Stable isotopes confirm the Banwell Bone Cave Mammal Assemblage Zone represents a MIS 5 fauna.

Rhiannon E. Stevens* and Hazel Reade
Institute of Archaeology, University College London, 31-34 Gordon Square, London, WC1H 0PY, UK.

*Corresponding author's e-mail: Rhiannon.stevens@ucl.ac.uk

Abstract:
The position of the Banwell Bone Cave mammal assemblage zone (MAZ) in the mammalian biostratigraphy of the British Isles has been the focus of debate for decades. Dominated by fauna typical of cold environments it was originally linked to the marine isotope stage (MIS) 4 stadial (c. 72-59 ka). Subsequently it was argued that the Banwell Bone Cave MAZ more likely relates to the temperate interstadial of marine isotope stage (MIS) 5a (c. 86–72 ka). It is envisioned that 'cold fauna' such as bison and reindeer moved into Britain during stadial MIS 5b (c. 90 ka) and were subsequently isolated by the rising sea level during MIS 5a. Here we investigate environmental conditions during the Banwell Bone Cave MAZ using bone collagen $\delta^{13}C$ and $\delta^{15}N$ and tooth enamel $\delta^{18}O$ and $\delta^{13}C$ isotope analysis. We analyse bison and reindeer from the MAZ type site, Banwell Bone Cave. Our results show unusually high $\delta^{15}N$ values, which we ascribe to arid conditions within a temperate environment. Palaeo-temperature estimates derived from enamel $\delta^{18}O$ indicate warm temperatures, similar to present day. These results confirm that the Banwell Bone Cave MAZ relates to a temperate interstadial and supports its correlation to MIS 5a rather than MIS 4.

Keywords: MIS 5a, stable isotope, carbon, nitrogen, oxygen, collagen, enamel, reindeer, bison, British Isles, Stage 5.

Introduction:

Mammalian biostratigraphy focuses on correlating and sequencing geological deposits based on the fossil mammal assemblages contained within them. Mammals are good biostratigraphic indicators due to their rapid morphological evolution and turnover (Schreve, 1997). Quaternary climate fluctuation has resulted in major shifts in the biogeography of many mammal species, resulting in discernible patterns of presence and absence in the fossil record of certain regions (Schreve, 1997). Currant and Jacobi (1997, 2001, 2002) outlined a mammalian biostratigraphic framework for the Late Pleistocene in the British Isles that described five mammal assemblage-zones (MAZ; distinctive fossil mammal bone assemblages), including the Banwell Bone Cave MAZ (hereafter the BBC MAZ). Named after the type-site, Banwell Bone Cave in Banwell, Somerset (Figure 1), the BBC MAZ is characterized by a low diversity fauna which consists primarily of tundra species. Reindeer (*Rangifer tarandus*) and bison (*Bison priscus*) dominate the fauna, with mountain hare (*Lepus timidus*), wolf (*Canis Lupus*), wolverine (*Gulo gulo*), and brown bear (*Ursus arctos*) being consistently present (Currant and Jacobi, 2001). Horse (*Equus ferus*) and traces of human presence are notably absent from this MAZ. The small mammal fauna from the BBC MAZ is restricted to a single species, the northern vole (*Microtus oeconomus*) (Currant and Jacobi 2011), which today inhabits a broad range of habitats including tundra, mixed forest, taiga and forest steppe biomes.

The BBC MAZ is known from locations widespread throughout England and Wales (Figure 1). Currant and Jacobi (2001:1710) argued that the BBC MAZ is 'clearly the vertebrate assemblage of a cold environment' and postulated that it correlated closely with the early part of the last cold stage, marine isotope stage 4 (MIS 4). However, in subsequent publications Gilmour *et al.* (2007) and Currant and Jacobi (2011) questioned this correlation and suggested that the BBC MAZ might actually relate to interstadial MIS 5a (the Brimpton interstadial dating to approximately 86–72 ka, Worsley *et al.* 1983, Bryant *et al.* 1983). Although typically characteristic of a fauna indicating cold tundra environments, many of the sites that contain the BBC MAZ also contain associated environmental proxies that indicate temperate climates, more characteristic of interstadial conditions. At Willment's Pit, Isleworth, Greater London, fossil Coleoptera provide evidence of interstadial climatic conditions (Coope and Angus, 1975), while pollen and plant macrosfossils indicate vegetation dominated by herbaceous species typical of grasslands that occur in treeless landscapes (Kerney *et al.* 1982). At Cassington in Oxfordshire, Coleoptera and pollen provide evidence of an interstadial open tundra environment, with vegetation dominated by Arctic steppe/tundra herbaceous species (Maddy *et al.* 1998). Amino acid racemization dating has tentatively correlated these deposits with MIS 5c and MIS 5a, respectively (Penkman *et al.* 2011, 2013). Further, TIMS dating of stalagmite flowstone enclosing the BBC MAZ at Stump Cross Caverns in North Yorkshire, gave a date of 73.86 +1.20/-1.19 kyr, supporting an interstadial MIS 5a correlation for this assemblage (Gilmour *et al.* 2007).

Evidence from raised beaches, which indicate higher sea levels, suggest Britain was not joined to continental Europe for most of MIS 5 (Keen 1995). Gilmour *et al.* (2007) and Currant and Jacobi (2011) argue that the temperate faunal species typical of interglacial conditions survived in Island Britain up until MIS 5c, then during cold MIS 5b Britain became temporarily reconnected to the continent and a major faunal change occurred, with the loss of most temperate mammal species and the gain of species typical of arctic conditions (arctic fox (*Vulpes lagopus*), wolverine (*Gulo gulo*), and reindeer (*Rangifer tarandus*)). With the onset of MIS 5a, they argue that the new fauna became trapped in Britain by the higher sea-levels and the return of Britain to being an island. The presence of a faunal assemblage typical of cold conditions, alongside palaeoclimate indicators of interstadial conditions, a restricted range of species and the absence of woolly mammoth (*Mammuthus primigenius*), wild horse (*Equus ferus*), woolly rhinoceros (*Coelodonta antiquitatis*), hominin remains and archaeology, which are present in MIS 5a on the European continent are all suggested to be evidence of Britain being an island isolated from the continent at this time (Currant and Jacobi 2011).

The possibility that the BBC MAZ represent fauna typical of cold environments living in temperate conditions has implications both for the technique of mammalian biostratigraphy and for our understanding of the Quaternary history of the British Isles. Thus, further investigation is required to confirm whether the BBC MAZ relates to cold or temperate environmental conditions. Here we undertake stable isotope analysis of bison and reindeer bone and teeth from Banwell Bone Cave in order to establish the environmental context in which these animals lived.

1.1 Background to stable isotopes:

Palaeoclimatic and palaeoenvironmental data can be obtained from fossil tooth enamel and bone through stable isotope analyses. The measured isotopic signals are underpinned by dietary specialisation, animal behaviour and environmental conditions. This approach has enabled the reconstruction of Late Pleistocene palaeoenvironmental conditions at a range of archaeological and palaeontological sites (e.g. Sponheimer and Lee Thorpe, 2003; Hedges *et al.* 2005, Stevens and Hedges, 2004; Drucker *et al.* 2008, 2011; Stevens *et al.* 2008, 2014; Szpak *et al.* 2010; Reade *et al.* 2016, 2020a; Fabre *et al.* 2011; Jones *et al.* 2018, 2019; Britton *et al.* 2019).

Skeletal carbon is acquired through the animal's diet and in herbivores is ingested directly from plant tissue (Gannes *et al.* 1997). Within the context of Late Pleistocene Europe, where plants used the C_3 photosynthetic pathway and C_4 and CAM plants were most likely absent (Wißing *et al.* 2016), plant $\delta^{13}C$ would have been influenced by a variety of climatic/environmental variables such as temperature, precipitation, relative humidity, atmospheric carbon dioxide concentrations and the canopy effect (Heaton, 1999; Kohn, 2010). Thus, faunal $\delta^{13}C$ reflects underlying environmental conditions, mediated by species-specific dietary behaviours, such as grazing versus browsing (Heaton, 1999). Bone collagen $\delta^{13}C$ signatures primarily reflect dietary protein whereas enamel carbonate $\delta^{13}C$ reflects the whole diet (Ambrose and Norr, 1993). Relative to the plants consumed, herbivore bone collagen $\delta^{13}C$ ($\delta^{13}C_{coll}$) are approximately +5‰ enriched and enamel carbonate $\delta^{13}C$ ($\delta^{13}C_{enamel}$) are approximately +14‰ enriched (Lee Thorpe *et al.* 1989; Cerling and Harris, 1999). Nutritional stress has also been suggested to influence animal $\delta^{13}C$ values but the evidence for this is equivocal (Doi *et al.* 2017).

Herbivore nitrogen is acquired from the plants in the animal's diet (Gannes *et al.* 1997). Globally, plant $\delta^{15}N$ has been shown to increase with decreasing mean annual precipitation, with plants growing in arid locations having higher $\delta^{15}N$ values than those growing in wetter locations (Austin and Vitousek, 1998; Handley *et al.* 1999; Amundson *et al.* 2003; Szpak, 2014). Furthermore, plant $\delta^{15}N$ values have been shown to be positively correlated with local temperatures, with plants growing in cooler ecosystems have lower $\delta^{15}N$ values than those growing in warmer ecosystems (Martinelli *et al.* 1999; Amundson *et al.* 2003; Pardo *et al.* 2006; Szpak 2014). However, at mean annual temperatures of <-0.5°C the relationship between temperature and plant $\delta^{15}N$ deteriorates (Craine *et al.* 2009). The relationships between plant $\delta^{15}N$ and climatic variables are thought to be linked to mycorrhizal associations, N availability and greater relative importance of fractionating losses of N in hot, dry ecosystems compared to cold, wet ecosystems (Craine *et al.* 2015). As for carbon, the $\delta^{15}N$ signatures of the vegetation are passed on to the herbivore consumers and are recorded in their body tissues. Thus herbivore $\delta^{15}N$ reflect the underlying environmental conditions. Relative to the plants consumed, herbivore bone $\delta^{15}N$ are typically +3 to 5‰ enriched (Bocherens and Drucker, 2003). Nutritional stress can also affect animal $\delta^{15}N$, but the direction and magnitude of these effects depends on whether the animal is undergoing protein catabolism when they are starving or relying more heavily on fat reserves or other processes that conserve protein during fasting (Hobson *et al.* 1993; Polischuk *et al.* 2001; Cherel *et al.* 2005; Fuller *et al.* 2005; Mekota *et al.* 2006; Lohuis *et al.* 2007; Newsome *et al.* 2010; Bowes *et al.* 2014; Gomez-Campos *et al.* 2011; Aguilar *et al.* 2014, Fleming *et al.* 2018).

Oxygen isotopes in mammal tooth enamel is linked to prevailing climatic and environmental conditions in the vicinity of the animal's habitat during the period of tooth formation (see Pederzani and Britton, 2019 for review). For most species, drinking water is typically the largest source of O to the $\delta^{18}O$ signature, but water contained in the diet and respiration also contribute (Bryant *et al.* 1995; Luz *et al.* 1984; Longinelli 1984; Luz and Kolodny, 1985). The relative contribution that each of these pools makes to an animal's body water depends on the physiological and behavioural characteristics of the species (Kohn, 1996; Kohn *et al.* 1996; Podlesak *et al.* 2008; Pederzani and Britton, 2019). For bison and reindeer (obligate drinkers and the species of focus in this study) empirical relationships between skeletal $\delta^{18}O$ and the $\delta^{18}O_{precip}$ have been demonstrated (Hoppe, 2006; Longinelli *et al.* 2003), which in turn displays a strong relationship to surface air temperatures in mid and high latitude environments (Rozanski, 1993). Here we measure $\delta^{18}O$ in tooth enamel carbonate. In medium-large sized mammals tooth formation typically lasts several months to a few years, thus a sample of enamel can provide information at either an annual or sub-annual resolution (Fricke *et al.* 1996).

Methods:

Ten bison and eleven reindeer bones along with eight bison and ten reindeer teeth were sampled for isotope analysis. All specimens came from the 2007 excavations at Banwell Bone Cave led by Roger Jacobi and Andy Currant as part of the Ancient Human Occupation of Britain (AHOB) project (Ashton and Stringer 2011). As the excavation was limited in size the recovered faunal assemblage was relatively small and it was not possible to select a single skeletal element to ensure any individual was only sampled once. However, the assemblage is thought to be a result of post-depositional mass movement as the bones were completely mixed, directly articulating elements were absent, and parts of the same animal did not occur even vaguely together within the sediments (Currant and Jacobi, 2011). Details of skeletal elements sampled are given in supplementary files 1 and 2. The reindeer teeth sampled include six teeth found *in situ* in their mandibular bones (three left mandibles, two teeth per mandible), thus a minimum of 3 individuals is represented.

2.1 Collagen extraction and analysis

Collagen was extracted from the bison and reindeer bone samples using a modified Longin (1971) method. Chunks of bone were cut using a dental drill with a small cutting wheel attachment. Each sample was cleaned by abrasion with aluminium oxide prior to collagen extraction. Bones were demineralised in 0.5M hydrochloric acid at 4°C until they had completely decalcified. Samples were then rinsed three times with deionized water and gelatinised in a pH3 aqueous solution for 48 hours at 75°C. The filtered supernatant containing the soluble collagen was then collected, frozen, and lyophilized. The collagen was weighed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. Analysis was performed at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge, using a Costech automated elemental analyser coupled to a Finnigan MAT253 isotope ratio mass spectrometer. Samples were analysed in duplicate, with carbon and nitrogen results being reported using the delta scale in units of 'per mil' (‰) relative to internationally accepted standards, VPDB and AIR respectively (Hoefs, 2009). Based on replicate analyses of international and laboratory standards, precision is better than ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

2.2 Enamel carbonate preparation and analysis

The tooth surfaces were cleaned with a brush and then lightly abraded using a tungsten drill bit. The enamel surface of each tooth was abraded from the apex to the cervix of the crown with a diamond-incrusted drill bit and the removed powder sample collected for analysis. Enamel powder samples were prepared according to Balasse *et al.* (2002). Samples were treated with 2–3% NaOCl for 24 hours (0.1ml/mg sample) then repeatedly rinsed with distilled water. Next 0.1 M acetic acid (0.1ml/mg sample) was added to the enamel powder and left for 4 hours. Samples were then thoroughly rinsed, frozen, and lyophilized. $\delta^{18}O$ and $\delta^{13}C$ analysis was performed at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge. Samples were reacted with 100% orthophosphoric acid for 10 minutes at 90°C in individual vessels in an automated cryogenic distillation system (PRISM), interfaced with a Finnigan MAT 253 isotope ratio mass spectrometer. Results are reported with reference to the international standard VPDB calibrated through the NBS19 standard (Coplen 1995) and the precision is better than ±0.10‰ for both $\delta^{18}O$ and $\delta^{13}C$.

