Proc. Univ. Bristol Spelaeol. Soc., 2020, 28 (2), 221-238

LATE GLACIAL PALAEOCLIMATE INVESTIGATIONS AT KING ARTHUR'S CAVE AND SUN HOLE

by

HAZEL READE, FIONA HOLLORAN, JENNIFER A. TRIPP, SOPHY CHARLTON, ANNE-LISE JOURDAN and RHIANNON E. STEVENS

ABSTRACT

King Arthur's Cave (Wye Valley) and Sun Hole (Cheddar Gorge) currently provide the earliest dates for a human presence in the British Isles after the Last Glacial Maximum. The earliest phase of activity at these sites has been dated to c. 15.2 to 14.6 thousand years cal. BP, which spans the onset of the Late Glacial Interstadial, a major global climate transition characterised by rapidly warming temperatures. Here we present stable isotope data from horse (*Equus ferus*) teeth found in the zooarchaeological assemblages at the sites. We also report two new radiocarbon dates on specimens from King Arthur's Cave. The *Equus* tooth enamel provides a record of climatic conditions during the animals' tooth formation. Evidence of human modification of the teeth (cut marks and fractures) chronologically tie these palaeoclimatic records to the earliest post-LGM archaeology at the two sites, thus informing on the climatic and environmental context under which human activity in these areas took place. Results indicate that people were present at the two sites during a period of climatic warming, with temperatures perhaps only marginally colder than present day conditions. However, suboptimal environmental conditions are suggested and may indicate changing vegetation dynamics within the local landscape.

INTRODUCTION

King Arthur's Cave (Wye Valley, Herefordshire, Figure 1) and Sun Hole (Cheddar Gorge, Somerset, Figure 1) provide the earliest dated human presence in the British Isles following the Last Glacial Maximum (LGM). An extensive radiocarbon dating programme targeting human remains and culturally modified faunal material has placed people at the sites at around 15.2 to 14.6 thousand years cal. BP (Jacobi and Higham, 2011). This coincides with a major global climate transition (the end of Greenland Stadial 2 (GS-2.1a) and the start of the Late Glacial Interstadial (GI-1e) (Rasmussen *et al.*, 2014)), and it is not currently clear whether human reoccupation of southwest Britain occurred prior to, during, or after the period of increasing temperatures. Here we investigate the climate and environment local to King Arthur's Cave and Sun Hole Cave during this phase of human activity, through stable isotope ($\delta^{18}O$ and $\delta^{13}C$) analysis of horse (*Equus ferus*) tooth enamel carbonate. The proliferation of horse remains in the faunal assemblages excavated from the two sites, many bearing marks of cultural modifications (cut marks and fractures), indicates horse was a key prey species exploited in both regions. Several of the teeth analysed in this study show such human-made fractures, thus the climatic and environmental data generated are directly linked to periods of human presence at both sites.

BACKGROUND

King Arthur's Cave is located in the Wye Valley in Herefordshire (Figure 1). First excavated in the 1870s, further excavations were conducted by UBSS between 1925-1929 and in 1952, and by Nick Barton in the 1990s (Taylor, 1928, ApSimon, 1992, Barton, 1997). The UBSS excavations recovered large faunal and lithic assemblages from stratified deposits. Palaeolithic artefacts from the site have been described as Late Upper Palaeolithic in character and include bi-truncated trapezoidal backed blades ('Cheddar points') (ApSimon, 1992; Jacobi and Higham, 2011). The Late Glacial faunal assemblage includes horse and red deer remains that show evidence of cut marks and cultural fractures, indicating exploitation and processing of these species by humans. Radiocarbon dating indicates that there were multiple, most likely sporadic, phases of human activity at the site. The earliest phase of human activity, predominately associated with wild horse exploitation, has been dated to between 15.2 and 14.7 thousand years cal. BP and its duration most likely did not exceed a few hundred years in total (Figure 2) (Jacobi and Higham, 2011).

