Spatio-temporal variation in the preservation of ancient faunal remains

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Palaeodemographic studies of animals using frequency distributions of radiocarbon dates are increasingly used in studies of Quaternary extinction but are complicated by taphonomic bias, or the loss of material through time. Current taphonomic models are based on the temporal frequency distributions of sediments, but bone is potentially lost at greater rates because not all sedimentary contexts preserve bone. We test the hypotheses that (i) the loss of bone over time is greater than that of sediment and (ii) this rate of loss varies geographically at large scales. We compiled radiocarbon dates on Pleistocene-aged bone from eastern Beringia (EB), the contiguous United States (CUSA) and South America (SA), from which we developed models of taphonomic loss. We find that bone is lost at greater rates than terrestrial sediment in general, but only for CUSA and SA. Bone in EB is lost at approximately the same rate as terrestrial sediments, which demonstrates the excellent preservation environments of arctic regions, presumably due to preservative effects of permafrost. These differences between bone and sediment preservation as well as between arctic and non-arctic regions should be taken into account by any research addressing past faunal population dynamics based on temporal frequency distributions.

1. Background

Determining the causes of Quaternary extinction events is a long-lasting and ongoing scientific debate. To properly contextualize these events, it is important to understand faunal population dynamics during and leading up to extinction [1–4]. Reconstructing population sizes of past species is complicated, but increasingly researchers are turning to frequency distributions of radiocarbon dates [3–5]. It is now evident that these records are complicated by taphonomic loss, or the progressive and time-dependent loss of geologic deposits [5–7]. As a result, old things are, in general, less common than young things in the fossil record. Surovell et al. [5] proposed a means of addressing this bias through a process termed ‘taphonomic correction’, in which abundance is measured as actual abundance in the archaeological (or fossil) record for a particular time period relative to the abundance of geologic deposits of the same age. Since being proposed, taphonomic correction has proved an effective tool for better understanding dynamics of human and faunal abundance in the distant past [8–11].

To develop a generalized global model of the temporal abundance of terrestrial sedimentary deposits, Surovell et al. [5] used a large database of radiocarbon dates associated with volcanic deposits [12], which have been deposited at a relatively constant rate over the last ca 40,000 years. The vast majority of those dates are on charcoal soil organic matter. As not all sedimentary contexts have geochemical conditions conducive to bone preservation, the loss of bone over time might be expected to be more severe than the loss of other materials in sediments, an observation that serves as the primary impetus for this study. Moreover, it is well known that there are large scale regional differences in soil and sedimentary geochemistry, such that different regions may be characterized by unique rates of taphonomic loss of bone. Following these concepts, we test two hypotheses: (i) bone is lost
from the fossil record at a greater rate than terrestrial sediments; (ii) there is large geographical scale variation in the loss of bone over time.

2. Material and methods
We use radiocarbon dates on North and South American Pleistocene faunas from ca 40 000 to 13 000 BP to test the hypotheses of this study. We use dates from modified versions of datasets originally compiled for Surovell et al. [13]. An ideal dataset for examining the taphonomic loss of bone over time would be composed of a large number of dates on fossil taxa whose natural abundance remained relatively constant through time, which would allow us to isolate the effects of taphonomic bias. Unfortunately, no such datasets exist. The past abundance of Pleistocene faunas almost certainly fluctuated over that time, owing to changes in climate and habitable land area. Still, we argue below that the dominant signal in the long-term pattern of abundance in the fossil record is a result of taphonomic loss. One major factor presumed to affect bone abundance over time is human predation [14,15], but except for the final one or two millennia prior to extinction, American Pleistocene faunal abundance should have remained unaffected by human predation.

We compiled radiocarbon dates on bone from extinct Pleistocene fauna for eastern Beringia (EB), the contiguous United States (CUSA) and South America (SA), excluding all dates from archaeological contexts. These groupings of dates are spatially separated by geographical gaps marked by the continental ice sheets in the north and Mesoamerica in the south. We also excluded dates on non-osseous materials, such as skin, hair, horn and dung. For each region, we vetted dates following Barnosky & Lindsey [16], and used only the highest quality dates (scoring 11 or 12). We derived most of our EB dates from Guthrie [17], and the majority of South American dates from Barnosky & Lindsey [16]. We also excluded all dates from the Rancho La Brea because this locality has unique preservation conditions and a very large number of radiocarbon ages that are highly clustered in time [18], which in combination could add considerable bias to the CUSA dataset. The resulting databases include 243 dates from EB, 87 dates from CUSA and 50 dates from SA. We do not consider these samples to be geographically unbiased within each region but instead they tend to be biased toward areas where fossil remains are commonly found. In that sense, they are intended to be a representative sample of the sample of dates that exists. We calibrated all dates using OxCal v. 4.2 [19] and the IntCal13 [20] calibration curve to produce 2σ contiguous age ranges. We used the centroid of the contiguous 2σ age range for the age of each specimen.