Results:

Collagen carbon and nitrogen:

Collagen was successfully extracted from all bones and had C/N atomic ratios between 2.9 and 3.6, which indicates good collagen preservation (DeNiro, 1985). The $\delta^{13}C_{coll}$ and $\delta^{15}N$ values of bison and reindeer are listed in supplementary file 1 and shown in figure 2. Additional published bison $\delta^{13}C_{coll}$ and $\delta^{15}N$ data from two specimens from Banwell Bone Cave were added to the dataset (Higham *et al.* 2006). Bison $\delta^{13}C_{coll}$ values range from -21.4‰ to -20.3‰ with a mean of -20.7 ± 0.3 ‰ and $\delta^{15}N$ values range from 9.1‰ to 10.8‰ with a mean of 9.8 ± 0.5 ‰. Reindeer $\delta^{13}C_{coll}$ values are higher than those of the bison, ranging from -19.9‰ to -19.6‰ with a mean of -19.8 ± 0.1 ‰, whereas reindeer $\delta^{15}N$ values are generally lower and more variable than those of the bison, ranging from 5.8‰ to 9.2‰ with a mean of 7.4 ± 1.3 ‰. Mann-Whitney U tests show there is a significant difference between bison and reindeer $\delta^{15}N$ (W=128, $p < 0.001$) and $\delta^{13}C_{coll}$ (W=0, $p < 0.001$).

Tooth carbonate carbon and oxygen:

Tooth $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ results are listed in supplementary file 2. Mean bison $\delta^{13}C_{enamel}$ is -11.5 ± 1.0 ‰, with individual values ranging from -10.1 to -12.6 ‰. As with the $\delta^{13}C_{coll}$ results, reindeer mean $\delta^{13}C_{enamel}$ is greater than that of the bison, being -10.5 ± 0.4 ‰. However, unlike the collagen, there is some overlap in reindeer and bison $\delta^{13}C_{enamel}$ values (Figure 3). Less variability is seen the in reindeer $\delta^{13}C_{enamel}$ (ranging from -10.1 to -11.0 ‰) than in that of the bison. $\delta^{18}O$ values range from -7.0 to -5.7 ‰ for bison (mean = -6.5 ± 0.4 ‰) and -8.2 to -5.0 ‰ for reindeer (mean = -6.6 ± 1.3 ‰). Mann-Whitney U tests show there is no significant difference between bison and reindeer $\delta^{13}C_{enamel}$ (W=25, $p > 0.05$) or $\delta^{18}O$ (W=40, $p > 0.05$).

Data conversions:

To facilitate direct comparison, $\delta^{13}C_{coll}$ and $\delta^{13}C_{enamel}$ were converted to $\delta^{13}C_{diet}$ by assuming a diet to collagen offset of +5‰, and diet to carbonate offset of +14‰ following Lee Thorpe *et al.* 1989 and Cerling and Harris 1999 (Figure 4, supplementary file 3). No significant difference was seen between estimated $\delta^{13}C_{diet}$ values reconstructed from tooth enamel and bone collagen for either bison (Mann-Whitney U test, W=44, $p > 0.05$) or reindeer (Mann-Whitney U test, W=46, $p > 0.05$).

To facilitate palaeo-drinking water estimates, we first converted $\delta^{18}O_{enamel}$ results from the V-PDB to the V-SMOW scale following (Coplen, 2011):

$$\delta^{18}O_{VSMOW} = 1.03091*\delta^{18}O_{VPDB}+30.91 \quad [1]$$

To estimate drinking water $\delta^{18}O$ for bison, we invert the empirically derived relationship between tooth enamel carbonate $\delta^{18}O$ ($\delta^{18}O_{carb}$) and local environmental water ($\delta^{18}O_{envi}$) given in Hoppe (2006) using the method recommended by Pryor *et al.* (2014):

$$\delta^{18}O_{envi} = (\delta^{18}O_{carb} - 30.057\ (\pm 0.58))/0.703\ (\pm 0.12) \quad [2]$$

For reindeer, we use a modified version of the relationship between skeletal phosphate $\delta^{18}O$ ($\delta^{18}O_{phos}$) and local environmental water ($\delta^{18}O_{envi}$) presented in Longinelli *et al.* (2003). Longinelli *et al.*'s dataset includes both tooth and bone samples and we note the relationship between $\delta^{18}O_{phos}$ and $\delta^{18}O_{envi}$ differs between the two sample types. In our study we have analysed only tooth enamel, so we derive a relationship between $\delta^{18}O_{phos}$ and $\delta^{18}O_{envi}$ based only on the tooth enamel data reported in Longinelli *et al.* (2003). Using inverted least-square regression (Pryor *et al.* 2014) the relationship between $\delta^{18}O_{envi}$ and $\delta^{18}O_{phos}$ is given by:

$$\delta^{18}O_{envi} = (\delta^{18}O_{phos} - 20.117(\pm 0.34)) / 0.683\ (\pm 0.11) \quad [3]$$

As this equation was derived for $\delta^{18}O_{phos}$, and we analysed the carbonate phase of enamel a conversion between the two bioapatite structures is required. $\delta^{18}O_{carb}$ covaries strongly with $\delta^{18}O_{phos}$ and we estimate $\delta^{18}O_{phos}$ for our results following Zazzo *et al.* (2004, equation 2):

$$\delta^{18}O_{phos} = (0.973 * \delta^{18}O_{carb}\ (\pm 0.01)) - 8.121(\pm 0.36) \quad [4]$$

The calculated palaeo-$\delta^{18}O_{envi}$ values are assumed to provide a satisfactory approximation of local palaeo-precipitation $\delta^{18}O$ ($\delta^{18}O_{precip}$). Assuming the empirical relationship that exists in the modern environment between $\delta^{18}O_{precip}$ and mean annual air temperature (e.g. Rozanski et al, 1993) is applicable to the past, palaeo-$\delta^{18}O_{precip}$ can be used to estimate palaeo-air temperature. However, this observed relationship is geographically variable. Here, we use the relationship derived from European data originating at sites below 500m of altitude by Pryor *et al.* (2014):

$$\text{Temperature (°C)} = (\delta^{18}O_{precip} - 13.74\ (\pm 0.16)) / 0.53\ (\pm 0.08) \quad [5]$$

Each data conversion has an associated uncertainty. We use the error propagation tool presented in Pryor *et al.* (2014) to calculate the compound uncertainty associated with our palaeo-$\delta^{18}O_{precip}$ and palaeotemperature estimates.

Discussion

Carbon:

The bone collagen and tooth enamel $\delta^{13}C$ values confirm a C_3 plant-based diet, typical of the steppe-tundra grasslands of the Late Pleistocene. The significantly higher reindeer $\delta^{13}C_{coll}$ relative to bison $\delta^{13}C_{coll}$ (Figure 2) follows a pattern often observed in Late Pleistocene contexts, where reindeer have higher $\delta^{13}C_{coll}$ than other contemporary herbivores including bovids, equids and other cervids such as red deer (e.g. Fizet *et al.* 1995; Drucker *et al.* 2003; Stevens *et al.* 2009). This has been attributed to their consumption of lichens, which exhibit higher $\delta^{13}C$ values than sympatric C_3 vascular plants (Park and Epstein, 1960; Maguas and Brugnoli, 1996; Drucker *et al.* 2001). The overlap of bison and reindeer $\delta^{13}C_{enamel}$ values potentially indicates ecological niche overlap and suggests a lichen component in the bovid diet which is not obvious from the $\delta^{13}C_{coll}$ values. Lichens are a rich source of carbohydrate and poor source of protein. As $\delta^{13}C_{enamel}$ reflect whole diet $\delta^{13}C$ (Ambrose and Norr, 1993; Tieszen and Fagre, 1993) low lichen consumption is more likely to be visible in $\delta^{13}C_{enamel}$ than in $\delta^{13}C_{coll}$, which primarily reflect dietary protein $\delta^{13}C$ (Krueger & Sullivan, 1984). Overlap between bovid and reindeer dietary niche and potential lichen consumption by bovids has previously been suggested in other Late Pleistocene contexts (Bocherens *et al.* 2015; Julien *et al.* 2012; Reade *et al.,* 2020b), and has been observed also in some modern bison populations (Larter and Gates, 1991). Overlapping reindeer and bison $\delta^{13}C_{enamel}$ values could also be produced by species-specific differences in tooth growth and enamel mineralisation rates. A full year of tooth growth is represented in the majority of analysed bison teeth, such that the derived dietary signal will represent an average spanning this time period. In comparison, the majority of the analysed reindeer teeth formed between late spring and autumn, and thus represent a dietary signature biased toward the summer months (see supplementary file 2). In modern reindeer populations, lichen is less heavily relied upon in summer compared to in the winter (Holleman *et al.* 1979). Together tooth and bone $\delta^{13}C$ data suggest the BBC MAZ was deposited at a time when steppe-tundra grasslands likely covered the local landscape.

Nitrogen:

Both the reindeer and bison $\delta^{15}N$ values are high for herbivore species. Notably the reindeer $\delta^{15}N$ values are higher than all published Late Pleistocene reindeer $\delta^{15}N$ values from the UK (Figure 5, supplementary file 4). Comparatively high reindeer $\delta^{15}N$ values are relatively rare in Late Pleistocene Europe but are found in reindeer from southwest France during MIS 3 (Figure 5, Bocherens *et al.* 2014). From the 97 Late Pleistocene European bison we found in the published literature, only two examples have $\delta^{15}N$ values comparative to those observed at Banwell Bone Cave (Figure 6, supplementary file 5). One is from southwest France (Les Pradelles / Marillac $\delta^{15}N$ = 9.3‰, Fizet *et al.* 1995) and another from Crimea, (Emine-Bair-Khosar, $\delta^{15}N$ = 9.1‰, Gasiorowski *et al.* 2014); both date to MIS 3. Thus, the range in bison $\delta^{15}N$ observed in the Banwell Bone Cave material is extremely rare for Late Pleistocene Europe.

Two possible explanations exist for such high herbivore $\delta^{15}N$ values. First, elevated $\delta^{15}N$ can be produced by nutritional stress. However, for such high bone collagen $\delta^{15}N$ to be solely indicative of nutritional stress long periods of fasting/starvation for both reindeer and bison would be required. Given the abundance of the bison and reindeer remains at Banwell Bone Cave and at other site containing the BBC MAZ, it seems that the environment was suitable for long-term co-existence of the two species and does not suggest the environment was so nutritionally poor as to result in significant periods of starvation. Furthermore, where comparable reindeer $\delta^{15}N$ values are seen in southwest France during MIS 3 (Bocherens *et al.* 2014), reindeer were also extremely abundant, often being the dominant fauna in zooarchaeological assemblages (Mellars, 2004). Such abundance is unlikely in an environment in which animals are starving.

The alternative and most parsimonious explanation is that the elevated reindeer and bison $\delta^{15}N$ values are linked to environmental conditions. Plant to herbivore $\delta^{15}N$ fractionation has been shown to be constant (Männel *et al.* 2007; Kuitems *et al.* 2015; Bocherens *et al.* 2014), and relationships between herbivore $\delta^{15}N$ and temperature and/or aridity have been shown to be driven by the $\delta^{15}N$ of the plants the animals consume (Murphy and Bowman, 2006; Hartman, 2011). Today, high plant $\delta^{15}N$ are linked to low precipitation (aridity) and higher temperatures. However, in southwest France, the high MIS 3 reindeer $\delta^{15}N$ values were found alongside elevated $\delta^{15}N$ values in contemporary herbivores and carnivores and were interpreted as being indicative of an environment for which no modern analogue is known. The contemporary palaeoclimate proxies indicted relatively low temperatures, thus the elevated $\delta^{15}N$ values were ascribed to aridity (Fizet *et al.* 1995; Richards *et al.* 2008; Bocherens *et al.* 2014). Similarly, the beetle, pollen and plant macrofossil data from BBC MAZ sites, along with the bison and reindeer oxygen isotope data (see below) do not indicate very high temperatures (Coope and Angus, 1975; Coope *et al.* 1997; Maddy *et al.* 1998). Thus, the Banwell Bone Cave reindeer and bison $\delta^{15}N$ likely also indicate arid conditions. The rarity of comparable bison $\delta^{15}N$ values from Late Pleistocene Europe support the notion that the BBC MAZ was deposited under non-analogue environmental conditions.

Oxygen:

Mean $\delta^{18}O_{enamel}$ values are similar for both species (-6.5 ± 0.4 ‰ for bison and -6.5 ± 1.3 ‰ for reindeer). As with the $\delta^{13}C_{enamel}$ and $\delta^{15}N_{coll}$, reindeer $\delta^{18}O_{enamel}$ is more variable than that of bison, ranging from -8.2 to -5.0 ‰, compared to -7.0 to -5.7 ‰. The higher variability in the reindeer $\delta^{18}O_{enamel}$ is likely attributable to the different time periods each tooth represents, with the bison $\delta^{18}O_{enamel}$ values relating to approximately a full annual cycle, and the reindeer $\delta^{18}O_{enamel}$ signatures being biased toward the summer months (Supplementary file 2).

Using the discussed data conversions, we estimate a mean palaeo-$\delta^{18}O_{precip}$ of -8.3 ± 1.3 ‰ from the bison data and -7.0 ± 1.6 ‰ from the reindeer data. For individual samples, palaeo-$\delta^{18}O_{precip}$ estimates range from -9.1‰ to -7.1‰ for bison and -9.3‰ to -4.6‰ for reindeer, with associated uncertainties between 2.4‰ and 2.8‰ (Supplementary file 2). For comparison, modern mean annual $\delta^{18}O_{precip}$ in the UK ranges from approximately -8.5 to -6.5 ‰ (IAEA GNIP). Estimated palaeo-$\delta^{18}O_{precip}$ therefore indicates similar climatic conditions to the present day, i.e. temperate conditions, assuming that $\delta^{18}O_{precip}$ can be treated as a function of temperature. The palaeo-$\delta^{18}O_{precip}$ estimates made from the reindeer data include values higher than might be expected, and if taken at face value could indicate a climate far warmer than present. However, this conjecture should be treated cautiously. As the majority of our reindeer samples are believed to have formed only over the summer months, the occurrence of higher palaeo-$\delta^{18}O_{precip}$ estimates are not actually surprising. In fact, an estimated mean $\delta^{18}O_{precip}$ of -4.6‰ is not that dissimilar to modern mean monthly maximum values for the UK of approximately -4.5 to -2.0 ‰ (IAEA, GNIP). Regardless, the $\delta^{18}O_{enamel}$ results only show evidence of $\delta^{18}O_{precip}$ values associated with temperate environments, and we find no indication of colder conditions.