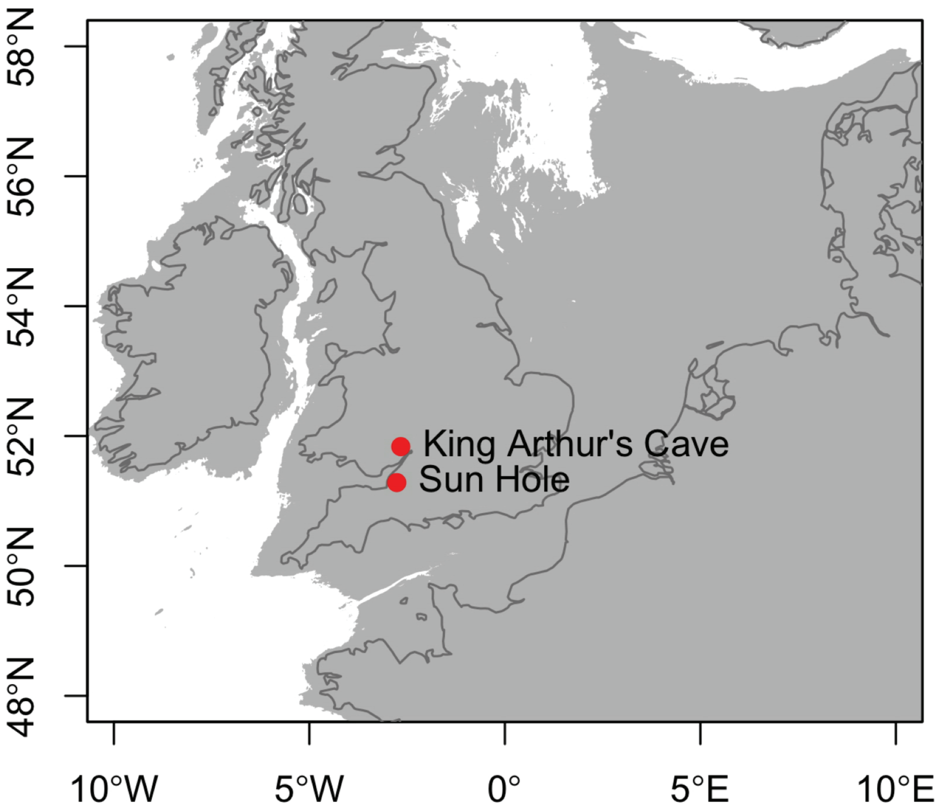

Figure 1. *Map of Britain and adjacent areas of northwest Europe, showing location of King Arthur's Cave and Sun Hole. Approximate position of the palaeocoastlines for GS-2.1a/GI-1 (-80m below modern sea-level) is derived from Zickel* et al. *(2016).*

Sun Hole is a small fissure cave located in Cheddar Gorge, Somerset (Figure 1). Several excavations took place at the site during the 20th century, which yielded small faunal and lithic assemblages. Unfortunately, some of this material was destroyed during a bombing raid at the UBSS museum in 1940. Of the small number of artefacts that remain, key tool-forms that represent the earliest Late Upper Palaeolithic technology in Britain are present (Jacobi and Higham 2009; 2011). Among the surviving faunal assemblage are culturally modified horse teeth and bones, and most significantly, a human ulna. Radiocarbon dating of this material places human presence at Sun Hole between 15.1 and 14.6 thousand years cal. BP, although as with King Arthur's Cave, activity at the site may have been limited in duration to only a few hundred years (Figure 2) (Jacobi and Higham, 2011).