To examine taphonomic loss, we binned each dataset into 500-year intervals. We clipped the CUSA and SA datasets to the oldest bone containing at least one date younger than 40 000 BP. Finally, we created taphonomic models for each region by nonlinear regression in R using the nls function following the general model developed by Surovell et al. [5]:

\[ f = a(t + b)^{-c}, \]

where \( f \) is the frequency of faunal specimens occurring at time \( t \), and \( a, b \) and \( c \) are coefficients. This model shows a greater degree of fit to temporal frequency distributions than other and simpler models [5]. We then compared each taphonomic model to each other as well as to the global taphonomic model previously developed by Surovell et al. [5].

3. Results
Both hypotheses are supported by our analysis. Since our data span several oscillations of environmental change that should have produced corresponding changes to faunal populations, it appears as though these distributions are primarily a reflection of taphonomic loss, although small shifts in abundance may still be visible in our data. This is especially true of EB, where the model of taphonomic loss is loosely constrained (figure 1c). Much of the noise in the regression may reflect environmentally caused changes in faunal populations or be an artefact of small sample size. Either way, we suggest that the long-term trend results from taphonomic loss. Supporting that contention is that the best-fit taphonomic curve for bone loss in EB (figure 1c, table 1) is very similar to the global model of sedimentary loss developed by Surovell et al. [5] (figure 1d), a congruence that would be very unlikely to result from faunal population dynamics. This suggests, not surprisingly, that conditions for bone preservation in the Arctic are excellent and essentially equivalent to conditions for the preservation of other dateable materials preserved within clastic sediments (e.g. charcoal and soil organic matter).

For the CUSA (figure 1a, table 1) and SA (figure 1b, table 1) datasets, loss of bone occurs at much greater rates than the loss of sedimentary contexts (figure 1d). As an example, over the 10 000 year period from 25 000 to 15 000 BP the Surovell et al. [5] sedimentary model and our EB bone model developed herein suggest approximately 47% loss of material, while for the SA and CUSA bone models, approximately 93 to 99% loss is indicated. Put another way, 100 fossils dating to 25 000 BP in Alaska would be equivalent in abundance to ca 189 fossils at 15 000 BP. For CUSA and SA, 100 fossils dating to 25 000 BP are equivalent to more than 3000 at 15 000 BP. Although it could be argued that the observed differences between EB and non-arctic regions are due to differences in faunal abundance through time resulting from changes in habitable land area related to glaciation, if that were the case, CUSA and EB would be expected to group together, as both were subject to continental glaciation, in contrast with SA. Because CUSA and SA show similar trends and differ substantially from EB, taphonomic loss and differences in geochemistry provide the most parsimonious explanation for these differences. Two-sample Kolmogorov–Smirnov tests indicate that all three samples are significantly different from each other as well as from the Bryson et al. [12] radiocarbon database from which the Surovell et al. [5] model was developed (table 2).

4. Discussion and conclusion
Palaeodemographic reconstructions of past animals are complicated by taphonomic bias, or the progressive loss of material through time. To date, models of taphonomic loss have only considered temporal frequency distributions of sediments, which may or may not preserve bone. To account for taphonomic bias in reconstructions of the dynamics of past animal populations using frequency distributions of radiocarbon dates will require the development of taphonomic models specific to bone, and this study is a first attempt to do so. Understanding how bone is lost through time and across space is especially critical to studies of Quaternary extinctions that use radiocarbon databases to infer the causes of extinction [3–5,13]. Towards that end, we can say with some confidence that the global model of sedimentary loss can be applied to EB, and very likely to circumpolar regions in general, but not to CUSA and SA. Importantly, at this point, we caution against the use of the models presented in table 1 for taphonomic...
correction. Particularly for the CUSA and SA datasets, small sample sizes result in very poor definition of long-term trends of taphonomic loss, particularly in the deep past in the right tails of the distributions. Applying these models may result in systematic over- or under-representation through time in temporal frequency distributions as discussed by Williams [7].