Using species mean palaeo-$\delta^{18}O_{precip}$ estimates we derive palaeo-temperature estimates of 10.3 ± 2.5 ºC from the bison data and 12.8 ± 3.1 ºC from the reindeer data. These temperatures are comparable to the recent (1981-2010) 30-year mean annual air temperature for southwest England of 10.5ºC (https://www.metoffice.gov.uk/). Similarities are also apparent between our palaeotemperature estimates and others from Late Pleistocene interglacial deposits. Coleoptera-based estimates from lithofacies B at Cassington, which contained a bison-reindeer fauna attributed to the BBC MAZ and has been dated to interstadial MIS 5a, range from 17 - 18 ºC for the warmest month to -4 – 4 ºC for the coldest month (Maddy,1998; Penkman 2011, 2013). Comparatively, Coleoptera-based temperature estimates from lithofacies D at the site, correlated to stadial MIS 4, range from 7 - 11 ºC for the warmest month to -30 – -10 ºC for the coldest month (Maddy,1998). Likewise, molluscs from the organic silts at Willment's Pit, Isleworth, which also contains mammalian fauna assigned to the BBC MAZ and tentatively correlated to interstadial MIS 5c, suggest mean July temperature of no lower than 15ºC (Kerney, 1982; Penkman 2011, 2013). Based on these independent data, our palaeo-temperature estimates clearly fall within the expected range of a Late Pleistocene interstadial climate, and outside of the range expected of a Late Pleistocene stadial climate.

Conclusion:

The results of the stable isotope analyses conducted in this study confirm that the Banwell Bone Cave faunal assemblage relates to a temperate rather than cold environment. Our study is the first to derive palaeoclimate information directly from the fauna itself, providing evidence that the bison-reindeer fauna, typically thought of as a cold climate assemblage, existed under temperate climate conditions at Banwell Bone Cave. Our results support the correlation of the BBC MAZ to interstadial MIS 5a rather than to the succeeding stadial of MIS 4.

The $\delta^{13}C$ values of bison and reindeer fauna indicate C_3 plant-based diets, typical of the steppe-tundra grasslands of the Late Pleistocene. Lichen appears to have been important for reindeer and potentially also a component of the bison diet, thus indicating some possible ecological niche overlap. The $\delta^{15}N$ values of both bison and reindeer are unusually high and likely represent arid conditions within a temperate environment. Mean palaeo-temperature estimates derived from bison and reindeer tooth enamel $\delta^{18}O$ indicate that temperate conditions similar to the present day prevailed during the deposition of the fauna at Banwell Bone Cave.

Confirmation that fauna from the Banwell Bone Cave lived in conditions consistent with the temperate interstadial MIS 5a rather than the succeeding cool stadial MIS 4, lends support to the hypothesis that the BBC MAZ represents an island fauna and that a mismatch between British and other European mammal faunas existed during MIS 5 (Gilmour *et al.* 2007). Finally, this study provides a cautionary tale for the use of particular species as climatic indicators. The presence or absence of geographical barriers may substantially influence the species composition of a faunal assemblage to the extent that species may have existed in environments beyond their current environmental limits, or in environments for which there are no modern analogues.

Acknowledgments:

RS and HR are funded by an ERC consolidator grant to RS (ERC-CG-617777: UP-North). We thank Delfin Weis and Elizabeth Rutherford for assistance with sample preparation and James Rolfe for assistance with analysis. We are grateful to Delphine Fremondeau for assistance with ZooMs analysis. Rebecca Kearney is thanked for assistance with formatting. We are very grateful to Andy Currant and the late Roger Jacobi for providing newly excavated material for analysis and for encouraging us to undertake research on the Late Pleistocene fauna of the British Isles. The excavations at Banwell Bone Cave were conducted as part of the Ancient Human Occupation of Britain (AHOB) Project funded by the Leverhulme Trust.

Bibliography:

Aguilar, A., Giménez, J., Gómez–Campos, E., Cardona, L., Borrell, A., 2014. $\delta^{15}N$ value does not reflect fasting in mysticetes. PLoS One 9(3), e92288.

Ambrose, S. H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J., Grupe, G. (Eds.), Prehistoric human bone: Archaeology at the molecular level. Springer, New York, pp. 1-37.

Amundson R., Austin A. T., Schuur E. A. G., Yoo K., Matzek V., Kendall C., Uebersax, A., Brenner, D. Baisden, W.T., 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochemical Cycles 17(1), 1031.

Ashton, N.M., Lewis, S.G.,Stringer, C.B. (eds) The Ancient Human Occupation of Britain. Elsevier, Amsterdam.

Austin A. T., Vitousek P. M., 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113(4), 519–529.

Balasse, M., Ambrose, S.H., Smith, A.B., Price, T.D., 2002. The seasonal mobility model for prehistoric herders in the South-Western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. Journal of Archaeological Science 29(9), 917–932.

Bocherens, H., Drucker, D., 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. International Journal of Osteoarchaeology 13(1–2), 46–53.

Bocherens, H., Drucker, D.G., Germonpré, M., Lázničková-Galetová, M., Naito, Y.I., Wissing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C, ^{15}N, ^{34}S) of bone collagen. Quaternary International 359, 211-228.

Bocherens, H., Drucker, D.G., Madelaine, S., 2014. Evidence for a ^{15}N positive excursion in terrestrial foodwebs at the Middle to Upper Palaeolithic transition in south-western France: implications for early modern humans. Journal of Human Evolution 69, 31-43.

Bowes, R. E., Lafferty, M. H., Thorp, J. H., 2014. Less means more: nutrient stress leads to higher $\delta^{15}N$ ratios in fish. Freshwater Biology 59, 1926–1931.

Britton, K., Pederzani, S., Kindler, L., Roebroeks, W., Gaudzinski-Windheuser, S., Richards, M. P., Tütken, T., 2019. Oxygen isotope analysis of Equus teeth evidences early Eemian and early Weichselian palaeotemperatures at the Middle Palaeolithic site of Neumark-Nord 2, Saxony-Anhalt, Germany. Quaternary Science Reviews 226, 106029.

Bryant, I.D., Holyoak, D.T., Moseley, K.A., 1983. Late Pleistocene deposits at Brimpton, Berkshire, England. Proceedings of the Geologists' Association 94(4), 321–343.

Bryant, J.D. Froelich, P., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimimica et Cosmochimica Acta 59(21), 4523-4537.

Cerling, T. E., Harris, J. M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120(3), 347-363.

Cherel, Y., Hobson, K. A., Baiileul, F., Groscolas, R., 2005. Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. Ecology 86(11), 2881–2888.

Coope, G.R., Angus, R.B., 1975. An ecological study of a temperate interlude in the Middle of the Last Glaciation, Based on Fossil Coleoptera from Isleworth, Middlesex. Journal of Animal Ecology 44(2), 365-391.

Coope, G.R., Gibbard, P.L., Hall, A.R., Preece, R.C., Robinson, J.E., Sutcliffe, A.J., 1997. Climatic and environmental reconstructions based on fossil assemblages from Middle Devensian (Weichselian) deposits of the River Thames at South Kensington, Central London, UK. Quaternary Science Reviews 16(10), 1163–1195.

Coplen, T. B., 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Communications in Mass Spectrometry 25(17), 2538–2560.

Coplen, T.B., 1995. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances — (technical report). Geothermics 24(5-6), 707-712.

Craine, J. M., Elmore, A. J., Aidar, M. P. M., Bustamante, M., Dawson, T. E., Hobbie, E. A., *et al.* 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytologist 183(4), 980–992.

Craine, J.M., Brookshire, E.N.J., Cramer, M.D., Hasselquist, N.J., Koba, K., Marin-Spiotta, E., Wang, L., 2015. Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. Plant and Soil 396, 1– 26.

Currant, A., Jacobi, R., 1997. Vertebrate faunas of the British Late Pleistocene and the chronology of human settlement. Quaternary Newsletter 82, 1–8.

Currant, A., Jacobi, R., 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. Quaternary Science Reviews 20, 1707–1716.

Currant, A., Jacobi, R., 2002. Human presence and absence in Britain during the early part of the Late Pleistocene. In: Tuffreau, A., Roebroeks, W. (Eds), Le Denier Interglaciaire et les occupations du Paléolithique moyen. Publications du CERP no. 8, Universite´ des Sciences et technologies de Lille, Villeneuve-d'Ascq, 105–113.

Currant, A.P., Jacobi, R.M., 2011. The mammalian faunas of the British late Pleistocene. In: Ashton, N.M., Lewis, S.G., Stringer, C.B. (Eds.), The Ancient Human Occupation of Britain. Elsevier, Amsterdam, pp. 165-180.

d'Angela, D., Longinelli, A., 1990. Oxygen isotopes in living mammal's bone phosphate: further results. Chemical Geology: Isotope Geoscience section 86, 75–82.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. Nature 317(6040), 806-809.

Doi, H., Akamatsu, F., González, A.L., 2017. Starvation effects on nitrogen and carbon stable isotopes of animals: An insight from meta-analysis of fasting experiments. Royal Society Open Science 4(8), 170633.

Drucker, D., Bocherens, H., Bridault, A.,Billiou, D., 2003. Carbon and nitrogen isotopic composition of red deer (*Cervus elaphus*) collagen as a tool for tracking palaeoenvironmental change during the Late-Glacial and Early Holocene in the northern Jura (France). Palaeography, Palaeoclimatology, Palaeoecology 195(3-4), 375-388.

Drucker, D., Bocherens, H., Pike-Tay, A., Mariotti, A., 2001. Isotopic tracking of seasonal dietary change in dentine collagen: preliminary data from modern caribou. Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science 333(5), 303-309.

Drucker, D.G., Bridault, A., Cupillard, C., Hujic, A., Bocherens, H., 2011. Evolution of habitat and environment of red deer *(Cervus elaphus)* during the Late-glacial and early Holocene in eastern France (French Jura and the western Alps) using multi-isotope analysis ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, $\delta^{34}S$) of archaeological remains. Quaternary International 245(2), 268-278.

Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E., Bocherens, H., 2008. Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266(1-2), 69–82.

Fabre, M., Lécuyer, C., Brugal, J.P., Amiot, R., Fourel, F., Martineau, F., 2011. Late Pleistocene climatic change in the French Jura (Gigny) recorded in the $\delta^{18}O$ of phosphate from ungulate tooth enamel. Quaternary Research 75(3), 605-613.

Fizet, M., Mariotti, A., Bocherens, H., 1995. Effect of Diet, Physiology and Climate on Carbon and Nitrogen Stable Isotopes of Collagen in a Late Pleistocene anthropic palaeoecosystem: Marillac, Charente, France. Journal of Archaeological Science 22(1), 67-79.

Fleming, A.H., Kellar, N.M., Allen, C.D., Kurle, C.M., 2018. The utility of combining stable isotope and hormone analyses in marine megafauna research. Frontiers in Marine Science 5, 338.

Fricke, H.C., D'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126, 91-99.

Fuller, B.T., Fuller, J.L., Sage, N.E., Harris, D.A., O'Connell, T.C., Hedges, R.E., 2005. Nitrogen balance and $\delta^{15}N$: why you're not what you eat during nutritional stress. Rapid Communications in Mass Spectrometry 19(18), 2497–2506.

Gannes, L.Z., Del Rio, C.M., Koch, P., 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comparative biochemistry and physiology Part A: Molecular & integrative physiology 119(3), 725–737.

Gąsiorowski, M., Hercman, H., Ridush, B., Stefaniak, K., 2014. Environment and climate of the Crimean Mountains during the Late Pleistocene inferred from stable isotope analysis of red deer (*Cervus elaphus*) bones from the Emine-Bair-Khosar Cave. Quaternary International 326, 243-249.

Gilmour, M., Currant, A.P., Jacobi, R.M., Stringer, C.B., 2007. Recent TIMS dating results from British Late Pleistocene vertebrate faunal localities: Context and interpretation. Journal of Quaternary Science 22(8), 793–800.

Gomez-Campos, E., Borrell, A., Aguilar, A., 2011. Nitrogen and carbon stable isotopes do not reflect nutritional condition in the striped dolphin. *Rapid Communication in Mass Spectrometry* 25(9), 1343–1347.

Handley, L. L., Austin, A. T., Stewart, G. R., Robinson, D., Scrimgeour, C. M., Raven, J. A., Heaton, T.H.E., Schmidt, S., 1999. The ^{15}N natural abundance ($\delta^{15}N$) of ecosystem samples reflects measures of water availability. Australian Journal of Plant Physiology 26(2), 185–199.

Hartman, G., 2011. Are elevated $\delta^{15}N$ values in herbivores in hot and arid environments caused by diet or animal physiology? Functional Ecology 25, 122-131.

Heaton, T.H.E., 1999. Spatial, species, and temporal variations in the $^{13}C/^{12}C$ ratios of C_3 plants: implications for palaeodiet studies. Journal of Archaeological Science 26(6), 637-649.

Hedges, R.E.M., Stevens, R.E., Kock, P.L., 2005. Isotopes in bones. In: Leng, M.J. (Ed), Isotopes in palaeoenvironmental research, Vol. 10. Springer, Dordrecht, pp. 117-145.

Higham, T. G., Jacobi, R. M., Bronk Ramsey, C., 2006. AMS radiocarbon dating of ancient bone using ultrafiltration. Radiocarbon 48(2), 179–195.

Hobson, K. A., Alisauskas, R. T., Clark, R. G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analysis of diet. Condor 95(2), 388–394.

Hoefs, J., 2009. Stable isotope geochemistry. Springer, Berlin.

Holleman, D. F., Luick,. R., White, R. G., 1979. Lichen intake estimates for reindeer and caribou during winter. Journal of Wildlife Management 43, 192-201.

Hoppe, K.A. 2006. Correlation between the oxygen isotope ratio of North American bison teeth and local waters: implication for paleoclimatic reconstructions. Earth Planetary Science Letters 244 (1-2), 408-417.

IAEA/WMO, 2019. Global Network of Isotopes in Precipitation. The GNIP Database. Accessible at: https://nucleus.iaea.org/wiser

Jones, J.R., Richards, M.P., Reade, H., de Quirós, F.B., Marín-Arroyo, A.B., 2019. Multi-Isotope investigations of ungulate bones and teeth from El Castillo and Covalejos caves (Cantabria, Spain): Implications for paleoenvironment reconstructions across the Middle-Upper Palaeolithic transition. Journal of Archaeological Science: Reports 23, 1029-1042.

