to the mammoth distribution in North Asia, indicating that humans were responding to the availability of prey. A micromammal distribution from SE US also showed an increase in micromammal abundances at H1, indicating that Heinrich Events favorably affected several trophic levels in the food chain.

Our observations indicate that the relationship of megafauna to climate is much more complex than previously thought. Contrary to the predictions of HLH, MNH, CED and SOI, rapid climate change actually increases the abundance of megafauna. The megafauna extinctions must have been caused by human interaction or a climatic variable that did not affect them during Heinrich Events.

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