Despite the practical limitations of these models, we have shown that for the Late Pleistocene, bone is lost at considerably greater rates for CUSA and SA, as compared with EB. The simplest explanation for the excellent state of bone preservation in arctic regions is cold temperatures and the presence of permafrost, which retard organic and inorganic diagenesis of osseous materials. Assuming the global model of taphonomic bias developed by Surovell et al. [5] is a good description of the age distribution of sedimentary contexts in EB, bone apatite in arctic environments appears to preserve as well as all other dateable materials within clastic sediments. For areas farther south, considerably more bone has been lost over time.

While regional and temporal differences in bone preservation are clear for the Pleistocene, we do not know to what extent they also apply to the Holocene, and we caution researchers from simply extrapolating these patterns forward or backward in time. This highlights the need for research examining trends in bone loss through the Holocene, as well as increased numbers of radiocarbon dates on Holocene palaeontological fauna in general, of which there are few. Finally, both hypotheses are supported by this work. Outside of arctic environments, bone is lost from the fossil record at greater rates than terrestrial sediments. We expect additional

**Figure 1.** Taphonomic loss of bone over the Late Pleistocene for (a) the contiguous United States, (b) South America, and (c) Beringia. Scatter plots show the frequency of calibrated (cal.) radiocarbon ages in 500 year bins, and lines are best-fit models for each region. (d) Best-fit models for all three regions compared with the Surovell et al. [5] global model of taphonomic loss (volc.; see footnote to table 2). All models have been standardized to their maximum value at 13 000 BP. (Online version in colour.)

**Table 1.** Best-fit models of taphonomic loss of bone for eastern Beringia, the contiguous United States and South America.

<table>
<thead>
<tr>
<th>region</th>
<th>best-fit model</th>
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<tbody>
<tr>
<td>eastern Beringia</td>
<td>freq. = 2.857 \times 10^{5.427}(t + 63 660)^{-5.427}</td>
</tr>
<tr>
<td>contiguous United States</td>
<td>freq. = 2.055 \times 10^{6.405}(t + 2914)^{-6.405}</td>
</tr>
<tr>
<td>South America</td>
<td>freq. = 5.691 \times 10^{5.927}(t + 7934)^{-5.927}</td>
</tr>
</tbody>
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Table 2. Pairwise Kolmogorov–Smirnov tests for all radiocarbon datasets.

<table>
<thead>
<tr>
<th>comparison</th>
<th>age range (yr BP)</th>
<th>sample sizes</th>
<th>results</th>
</tr>
</thead>
<tbody>
<tr>
<td>volcanic versus EB</td>
<td>13 000–40 000</td>
<td>$n_1 = 365$, $n_2 = 246$</td>
<td>$Z = 2.275; p &lt; 0.001$</td>
</tr>
<tr>
<td>volcanic versus CUSA</td>
<td>12 500–40 000</td>
<td>$n_1 = 383$, $n_2 = 87$</td>
<td>$Z = 4.44; p &lt; 0.001$</td>
</tr>
<tr>
<td>volcanic versus SA</td>
<td>12 500–28 000</td>
<td>$n_1 = 269$, $n_2 = 50$</td>
<td>$Z = 2.373; p &lt; 0.001$</td>
</tr>
<tr>
<td>EB versus CUSA</td>
<td>13 000–40 000</td>
<td>$n_1 = 246$, $n_2 = 63$</td>
<td>$Z = 3.659; p &lt; 0.001$</td>
</tr>
<tr>
<td>EB versus SA</td>
<td>13 000–28 000</td>
<td>$n_1 = 200$, $n_2 = 41$</td>
<td>$Z = 2.707; p &lt; 0.001$</td>
</tr>
<tr>
<td>CUSA versus SA</td>
<td>12 500–28 000</td>
<td>$n_1 = 79$, $n_2 = 50$</td>
<td>$Z = 1.441; p = 0.037$</td>
</tr>
</tbody>
</table>

The volcanic dataset is the Bryson et al. [12] global database of radiocarbon dates associated with volcanic deposits that was used to construct the Surovell et al. [5] model of taphonomic bias.

geographical differences to become evident in the near future. For example, a similar study comparing taphonomic loss of bone between humid and arid environments would probably also be fruitful, although there are presently far too few dates from arid regions to establish robust models of taphonomic loss.

Data accessibility. The data are available as the electronic supplementary material.

References


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