Jones, J.R., Richards, M.P., Straus, L.G., Reade, H., Altuna, J., Mariezkurrena, K., Marín-Arroyo, A.B., 2018. Changing environments during the Middle-Upper Palaeolithic transition in the eastern Cantabrian Region (Spain): direct evidence from stable isotope studies on ungulate bones. Scientific Reports 8, 14842.

Julien, M.A., Bocherens, H., Burke, A., Drucker, D.G., Patou-Mathis, M., Krotova, O., Péan, S., 2012. Were European steppe bison migratory? ^{18}O, ^{13}C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. Quaternary International 271, 106-119.

Keen, D.H., 1995. Raised beaches and sea-levels in the English Channel in the Middle and Late Pleistocene: Problems of interpretation and implications for the isolation of the British Isles. In: Preece, R.C. (Ed.), Island Britain: A Quaternary Perspective. Geological Society of London Special Publication 96, 63–74.

Kerney, M.P., Gibbard, P.L., Hall, A.R. and Robinson, J.E., 1982. Middle devensian river deposits beneath the 'upper floodplain' terrace of the river Thames at Isleworth, west London. Proceedings of the Geologists' Association 93(4), 385-393.

Kohn, M.J., 1996. Predicting animal $\delta^{18}O$: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60(23), 4811-4829.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proceedings of the National Academy of Science 107(46), 19691-19695.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. Geochimica et Cosmochimica Acta 60(20), 3889-3896.

Krueger, H.W., Sullivan, C.H., 1984. Models for carbon isotope fractionation between diet and bone. In: Turnland, J., Johnson, P.E. (Eds.), Stable Isotopes in Nutrition. American Chemical Society, Washington DC, pp. 205-222.

Kuitems, M., van Kolfschoten, T. and van der Plicht, J., 2015. Elevated $\delta^{15}N$ values in mammoths: a comparison with modern elephants. Archaeological and Anthropological Sciences 7(3), 289–295.

Larter, N.C., Gates, C.C., 1991. Diet and habitat selection of wood bison in relation to seasonal-changes in forage quantity and quality. Canadian Journal of Zoology 69(10), 2677-2685.

Lee-Thorp, J. A., Sealy, J. C., van der Merwe, N. J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite and their relationship to diet. Journal of Archaeological Science 16(6), 585-599.

Lohuis, T. D., Harlow, H. J., Beck, T. D. I., 2007. Hibernating black bears (*Ursus americanus*) experience skeletal muscle protein balance during winter anorexia. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology 147(1), 20–28.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. Nature

230(5291), 241–242.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? *Geochimica et Cosmochimica Acta* 48(2), 385-390.

Longinelli, A., Iacumin, P., Davanzo, S., Nikolaev, V., 2003. Modern reindeer and mice: revised phosphate–water isotope equations. Earth and Planetary Science Letters 214(3-4), 491-498.

Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth and Planetary Science Letters 75(1), 29-36.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta 48(8),1689-1693.

Maddy, D., Lewis, S.G., Scaife, R.G., Bowen, D.Q., Coope, G.R., Green, C.P., Hardaker, T., Keen, D.H., Rees-Jones, J., Parfitt, S., Scott, K., 1998. The Upper Pleistocene deposits at Cassington, near Oxford, England. Journal of Quaternary Science: Published for the Quaternary Research Association 13(3), 205-231.

Maguas, C., Brugnoli, E. 1996. Spatial variation in carbon isotope discrimintation across the thalli of several lichen species. Plant, Cell & Environment 19(4), 437- 446.

Männel, T.T., Auerswald, K., Schnyder, H., 2007. Altitudinal gradients of grassland carbon and nitrogen isotope composition are recorded in the hair of grazers. Global Ecology and Biogeography 16(5), 583-592.

Martinelli, L.A., Piccolo, M.D.C., Townsend, A.R., Vitousek, P.M., Cuevas, E., McDowell, W., Robertson, G.P., Santos, O.C., Treseder, K., 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. Biogeochemistry 46(1-3), 45-65.

Mekota, A.M., Grupe, G., Ufer, S. and Cuntz, U., 2006. Serial analysis of stable nitrogen and carbon isotopes in hair: monitoring starvation and recovery phases of patients suffering from anorexia nervosa. Rapid Communications in Mass Spectrometry 20(10), 1604-1610

Mellars, P.A., 2004. Reindeer specialization in the early Upper Palaeolithic: the evidence from south west France. Journal of Archaeological Science 31(5), 613-617.

Murphy, B.P., Bowman, D.M., 2006. Kangaroo metabolism does not cause the relationship between bone collagen $\delta^{15}N$ and water availability. Functional Ecology 20(6), 1062-1069.

Newsome, S. D., Clementz, M. T., Koch, P. L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, 26(3), 509–572.

Pardo L. H., Templer P. H., Goodale C. L., Duke S., Groffman P. M., Adams M. B., *et al.* 2006. Regional assessment of N saturation using foliar and root $\delta^{15}N$. Biogeochemistry 80, 143–171.

Park, R., Epstein, S., 1960. Carbon isotope fractionation during photosynthesis. Geochimica et Cosmochimica Acta 21, 110-126.

Pederzani, S., Britton, K., 2019. Oxygen isotopes in bioarchaeology: Principles and applications, challenges and opportunities. Earth-science reviews 188, 77-107.

Penkman, K.E.H., Preece, R.C., Bridgland, D.R., Keen, D.H., Meijer, T., Parfitt, S.A. *et al.* 2011. A chronological framework for the British Quaternary based on Bithynia opercula . Nature 476, 446-449.

Penkman, K.E.H., Preece, R.C., Bridgland, D.R., Keen, D.H., Meijer, T., Parfitt, S.A. *et al.* 2013. An aminostratigraphy for the British Quaternary based on Bithynia opercula. Quaternary Science Reviews 61, 111-134.

Podlesak, D.W., Torregrossa, A.M., Ehleringer, J.R., Dearing, M.D., Passey, B.H., Cerling, T.E., 2008. Turnover of oxygen and hydrogen isotopes in the body water, CO2, hair, and enamel of a small mammal. Geochimica et Cosmochimica Acta 72, 19-35.

Polischuk, S.C., Hobson, K.A., Ramsay, M.A., 2001. Use of stable-carbon and-nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology 79(3), 499-511.

Pryor, A.J., Stevens, R.E., O'Connell, T.C., Lister, J.R., 2014. Quantification and propagation of errors when converting vertebrate biomineral oxygen isotope data to temperature for palaeoclimate reconstruction. Palaeogeography, palaeoclimatology, palaeoecology 412, 99-107.

Reade, H., O'Connell, T.C., Barker, G., Stevens, R.E., 2016. Pleistocene and Holocene palaeoclimates in the Gebel Akhdar (Libya) estimated using herbivore tooth enamel oxygen isotope compositions. Quaternary International 404, 150-162.

Reade, H., Tripp, J.A., Charlton, S., Grimm, S., Sayle, K.L., Fensome, A., Higham, T.F., Barnes, I., Stevens, R.E., 2020a. Radiocarbon chronology and environmental context of Last Glacial Maximum human occupation in Switzerland. Scientific Reports 10(1), 4694.

Reade, H., Tripp, J.A., Charlton, S., Grimm, S., Leesch, D., Müller, W., Sayle, K.L., Fensome, A., Higham, T.F., Barnes, I., Stevens, R.E., 2020b. Deglacial landscapes and the Late Upper Palaeolithic of Switzerland. Quaternary Science Reviews 239, 106372.

Richards, M.P., Taylor, G., Steele, T., McPherron, S.P., Soressi, M., Jaubert, J., Orschiedt, J., Mallye, J.B., Rendu, W., Hublin, J.J., 2008. Isotopic dietary analysis of a Neanderthal and associated fauna from the site of Jonzac (Charente-Maritime), France. Journal of Human Evolution 55, 179-185.

Rozanski, K.L., Araguás-Araguás, L., Conginatini, R., 1993. Isotopic Patterns in Modern Global Precipitation. In: Swart, P.K., Lohmann, K.C., Mckenzie, J., Savin, S. (Eds.), Climate Change in Continental Isotopic Records. Geophysical Monograph Series Vol. 78, American Geophysical Union, Washington DC, pp. 1-36.

Schreve, D.C., 1997. Mammalian biostratigraphy of the later Middle Pleistocene in Britain. Unpublished Doctoral thesis, University College London.

Sponheimer, M., Lee-Thorp, J.A., 2003. Using carbon isotope data of fossil bovid communities for palaeoenvironmental reconstruction: research articles: human origins research in South Africa. South African Journal of Science 99(5), 273-275.

Stevens, R.E., Hedges, R.E., 2004. Carbon and nitrogen stable isotope analysis of northwest European horse bone and tooth collagen, 40,000 BP–present: Palaeoclimatic interpretations. Quaternary Science Reviews 23(7-8), 977-991.

Stevens, R.E., Hermoso-Buxán, X.L., Marín-Arroyo, A.B., González-Morales, M.R., Straus, L.G., 2014. Investigation of Late Pleistocene and Early Holocene palaeoenvironmental change at El Mirón cave (Cantabria, Spain): Insights from carbon and nitrogen isotope analyses of red deer. Palaeogeography, Palaeoclimatology, Palaeoecology, 414, 46-60.

Stevens, R.E., Jacobi, R., Street, M., Germonpré, M., Conard, N.J., Münzel, S.C. and Hedges, R.E., 2008. Nitrogen isotope analyses of reindeer (*Rangifer tarandus*), 45,000 BP to 9,000 BP: Palaeoenvironmental reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology 262(1-2), 32-45.

Stevens, R.E., O'Connell, T.C., Hedges, R.E., Street, M., 2009. Radiocarbon and stable isotope investigations at the Central Rhineland sites of Gönnersdorf and Andernach-Martinsberg, Germany. Journal of Human Evolution 57(2), 131-148.

Szpak, P., 2014. Complexities of nitrogen isotope biogeochemistry in plant-soil systems: implications for the study of ancient agricultural and animal management practices. Frontiers in Plant Science 5(288), 1-19.

Szpak, P., Gröcke, D.R., Debruyne, R., MacPhee, R.D., Guthrie, R.D., Froese, D., Zazula, G.D., Patterson, W.P., Poinar, H.N., 2010. Regional differences in bone collagen $\delta^{13}C$ and $\delta^{15}N$ of Pleistocene mammoths: implications for paleoecology of the mammoth steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 286(1-2), 88-96.

Tieszen, L.L., Fagre, T., 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite and soft tissues. In: Lambert, J., Grupe, G. (Eds.), Prehistoric Human Bone: Archaeology at the Molecular Level. Springer-Verlag, New York, 121-155.

Wißing, C., Rougier, H., Crevecoeur, I., Germonpré, M., Naito, Y.I., Semal, P., Bocherens, H., 2016. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. Quaternary International 411, 327-345.

Zazzo, A., Lécuyer, C., Sheppard, S.M., Grandjean, P., Mariotti, A., 2004. Diagenesis and the reconstruction of paleoenvironments: a method to restore original $\delta^{18}O$ values of carbonate and phosphate from fossil tooth enamel. Geochimica et Cosmochimica Acta 68(10), 2245-2258.

Figure 1: Sites in the British Isles containing a Banwell Bone Cave mammal assemblage-zone fauna. Red star = Banwell Bone Cave; 1 Stump Cross Cave; 2 Windy Knoll Cave; 3 Steetley Wood Cave; 4 Ash Tree Cave; 5 The Arch (aka Lion's Mouth); 6 Tattershall Castle; 7 Cassington; 8 Bosco's Den; 9 Port Eynon Point Cave; 10 Pen Park Quarry; 11 Kew Bridge Station; 12 Willment's Pit, Isleworth; 13 Windsor; 14 Limekiln Hill Quarry; 15 Brean Down; 16 Bleadon Quarry; 17 Picken's Hole; 18 Hyena Den; 19 Tornewton Cave. (After Current and Jacobi, 2001).

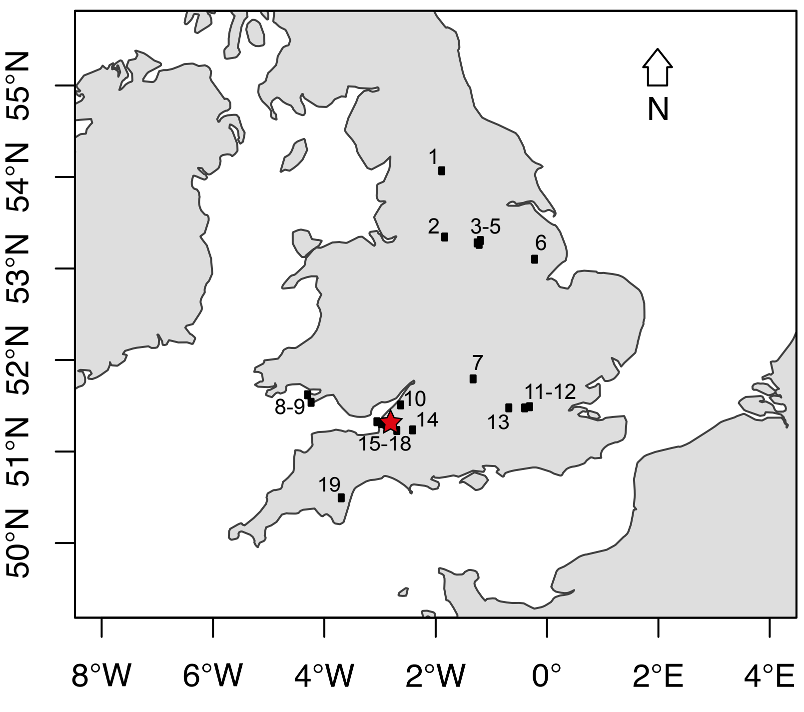


Figure 2: Banwell Bone Cave bison and reindeer bone collagen $\delta^{13}C$ and $\delta^{15}N$ results.

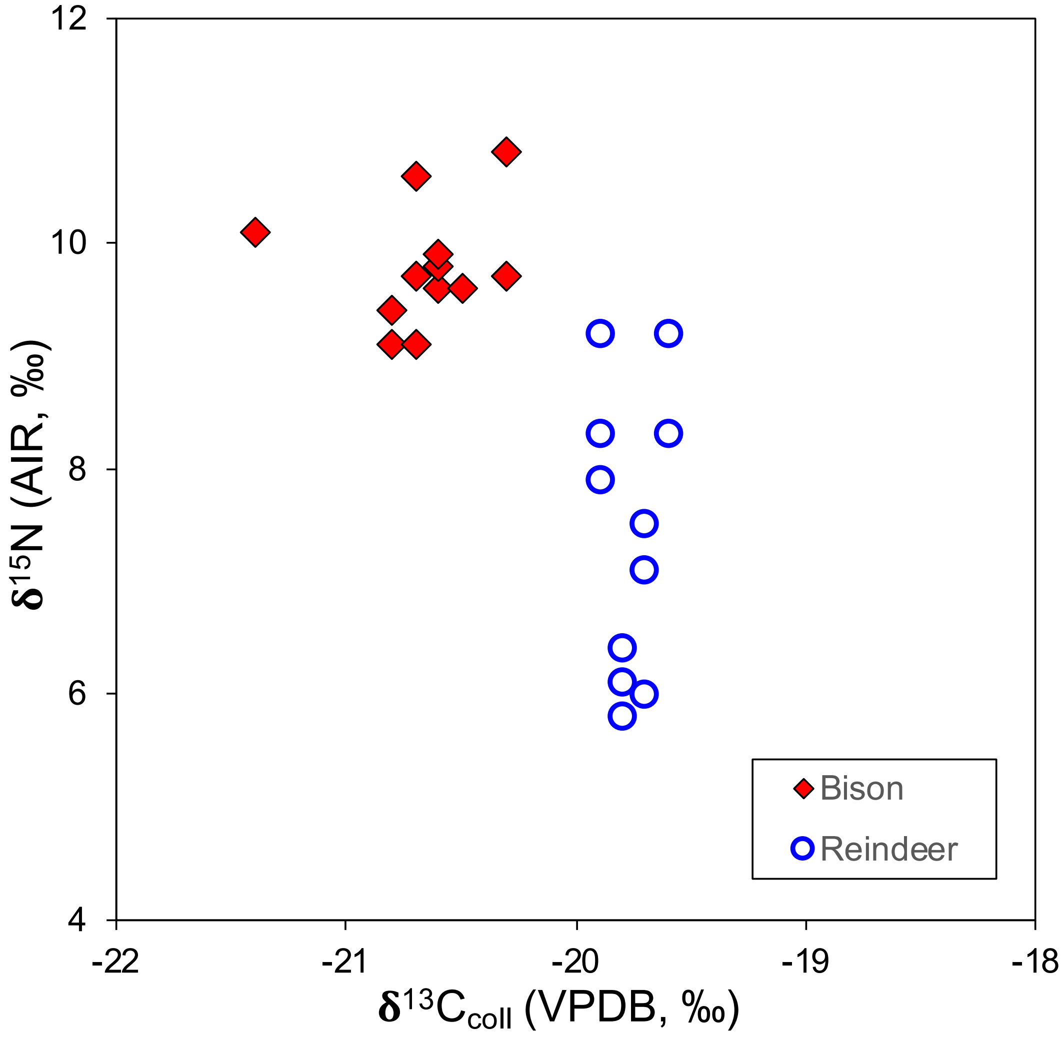


Figure 3: Bison and reindeer calculated drinking water $\delta^{18}O$ values plotted against enamel $\delta^{13}C$ (See supplementary file 3 for enamel $\delta^{18}O$ values).

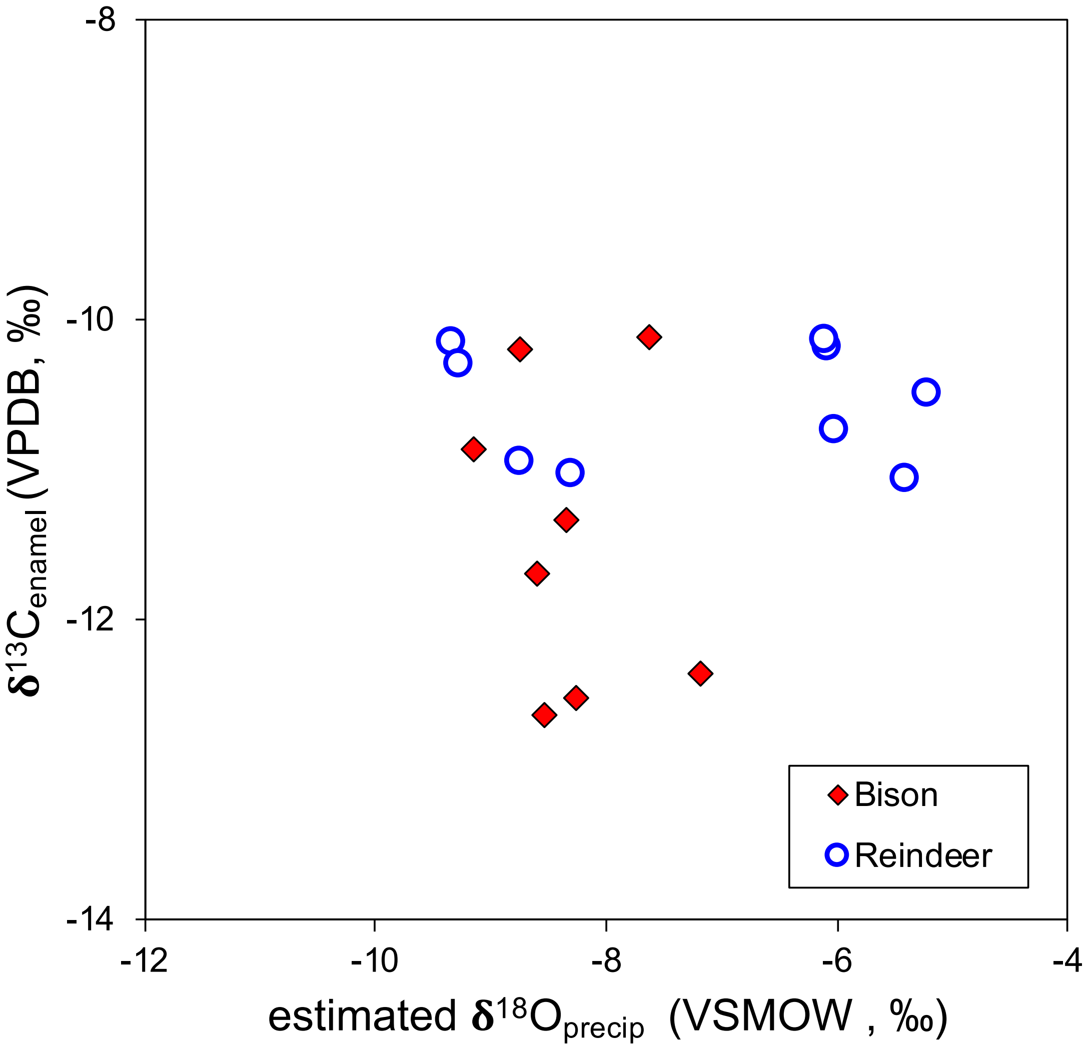


Figure 4: Calculated carbon isotope values of the diet consumed by Banwell Bone Cave bison and reindeer.

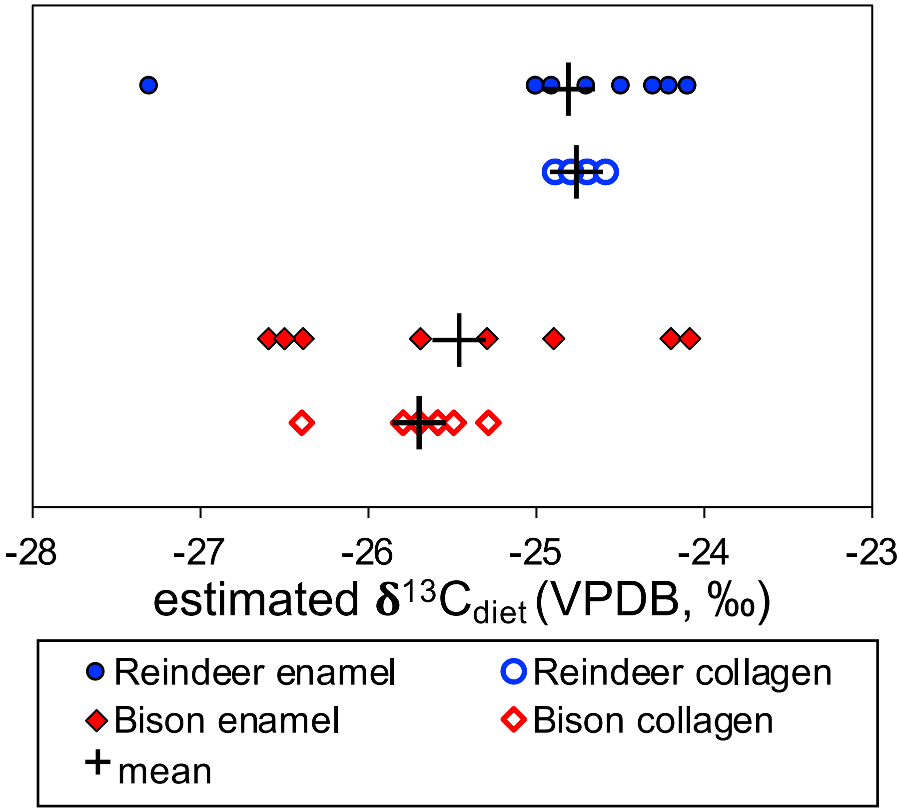


Figure 5: Bone collagen $\delta^{13}C$ and $\delta^{15}N$ of late Pleistocene reindeer from the UK and southwest France. Additional data not produced for this publication has been collated from the published literature (Full details are given in Supplementary file 4).

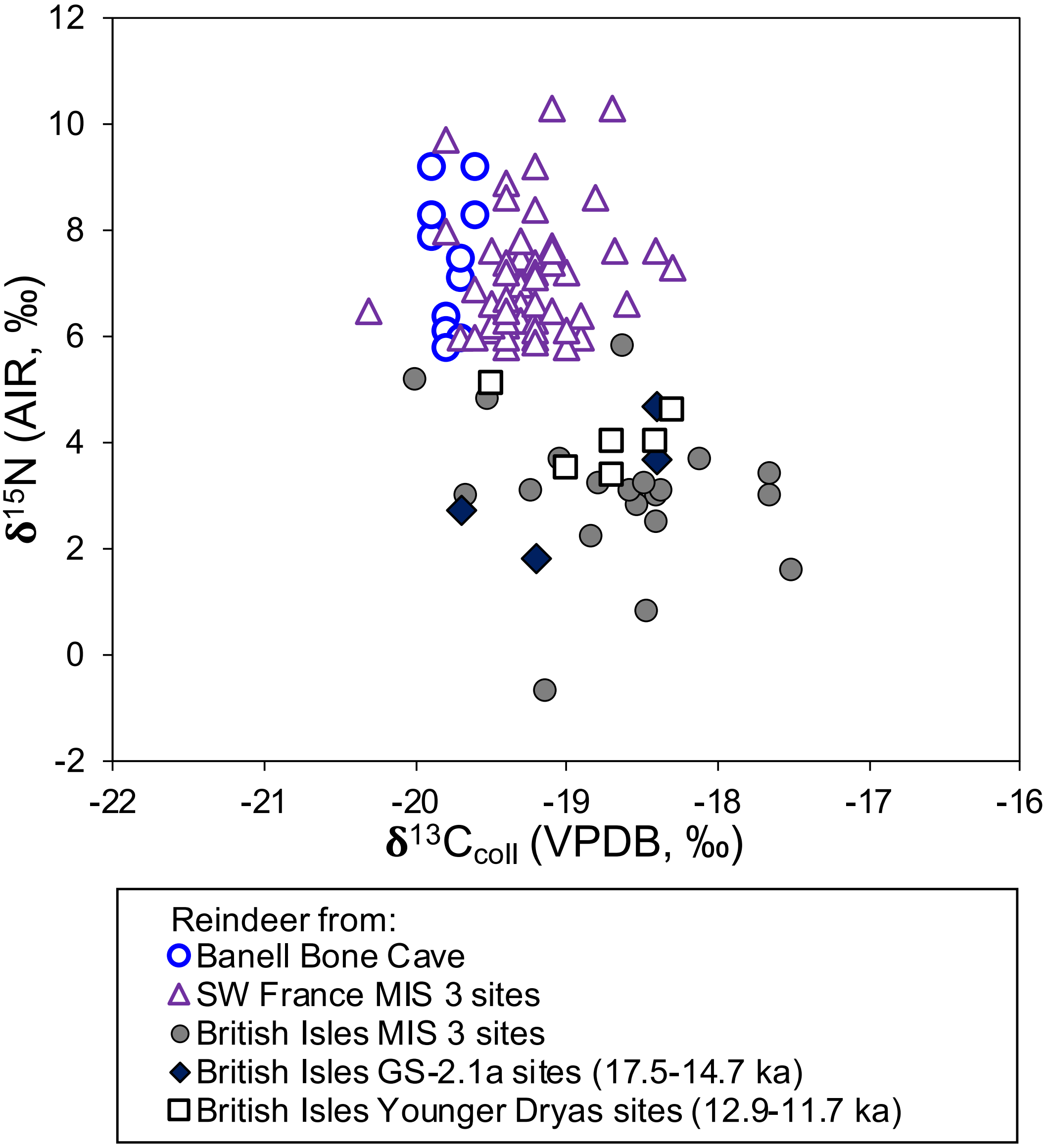
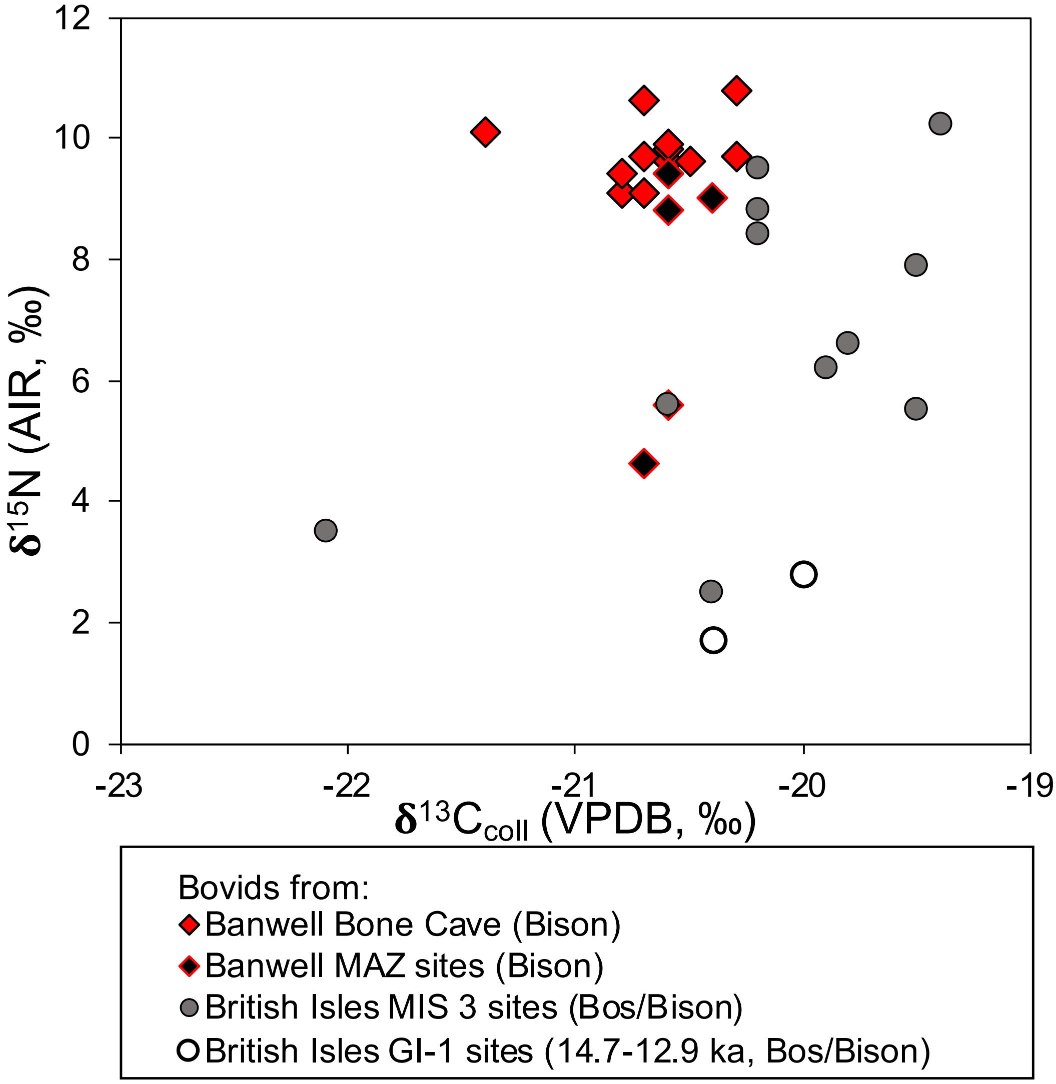


Figure 6: Bone collagen $\delta^{13}C$ and $\delta^{15}N$ of late Pleistocene Bovids from the UK and southwest France. Additional data not produced for this publication has been collated from the published literature (For full details see Supplementary file 5).



Supplementary text 1: ZooMS Methodology:

A recording error resulted in the failure to record the element used to identify select specimens to species. Due to Covid-19 restrictions preventing access to collections, the elements used to identify species could not be re-checked. To confirm initial species identifications collagen peptide fingerprints were obtained for these specimens. This was undertaken following methods adapted from Buckley et al. (2009) and Welker et al. (2015) using the acid-insoluble collagen. For each sample, around 100 ng of already extracted collagen were transferred to Eppendorf micro-tubes and gelatinised in 50 µl 50 mM Ammonium Bicarbonate for 1h at 65°C. Samples were then incubated overnight at 37°C with 0.4 µg of sequencing grade modified trypsin (Promega). Following trypsin digestion, samples were acidified with 0.5% trifluoroacetic acid (TFA) and purified using Pierce™ 100 µl C18 resin Tips (Thermo Scientific) using conditioning and eluting solutions composed of 50% acetonitrile and 0.1% TFA. Collagen was eluted in 50 µL.

For MALDI-TOF-MS, 0.5 µL of the trypsin-digested extract was spotted with 0.5 µL of α-cyano-hydroxycinnamic acid matrix solution (0.1% TFA in ACN/H2O 1:1 v/v) onto a 48 spot MALDI target plate, and air dried. MALDI-MS analyses were carried out in triplicate on a Shimadzu MALDI 8020 instrument, operating at up to 2000 laser shots per plate spot, over a m/z range of 900-4000. The mass spectra were calibrated against an adjacent MS standard spot containing eight calibrant peptides (TOFMix™) of 0.8 to 3.7 kiloDalton (kDa) range (Bradykinin 1-7, angiotensin II, angiotensin I, Glu1-fibrinopeptide B, N-acetyl Renin substrate, ACTH 1–17 clip, ACTH 18–39 clip and ACTH 7–38 clip) – of which seven were used (1.0 – 3.7 kDa range).

The obtained collagen fingerprints were manually inspected for the presence of relevant peptide markers (A-G) in mMass v. 5.5.0 (Strohalm et al., 2010), after filtering peaks with a signal-to-noise ratio (S/N) threshold of 3.0 (Kirby et al., 2013), and using previously published collagen peptide markers from reference spectra (Buckley et al. 2009, 2017; Welker et al., 2016).

All initial species identifications were confirmed by ZooMs analysis (See table S1.1 and S1.2)

Table S1.1 ZooMS results. Columns P1 to G1 indicate identified peaks in the mass spectra. ZooMS identification is based on these peaks

Sample ID	**P1**	**A**	**A'**	**B**	**C**	**P2**	**D**	**E**	**F**	**F'**	**G**	**G'**	**ZooMS ID**
BW1	1105.2		1209.3	1427.4	1580.4	1648.5	2130.9		2853.1				*Bison / Bos sp*
BW8	1105.4	1192.5	1208.5	1427.7	1580.7	1648.8	2131.2	2792.8	2853.8			*3035.1 - shifted by 1 amu*	*Bison / Bos sp*
BW11	1105.3			1427.5	1580.5	1648.6	2130.9			2899.4		*3094.7 - shifted by 1 amu*	*Capra sp / Rangifer*
BW12	1105.6	1150.6	1196.4	1427.7	1580.8	1648.8	2131.1					*3094.9 - shifted by 1 amu*	*Rangifer*
BW13	1105.6		1166.6	1427.9	1581.0	1649.0	2131.4		2883.0				*Rangifer*
BW17	1105.5			1427.6	1580.6	1648.7	2130.9		2883.1			3093.0	*Capra sp / Rangifer*
BW19	1105.6		1166.6	1427.7	1580.8	1648.8	2131.0		2883.5			3093.7	*Rangifer*
BW20	1105.6	1150.6		1427.7	1580.7	1648.8	2131.0		2883.3			3093.9	*Rangifer*

Table S1.2 Most probable identification based on macroscopic zooarchaeological, ZooMS and stratigraphic context.

Sample ID	**Macroscopic zooarchaeological identification**	**ZooMS identification**	**Most probable identification**[1]
BW1	*Bison*	*Bison / Bos sp*	*Bison*
BW8	*Bison*	*Bison / Bos sp*	*Bison*
BW11	*Rangifer tarandus*	*Capra sp / Rangifer*	*Rangifer tarandus*
BW12	*Rangifer tarandus*	*Rangifer*	*Rangifer tarandus*
BW13	*Rangifer tarandus*	*Rangifer*	*Rangifer tarandus*
BW17	*Rangifer tarandus*	*Capra sp / Rangifer*	*Rangifer tarandus*
BW19	*Rangifer tarandus*	*Rangifer*	*Rangifer tarandus*
BW20	*Rangifer tarandus*	*Rangifer*	*Rangifer tarandus*

Supplementary text 1 bibliography:

Buckley, M., Collins, M., Thomas-Oates, J., Wilson, J.C., 2009. Species identification by analysis of bone collagen using matrix-assisted laser desorption/ionisation time-of-flight mass spectrometry. Rapid Commun Mass Spectrom 23 (23), 3843–3854.

Buckley, M., Harvey, V.L., Chamberlain, A.T., 2017. Species identification and decay assessment of Late Pleistocene fragmentary vertebrate remains from Pin Hole Cave (Creswell Crags, UK) using collagen fingerprinting. Boreas 46, 402–411.

Kirby, D.P., Buckley, M., Promise, E., Trauger, S., Holdcraft, T.R., 2013. Identification of collagen-based materials in cultural heritage. Analyst 138 (17), 4849-4858.

Strohalm, M., Kavan, D., Novak, P., Volny, M., Havlicek, V., 2010. mMass 3: a crossplatform software environment for precise analysis of mass spectrometric data. Anal. Chem. 82 (11), 4648-4651.

Welker, F., Soressi, M., Rendu, W., Hublin, J.-J., Collins, M.J., 2015. Using ZooMS to identify fragmentary bone from the Late Middle/Early Upper Palaeolithic sequence of Les Cottés, France. J Archaeol Sci, 54, 279–286.

Welker, F., Hajdinjak, M., Talamo, S., Jaouen, K., Dannemann, M., David, F., Julien M., Meyer, M., Kelso, J., Barnes, I., Brace, S., Kamminga, P., Fischer, R., Kessler, B.M., Stewart, J.R., Pääbo, S., Collins, M.J., Hublin, J.-J., 2016. Palaeoproteomic evidence identifies archaic hominins associated with the Châtelperronian at the Grotte du Renne. PNAS, 113 (40): 11162-11167.

Supplementary Table 1: Sample details and bone collagen carbon and nitrogen stable isotope results.

Sample code	Sample no	Find no	Species	Element	%C	%N	$\delta^{13}C$	$\delta^{15}N$	C:N	source
BW1	39	43	Bison	*	33.6	12.3	-20.6	9.6	3.2	1
BW2	10	11 (a)	Bison	Phalange	38.6	14.2	-20.8	9.1	3.2	1
BW3	21	23	Bison	Astragalus	42.6	15.6	-21.4	10.1	3.2	1
BW4	26	25	Bison	Vertebrae	41.8	15.3	-20.7	9.7	3.2	1
BW5	10	16	Bison	Phalange	40.4	14.8	-20.6	9.8	3.2	1
BW6	39	40	Bison	Scapula	43.5	15.9	-20.3	9.7	3.2	1
BW7	1	8	Bison	Phalange	43.3	15.8	-20.6	9.9	3.2	1
BW8	10	11	Bison	*	47.3	17.4	-20.7	9.1	3.2	1
BW9	45	47	Bison	Vertebrae	43.8	16	-20.5	9.6	3.2	1
BW10	8	1	Bison	Vertebrae	44.6	16.3	-20.8	9.4	3.2	1
OxA-14136			Bison	calcaneum	41.2		-20.3	10.8	3.2	2
OxA-14138			Bison	calcaneum	41.1		-20.7	10.6	3.1	2
BW11	10	12	Reindeer	*	43.5	15.8	-19.9	9.2	3.2	1
BW12	18	19	Reindeer	*	41.6	15.2	-19.8	6.4	3.2	1
BW13		7	Reindeer	*	40.3	14.7	-19.8	6.1	3.2	1
BW14	33	38	Reindeer	Vertebrae	41.9	15.3	-19.7	7.1	3.2	1
BW15		5	Reindeer	Mandible	40.9	14.9	-19.6	8.3	3.2	1
BW16	45	46	Reindeer	Maxilla	42.3	15.4	-19.7	7.5	3.2	1
BW17	18	17	Reindeer	*	42.8	15.7	-19.7	6	3.2	1
BW18		14	Reindeer	Astragalus	46.3	17	-19.9	7.9	3.2	1
BW19	21	24	Reindeer	*	52.5	19.2	-19.9	8.3	3.2	1
BW20	60	61	Reindeer	*	49.5	18.1	-19.6	9.2	3.2	1
BW21	33	36	Reindeer	Scapula	43.3	15.8	-19.8	5.8	3.2	1

1: This study
2: Higham, T. G., Jacobi, R. M. & Bronk Ramsey, C. AMS radiocarbon dating of ancient bone using ultrafiltration. Radiocarbon 48, 179–195 (2006)

* Element not recorded so species identification was confirmed by ZooMs. See supplementary text 1

Supplementary Table 2: Sample details, tooth enamel oxygen and carbon isotope results, and results of conversion equations

Sample code	Species	Notes	Tooth	Animal age during formation (months)	Measured enamel carbonate $\delta^{13}C$	Measured enamel carbonate $\delta^{18}O$ vpdb	Calculated carbonate $\delta^{18}O$ vsmow (equation 1)	Calculated phosphate $\delta^{18}O$ vsmow (equation 2)	Calculated drinking water $\delta^{18}O$ vsmow (bison equation 3, reindeer equation 4)
ED1	Bison		Upper left P3/P4	9 months to c.30months	-10.9	-7.0	23.7	14.9	-9.1 ± 2.6
ED2	Bison		Upper left M1/M2	en utero to c.13 months	-12.6	-6.6	24.1	15.3	-8.5 ± 2.7
ED3	Bison		Lower right P3/P4	9 months to c.30months	-11.7	-6.7	24.0	15.3	-8.6 ± 2.6
ED4	Bison		Upper left M1/M2	en utero to c.13 months	-12.4	-5.7	25.0	16.2	-7.1 ± 2.7
ED5	Bison		Upper left M1/M2	en utero to c.13 months	-11.3	-6.5	24.2	15.5	-8.3 ± 2.7
ED11	Bison		Lower M1	en utero to c.4months	-12.5	-6.4	24.3	15.5	-8.2 ± 2.7
ED12	Bison		Upper left M3	9 months to c.24months	-10.2	-6.8	23.9	15.2	-8.7 ± 2.6
ED13	Bison		Upper Left M2	Birth to c.13 months	-10.1	-6.0	24.7	15.9	-7.6 ± 2.7
ED14	Reindeer		Lower Left M1/M2	3 to 9 months	-11	-5.1	25.6	16.8	-4.8 ± 2.8
ED15	Reindeer		Lower Left M1/M2	3 to 9 months	-10.1	-8.2	22.5	13.8	-9.3 ± 2.4
ED16	Reindeer	ED16, ED23 from same mandible	Left lower P2	13 to 18 months	-10.5	-5.0	25.8	17.0	-4.6 ± 2.8
ED17	Reindeer		Upper Left P2/dp2?	13 to 18 months	-13.3	-8.0	22.6	13.9	-9.1 ± 2.4
ED18	Reindeer		Upper right M3	9 to 26 months	-10.7	-5.6	25.1	16.3	-5.5 ± 2.7
ED19	Reindeer	ED19, ED20 from same mandible	Upper Left M3	9 to 26 months	-10.2	-5.6	25.1	16.3	-5.6 ± 2.7
ED20	Reindeer	ED19, ED20 from same mandible	Upper Left M2	13 to 18 months	-10.3	-8.1	22.5	13.8	-9.2 ± 2.4
ED21	Reindeer	ED21, ED22from same mandible	Lower left P3	13 to 18 months	-11	-7.4	23.3	14.6	-8.1 ± 2.5
ED22	Reindeer	ED21, ED22from same mandible	Lower Left P2	13 to 18 months	-10.9	-7.7	23.0	14.2	-8.6 ± 2.4
ED23	Reindeer	ED16, ED23 from same mandible	Left lower P3	13 to 18 months	-10.1	-5.7	25.1	16.3	-5.6 ± 2.7

Bison-based palaeo-δ^{18}Oprecip estimate									-8.3 ± 1.3
Reindeer-based palaeo-δ^{18}Oprecip estimate									-7.0 ± 1.6
Bison-based temperature estimate (ºC) (equation 5)									10.3 ± 2.5
Reindeer-based temperature estimate (ºC) (equation 5)									12.8 ± 3.1

Equation 1: $\delta^{18}O_{VSMOW} = 1.03091*\delta^{18}O_{VPDB}+30.91$ (Coplen 2011)

Equation 2: $\delta^{18}O_{phos} = 0.973*\delta^{18}O_{carb} - 8.12$ (Zazzo et al. 2004)

Equation 3: $\delta^{18}O_{envi} = (\delta^{18}O_{carb} - 30.057 (\pm 0.58))/0.703 (\pm 0.12)$ (based on Hoppe 2006)

Equation 4: $\delta^{18}O_{envi} = (\delta^{18}O_{phos} – 20.117(\pm 0.34)) / 0.683 (\pm 0.11)$ (based on Longinelli et al., 2003)

Equation 5: temperature (ºC) = ($\delta^{18}O_{precip}$ – 13.74 (±0.16)) / 0.53 (±0.08) (Pryor et al., 2014)

Timing of crown formation or enamel mineralization in Rangifer is estimated here based on known information for other deer species as this information is yet to be established for reindeer (Brown and Chapman, 1991a, b).

For Bison, these estimates are based on Gadbury et al. 2000.

Supplementary table 2 bibliography

Coplen, T. B., 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Communications in Mass Spectrometry 25(17), 2538–2560.

Zazzo, A., Lécuyer, C., Sheppard, S.M., Grandjean, P., Mariotti, A., 2004. Diagenesis and the reconstruction of paleoenvironments: a method to restore original $\delta^{18}O$ values of carbonate and phosphate from fossil tooth enamel. Geochimica et Cosmochimica Acta 68(10), 2245-2258.

Hoppe, K.A. 2006. Correlation between the oxygen isotope ratio of North American bison teeth and local waters: implication for paleoclimatic reconstructions. Earth Planetary Science Letters 244 (1-2), 408-417.

Longinelli, A., Iacumin, P., Davanzo, S., Nikolaev, V., 2003. Modern reindeer and mice: revised phosphate–water isotope equations. Earth and Planetary Science Letters 214(3-4), 491-498.

Pryor, A.J., Stevens, R.E., O'Connell, T.C., Lister, J.R., 2014. Quantification and propagation of errors when converting vertebrate biomineral oxygen isotope data to temperature for palaeoclimate reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 412, 99-107.

Brown, W.A.B., Chapman, N.G., 1991a. Age assessment of fallow deer (Dama dama) from a scoring scheme based on radiographs of developing permanent molariform teeth. Journal of Zoology 224(3), 367-379.

Brown, W.A.B., Chapman, N.G., 1991b. The dentition of red deer (Cervus elaphus): a scoring scheme to assess age from wear of the permanent molariform teeth. Journal of Zoology 224(4), 519-536.

Gadbury, C., Todd, L., Jahren, A.H., Amundson, R., 2000. Spatial and temporal variations in the isotopic composition of bison tooth enamel from the Early Holocene Hudson-Meng Bone Bed, Nebraska. Palaeogeography, Palaeoclimatology, Palaeoecology 157 (1-2), 79-93.

Supplementary Table 3: Results of conversion of collagen and carbonate $\delta^{13}C$ data to estimated $\delta^{13}C$ diet.

Sample code	Species	$\delta^{13}C$	Material	Calculated $\delta^{13}C$ diet
BW1	Bison	-20.6	Collagen	-25.6
BW2	Bison	-20.8	Collagen	-25.8
BW3	Bison	-21.4	Collagen	-26.4
BW4	Bison	-20.7	Collagen	-25.7
BW5	Bison	-20.6	Collagen	-25.6
BW6	Bison	-20.3	Collagen	-25.3
BW7	Bison	-20.6	Collagen	-25.6
BW8	Bison	-20.7	Collagen	-25.7
BW9	Bison	-20.5	Collagen	-25.5
BW10	Bison	-20.8	Collagen	-25.8
OxA-14136	Bison	-20.3	Collagen	-25.3
OxA-14138	Bison	-20.7	Collagen	-25.7
BW11	Reindeer	-19.9	Collagen	-24.9
BW12	Reindeer	-19.8	Collagen	-24.8
BW13	Reindeer	-19.8	Collagen	-24.8
BW14	Reindeer	-19.7	Collagen	-24.7
BW15	Reindeer	-19.6	Collagen	-24.6
BW16	Reindeer	-19.7	Collagen	-24.7
BW17	Reindeer	-19.7	Collagen	-24.7
BW18	Reindeer	-19.9	Collagen	-24.9
BW19	Reindeer	-19.9	Collagen	-24.9
BW20	Reindeer	-19.6	Collagen	-24.6
BW21	Reindeer	-19.8	Collagen	-24.8
ED1	Bison	-10.9	Enamel	-24.9
ED2	Bison	-12.6	Enamel	-26.6
ED3	Bison	-11.7	Enamel	-25.7
ED4	Bison	-12.4	Enamel	-26.4
ED5	Bison	-11.3	Enamel	-25.3
ED11	Bison	-12.5	Enamel	-26.5
ED12	Bison	-10.2	Enamel	-24.2
ED13	Bison	-10.1	Enamel	-24.1
ED14	Reindeer	-11	Enamel	-25
ED15	Reindeer	-10.1	Enamel	-24.1
ED16	Reindeer	-10.5	Enamel	-24.5
ED17	Reindeer	-13.3	Enamel	-27.3
ED18	Reindeer	-10.7	Enamel	-24.7
ED19	Reindeer	-10.2	Enamel	-24.2
ED20	Reindeer	-10.3	Enamel	-24.3
ED21	Reindeer	-11	Enamel	-25
ED22	Reindeer	-10.9	Enamel	-24.9
ED23	Reindeer	-10.1	Enamel	-24.1

$\delta^{13}C_{coll}$ and $\delta^{13}C_{enamel}$ were converted to $\delta^{13}C_{diet}$ by assuming a diet to collagen offset of +5‰, and diet to carbonate offset of +14‰ following Lee Thorpe *et al.* 1989 and Cerling and Harris 1999

Lee-Thorp, J. A., Sealy, J. C., van der Merwe, N. J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite and their relationship to diet. Journal of Archaeological Science 16(6), 585-599.
Cerling, T. E., Harris, J. M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120(3), 347-363.

Supplementary Table 4: Bone collagen δ^{13}C and δ ^{15}N of late Pleistocene reindeer from the UK and southwest France collated from published literature.

Site Name	Country	Element	Lab code	Direct ^{14}C date lab Code	Direct ^{14}C date	uncertainty on ^{14}C date	Age category	Collagen $\delta^{13}C$	Collagen $\delta^{15}N$	Collagen C:N ratio	Date reference	Carbon (coll) reference	Nitrogen (coll) reference
Sun Hole Cave	UK	1st phalange	OxA-14827	OxA-14827	10145	55	GS-1 (Younger Dryas)	-18.3	4.6	3.2	11	11	11
Kent’s Cavern	UK	1st phalange	OxA-14825	OxA-14825	10255	45	GS-1 (Younger Dryas)	-19.5	5.1	3.2	11	11	11
Chelm's Combe	UK	left dentary	A/CC/B/6	OxA-17831	10480	45	GS-1 (Younger Dryas)	-18.4	4	3.2	11	11	11
Foxhole Cave	UK	astragalus	OxA-8312	OxA-8312	10685	65	GS-1 (Younger Dryas)	-18.7	3.4	3.3	15	15	15
Foxhole Cave	UK	astragalus	OxA-25145	OxA-25145	10780	50	GS-1 (Younger Dryas)	-19	3.5	3.2	16	16	16
Foxhole Cave	UK	tibia	OxA-8311	OxA-8311	10785	65	GS-1 (Younger Dryas)	-18.7	4	3.4	15	15	15
Gough's Cave	UK	antler	OxA-18064	OxA-18064	12535	55	GS-2.1a	-19.2	1.8	3.2	11	11	11
Foxhole Cave	UK	astragalus	OxA-25146	OxA-25146	12555	55	GS-2.1a	-19.7	2.7	3.2	16	16	16
Kent’s Cavern	UK	astralagus, left	OxA-14826	OxA-14826	14395	60	GS-2.1a	-18.4	4.7	3.2	11	11	11
Reindeer Rift, Cattedown	UK	calcaneum, sin.	OxA-17160	OxA-17160	14550	55	GS-2.1a	-18.4	3.7	3.2	11	11	11
Goat's Hole (Paviland)	UK	bone	OxA-17560	OxA-17560	24240	110	OIS3	-17.7	3.4	3.3	12	12	12
Pontnewydd Cave	UK	1st phalange	OxA-13984	OxA-13984	25210	120	OIS3	-18.4	3.1	3.2	3	3	3
Goat's Hole (Paviland)	UK	antler	OxA- 7084	OxA-7084	28550	650	OIS3	-19.2	3.1	3.1	15	15	15
Pontnewydd Cave	UK	metacarpal	OxA-13993	OxA-13993	30240	230	OIS3	-18.5	3.2	3.2	3	3	3
Pontnewydd Cave	UK	tibia	OxA-11672	OxA-11672	31800	1000	OIS3	-17.7	3	3.3	3	3	3
Goat's Hole (Paviland)	UK	antler	OxA-13438	OxA-13438	31990	180	OIS3	-19	3.7	3.2	12	12	12
Kent’s Cavern	UK	antler	OxA-30162	OxA-30162	34850	600	OIS3	-18.8	3.2	3.4	14	14	14
Kent’s Cavern	UK	antler	OxA-30272	OxA-30272	35100	650	OIS3	-19.1	-0.7	3.3	14	14	14
Pontnewydd Cave	UK	tibia	OxA-11671	OxA-11671	35400	>	OIS3	-19.7	3	3.4	3	3	3
Pontnewydd Cave	UK	humerus (left)	OxA-11669	OxA-11669	36700	>	OIS3	-20	5.2	3.5	3	3	3
Goat's Hole (Paviland)	UK	antler	OxA-13658	OxA-13658	37350	320	OIS3	-18.6	5.8	3.2	12	12	12
Pin Hole	UK	antler	OxA-11980	OxA-11980	37760	340	OIS3	-19.5	4.8	3.3	13	13	13
Pontnewydd Cave	UK	right mandible	OxA-14052	OxA-14052	39600	900	OIS3	-18.6	3.1	3.4	3	3	3
Kent’s Cavern	UK	left dentary	OxA-13888	OxA-13888	40000	700	OIS3	-18.5	2.8	3.3	8	8	8
Pontnewydd Cave	UK	humerus (right)	OxA-11670	OxA-11670	40200	>	OIS3	-18.4	2.5	3.3	3	3	3
Goat's Hole (Paviland)	UK	antler	OxA-13439	OxA-13439	40570	370	OIS3	-18.8	2.2	3.2	12	12	12

Site Name	Country	Element	Lab code	Direct ^{14}C date lab Code	Direct ^{14}C date	uncertainty on ^{14}C date	Age category	Collagen $\delta^{13}C$	Collagen $\delta^{15}N$	Collagen C:N ratio	Date reference	Carbon (coll) reference	Nitrogen (coll) reference
Pin Hole	UK	antler	OxA-11797	OxA-11797	40650	500	OIS3	-18.5	0.8	3.4	8	8	8
Pontnewydd Cave	UK	astragalus	OxA-14055	OxA-14055	41400	1400	OIS3	-18.4	3	3.3	3	3	3
Pin Hole	UK	antler	OxA- 11796	OxA-11796	44200	800	OIS3	-17.5	1.6	3.3	8	8	8
Robin Hood's Cave	UK	bone	OxA-12772	OxA-12772	47300	1200	OIS3	-18.1	3.7	3.2	13	13	13
Kent's Cavern	UK	proximal radius	OxA-14714	OxA-14714	49600	2200	OIS3	-18.6	3.1	3.3	8	8	8
Abri Castanet	France	tibia	CST400	GifA 97312	32460	420	OIS 3	-19.5	7.6	3	2	2	2
Abri Castanet	France	metatarsus	CST600	GifA 97313	32750	460	OIS 3	-19.8	9.7	3.1	2	2	2
Abri Castanet	France	humerus	CST500	GifA 99165	31430	390	OIS 3	-19.2	9.2	3.1	2	2	2
Abri Castanet	France	tibia	CST300	GifA 99166	34320	520	OIS 3	-19.1	10.3	3.2	2	2	2
Abri Castanet	France	femur	CST200	GifA 99180	32950	520	OIS 3	-18.7	10.3	3	2	2	2
Abri Castanet	France	metatarsus	CST100				OIS 3	-18.8	8.6	3	2	2	2
Abri Castanet	France	humerus	CST-A1				OIS 3	-19.3	7.8	3.5	2	2	2
Abri Lartet	France	astragalus	LRT-2				OIS 3	-19.2	8.4	3.3	2	2	2
Abri Lartet	France	astragalus	LRT-3				OIS 3	-19.3	7.5	3.3	2	2	2
Abri Pasquet	France	calcaneum	PSQ-1				OIS 3	-19.4	8.9	3.5	2	2	2
Abri Pataud	France	Tibia	P-19918	OxA-21581	33550	550	OIS 3	-19.3	7.5	3.3	9	6	6
Abri Pataud	France	Metacarpal III-I	P-19931	OxA-21587	28150	290	OIS 3	-19.2	6	3.3	9	6	6
Abri Pataud	France	Central + fourth t	P-19932	OxA-21588	28250	280	OIS 3	-19.2	6	3.3	9	6	6
Abri Pataud	France	Tibia	P-19912	OxA-21599	34850	600	OIS 3	-18.6	6.6	3.3	9	6	6
Abri Pataud	France	Metatarsal III-I	P-19913	OxA-21600	34200	550	OIS 3	-19.2	7.4	3.3	9	6	6
Abri Pataud	France	Bone	P-21953	OxA-21670	33450	500	OIS 3	-19.2	7.2	3.4	9	6	6
Abri Pataud	France	Bone	P-21954	OxA-21671	34300	600	OIS 3	-19.1	7.5	3.3	9	6	6
Grotte XVI	France	metatarsus	G16-47				OIS 3	-19.1	7.7	3.3	2	2	2
Grotte XVI	France	metatarsus	G16-50				OIS 3	-19.3	7	3.2	2	2	2
Grotte XVI	France	tibia	G16-100				OIS 3	-19.3	6.6	3.3	2	2	2
Grotte XVI	France	mandible	G16-19				OIS 3	-19.5	6.1	3.4	2	2	2
Grotte XVI	France	radioulna	G16-20				OIS 3	-18.9	6	3.3	2	2	2
Grotte XVI	France	metatarsus	G16-23				OIS 3	-19	7.2	3.2	2	2	2
Grotte XVI	France	metatarsus	G16-24				OIS 3	-19.5	6.6	3.3	2	2	2

Site Name	Country	Element	Lab code	Direct ^{14}C date lab Code	Direct ^{14}C date	uncertainty on ^{14}C date	Age category	Collagen $\delta^{13}C$	Collagen $\delta^{15}N$	Collagen C:N ratio	Date reference	Carbon (coll) reference	Nitrogen (coll) reference
Grotte XVI	France	metacarpum	G16-25				OIS 3	-19.1	7.4	3.3	2	2	2
Grotte XVI	France	metatarsus	G16-26				OIS 3	-19.1	6.5	3.3	2	2	2
Grotte XVI	France	mandible	G16-37				OIS 3	-18.9	6.4	3.3	2	2	2
Grotte XVI	France	phalanx I	G16-70				OIS 3	-19	5.8	3.3	2	2	2
Grotte XVI	France	astragalus	G16-76				OIS 3	-19.8	8	3.3	2	2	2
Grotte XVI	France	metapodial	G16-93				OIS 3	-19.2	7.1	3.3	2	2	2
Grotte XVI	France	metacarpum	G16-94				OIS 3	-19.3	7.8	3.3	2	2	2
Grotte XVI	France	metacarpum	G16-95				OIS 3	-19.4	7.4	3.3	2	2	2
La Berbie	France	jawbone	LBR1100				OIS 3	-19.1	7.6	3.2	1	1	1
La Berbie	France	femur	LBR3400				OIS 3	-19.4	5.8	3.3	1	1	1
La Moustier	France	metacarpal	OxA-25170	OxA-25170	50000	3900	OIS 3	-19.4	6.2	3.5	10	10	10
La Quina	France	bone	OxA-21807	OxA-21807	45200	2200	OIS 3	-18.678	7.6	3.3	10	10	10
Le Moustier	France	calcaneum	G16-77				OIS 3	-19.3	6.3	3.3	2	2	2
Le Moustier	France	scapula	MST-12				OIS 3	-19.3	6.3	3.3	2	2	2
Les Peyrugues	France	humerus	PRG3900				OIS 3	-19.2	6.3	3.3	5	5	5
Les Peyrugues	France	radius	PRG5400				OIS 3	-19.4	6	3.1	5	5	5
Les Peyrugues	France	long bone	PRG5500				OIS 3	-19	6.1	3.3	5	5	5
Les Peyrugues	France	metatarsal	PRG5600				OIS 3	-19.7	6	3.2	5	5	5
Les Peyrugues	France	radius	PRG5800				OIS 3	-19.2	6.1	3.2	5	5	5
Les Pradelles / Marillac	France	bone	not given				OIS 3	-20.3	6.5	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.6	6.9	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.5	6.2	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.4	6.5	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.4	6.3	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.2	5.9	not given	7	7	7
Les Pradelles / Marillac	France	bone	not given				OIS 3	-19.2	6.6	not given	7	7	7
Mandrin	France	femur	OxA-21694	OxA-21694	47100	0	OIS 3	-19.5	6.6	3.4	10	10	10
Roc-de-Combe	France	metatarsus	RCM-22				OIS 3	-18.4	7.6	3.3	2	2	2

Site Name	Country	Element	Lab code	Direct ^{14}C date lab Code	Direct ^{14}C date	uncertainty on ^{14}C date	Age category	Collagen δ^{13}C	Collagen δ^{15}N	Collagen C:N ratio	Date reference	Carbon (coll) reference	Nitrogen (coll) reference
Roc-de-Combe	France	metatarsus	RCM-23				OIS 3	-19.4	8.6	3.3	2	2	2
Roc-de-Combe	France	metatarsus	RCM-24				OIS 3	-19.1	6.5	3.2	2	2	2
Roc-de-Combe	France	phalanx	RCM-25				OIS 3	-19.8	8	3.3	2	2	2
Roc-de-Combe	France	maxillary	RCM-26				OIS 3	-19.4	7.2	3.3	2	2	2
Saint-Césaire	France	metapodium	RPB7200				OIS 3	-18.3	7.3	3.2	1	1	1
Saint-Césaire	France	not given	RPB3100				OIS 3	-19.4	6.7	3.2	4	4	4
Saint-Césaire	France	not given	RPB3700				OIS 3	-19.4	6.5	3.2	4	4	4
Vergisson II	France	bone	OxA-7758	OxA-7758	35700	2400	OIS 3	-19.604	6	3	17	18	17

Supplementary table 4 bibliography

1: Bocherens, H., Drucker, D.G., Billiou, D., Patou-Mathis, M., Vandermeersch, B. 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: Review and use of a multi-source mixing model. Journal of Human Evolution 49: 71–87.

2: Bocherens, H., Drucker, D.G., Madelaine, S., 2014. Evidence for a ^{15}N positive excursion in terrestrial foodwebs at the Middle to Upper Palaeolithic transition in south-western France: implications for early modern humans. Journal of Human Evolution 69, 31-43.

3: Debenham, N.C., Pettitt, P.B., Housley, R.A., Higham, T.F.G., Rowe, N.P., Atkinson, T., Hebden, N. 2012. Neanderthals in Wales: Pontnewydd and the Elwy Valley. ed. / S.H.R. Aldhouse-Green; Rick Peterson; K.E. Walker. Cardiff : Oxbow Books in association with The National Museum of Wales, 302-320.

4: Drucker, D., Bocherens, H., Mariotti, A., Lévêque, F., Vandermeersch, B., Guadelli. J.-L., 1999. Conservation des signatures isotopiques du collagène d'os et de dents du Pléistocène supérieur (Saint-Césaire, France) : implications pour les reconstitutions des régimes alimentaires des néandertaliens. Bulletins et Mémoires de la Société d'Anthropologie de Paris, Nouvelle Série, tome 11 fascicule 3-4, pp. 289-305.

5: Drucker, D., Bocherens, H., Biliou, D. 2003. Evidence for shifting environmental conditions in Southwestern France from 33 000 to 15 000 years ago derived from carbon-13 and nitrogen-15 abundances in collagen of large herbivores. *Earth Planetary Science Letter* 216, 163–173.

6: Drucker, D.G., Vercoutere, C., Chiotti, L., Nespole, R., Crepin, L., Condard, N.J., Munzel, S.C., Higham, T., Plicht, J., Laznickova-Galetova, M. and Bochrens, H. 2015 Tracking possible decline of woolly mammoth during the Gravettian in Dordogne (France) and the Ach Valley (Germany) using multi-isotope tracking (13C, 14C, 15N, 34S, 18O). Quaternary International, 359, 304-317.

7: Fizet, M., Mariotti, A., Bocherens, H., 1995. Effect of Diet, Physiology and Climate on Carbon and Nitrogen Stable Isotopes of Collagen in a Late Pleistocene anthropic palaeoecosystem: Marillac, Charente, France. Journal of Archaeological Science 22(1), 67-79.

8: Higham, T.G., Jacobi, R.M., Bronk Ramsey, C., 2006. AMS radiocarbon dating of ancient bone using ultrafiltration. Radiocarbon 48(2), 179–195.

9: Higham, T., Jacobi, R., Basell, L., Bronk Ramsey, C., Chiotti, L., Nespoulet, R. 2011. Precision dating of the Palaeolithic: A new radiocarbon chronology for the Abri Pataud (France), a key Aurignacian sequence. Journal of human evolution, 61(5) 549-563.

10: Higham T, Douka K, Wood R, Ramsey CB, Brock F, Basell L, et al. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature. 2014; 512: 306–309.

11: Jacobi, RM, Higham T. 2009. The early Late glacial re-colonization of Britain: new radiocarbon evidence from Gough's Cave, southwest England. Quaternary Science Reviews, 28 : 1895-1913

12: Jacobi, R.M., Higham, T.F.G. 2008. The 'Red Lady' ages gracefully: new ultrafiltration AMS determinations from Paviland. Journal of Human Evolution, 55: 898-907.

13: Jacobi, R.M., Higham, T.F.G., Bronk Ramsey, C. 2006. AMS radiocarbon dating of Middle and Upper Palaeolithic bone in the British Isles: improved reliability using ultrafiltration. *Journal of Quaternary Science*. 21 (5): 557–573.

14: Proctor, C., Douka, K., Proctor, J.W. and Higham, T. 2017. The Age and Context of the KC4 Maxilla, Kent's Cavern, UK. European Journal of Archaeology 20 (1) 2017, 74–97.
15: Richards, M. P. 2000. Human and faunal stable isotope analyses from Goat's Hole and Foxhole caves, Gower. Pp. 71-75 in S. Aldhouse-Green (ed.), Paviland Cave and the "Red Lady": a definitive report. Western Academic and Specialist Press, Ltd.: Bristol.

16: Schulting, R.J., Fibiger, L., Macphail, R.I., McLaughlin, R., Murray, E.V., Price, C., Walker, E.A. 2013a. Mesolithic and Neolithic humans remains from Foxhole Cave (Gower, South Wales). Antiquaries Journal 93: 1-23.

17: Stevens, R.E. Jacobi, R., Street, M., Germonpré, M., Conard, N.J., Münzel, S.C. Hedges, R.E.M. 2008 Nitrogen isotope analyses of reindeer (Rangifer tarandus), 45,000 BP to 9,000 BP: Palaeoenvironmental reconstructions.Palaeogeography, Palaeoclimatology, Palaeoecology , 262 (1-2) pp. 32-45.

18: ORAU database: https://c14.arch.ox.ac.uk/database/db.php?page=checkDate&oxa=7758&auto=true

Supplementary Table 5: Bone collagen δ^{13}C and δ ^{15}N of late Pleistocene Bovids from the UK and southwest France collated from published literature.

Site Name	Country	Species	Element	Lab code	Direct ^{14}C date Lab Code	Direct ^{14}C date	Age category	Collagen δ^{13}C	Collagen δ^{15}N	Collagen C:N ratio	Date reference	Carbon (coll) reference	Nitrogen (coll) reference
Ash Tree Cave	UK	Bison priscus	cervical vertabra	OxA-15003	57700	>	Banwell MAZ site	-20.6	5.6	3.2	1	1	1
Windy Knoll	UK	Bison priscus	radius	OxA-15001	51700	>	Banwell MAZ site	-20.7	4.6	3.2	1	1	1
Steetley Quarry	UK	Bison priscus	metacarpal	OxA-15000	53200	>	Banwell MAZ site	-20.6	9.4	3.2	1	1	1
Ash Tree Cave	UK	Bison priscus	metatarsal	OxA-13800	54100	>	Banwell MAZ site	-20.4	9	3.3	1	1	1
Banwell Bone Cave	UK	Bison priscus	calcaneum	OxA-14136	59500	>	Banwell MAZ site	-20.3	10.8	3.2	1	1	1
Banwell Bone Cave	UK	Bison priscus	calcaneum	OxA-14138	53900	>	Banwell MAZ site	-20.7	10.6	3.1	1	1	1
Hunter's Lodge Inn Sink	UK	Bison priscus	scapula	OxA-13566	54800	>	Banwell MAZ site	-20.6	8.8	3.2	1	1	1
Goat's Hole (Paviland)	UK	Bison	not given	OxA-6932	32600	950	OIS3	-20.2	9.5	2.9	2	2	2
Kendrick's Cave	UK	Bovine	humerus	OxA-11726	12310	50	GI-1ed	-20	2.8	3.2	3	3	3
Goat's Hole (Paviland)	UK	Bison	not given	OxA-13435	30320	170	OIS3	-19.4	10.2	3.2	4	4	4
Goat's Hole (Paviland)	UK	Bison	not given	OxA-13418	31250	230	OIS3	-20.2	8.4	3.3	4	4	4
Goat's Hole (Paviland)	UK	Bison	not given	OxA-6924	31600	850	OIS3	-19.5	7.9	2.9	2	2	2
Goat's Hole (Paviland)	UK	Bos/Bison	not given	OxA-6926	26820	460	OIS3	-20.2	8.8	3	2	2	2
Goat's Hole (Paviland)	UK	Bos/Bison	not given	OxA-6925	29850	700	OIS3	-19.9	6.2	3	2	2	2
Foxhole Cave	UK	Bos/Bison	sacrum	OxA-25158	28310	290	OIS3	-22.1	3.5	3.2	5	5	5
Foxhole Cave	UK	Bos/Bison	scapula	OxA-25157	30750	390	OIS3	-19.5	5.5	3.2	5	5	5
Pin hole Cave	UK	Bovini	partial right tibia	OxA-11976	40720	390	OIS3	-20.4	2.5	3.3	1	1	1
Pin hole Cave	UK	Bovini	left radius/ulna	OxA-13591	48000	1000	OIS3	-19.8	6.6	3.1	1	1	1

Supplementary table 5 bibliography

1: Higham, T.G., Jacobi, R.M., Bronk Ramsey, C., 2006. AMS radiocarbon dating of ancient bone using ultrafiltration. Radiocarbon 48(2), 179–195.

2: Richards, M. P. 2000. Human and faunal stable isotope analyses from Goat's Hole and Foxhole caves, Gower. Pp. 71-75 in S. Aldhouse-Green (ed.), Paviland Cave and the "Red Lady": a definitive report. Western Academic and Specialist Press, Ltd.: Bristol.

3: Jacobi, R.M., and Higham, T.F.G., 2011. The British Earlier Upper Palaeolithic: Settlement and Chronology. AHOB. Developments in Quaternary Science: 14 ISSN 1571-0866

4: Jacobi, R.M. and Higham, T.F.G. 2008. The 'Red Lady' ages gracefully: new ultrafiltration AMS determinations from Paviland. Journal of Human Evolution, 55: 898-907.

5: Schulting, R.J., Fibiger, L., Macphail, R.I., McLaughlin, R., Murray, E.V., Price, C. and Walker, E.A. 2013. Mesolithic and Neolithic humans remains from Foxhole Cave (Gower, South Wales). Antiquaries Journal 93: 1-23.