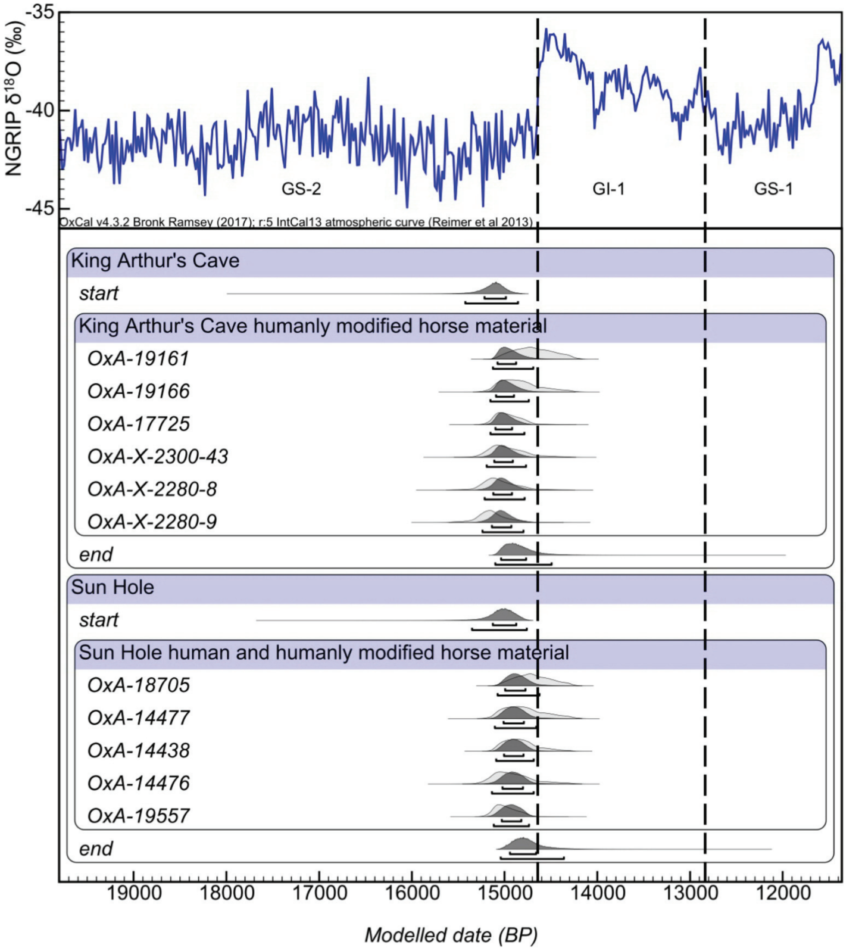

Figure 2. *Modelled probability distribution of dated human and humanly modified Equus ferus remains from King Arthur's Cave and Sun Hole Cave. Dates originally published in Jacobi and Higham (2011). The Greenland ice core (NGRIP) $\delta^{18}O$ record is displayed for comparison. Human presence in the British Isles appears to occur prior to the warming signal in the NGRIP record.*

The dates of human activity at King Arthur's Cave and Sun Hole span the onset of the Late Glacial Interstadial (GI-1), which occurred at c. 14.7 thousand years BP, based on the Greenland Ice Core Chronology (Rasmussen *et al*., 2014). During this time global air temperatures rose rapidly, resulting in significant biotic responses, such as changes in floral and faunal compositions and an increase in biodiversity in some regions (Binney *et al*., 2017; Kindler *et al*., 2014; Lister and Stuart, 2008). However, the timing and magnitude of these climatic changes and environmental responses have long been known to be regionally variable (e.g. Coope and Lemdahl, 1995; Walker *et al*., 1994; 2003). Within the British Isles there have been numerous studies into Late Glacial climate and environment (e.g. Lowe *et al*., 1999, Brooks and Langdon, 2014, Elias and Matthews, 2014), but there is a paucity of records that span the stadial-interstadial transition and that can be linked to the archaeological record. This is partly due to the major changes in sedimentation regimes and biological productivity that characterise the GS-2.1a to GI-1 transition.

Establishing the climatic and environmental context of human activity at King Arthur's Cave and Sun Hole is particularly important for understanding the subsistence strategies, mobility/settlement patterns, and landscape experiences of these early colonising populations. In this study we use stable isotope ($\delta^{18}O$ and $\delta^{13}C$) analysis of horse tooth enamel carbonate from King Arthur's Cave and Sun Hole to infer climatic and environmental conditions local to the sites. The oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotope signature of tooth enamel relates to the vegetation and water the animal consumed during the period of tooth formation, which is linked to prevailing climatic and environmental conditions in the vicinity of the animal's habitat and is influenced by animal physiology and behaviour (Pederzani and Britton, 2019). Horse physiology necessitates regular access to drinking water and their behavioural ecology favours landscapes with grass and sedge vegetation (Crane *et al*., 1997; King, 2002). Horse teeth form over several years, developing progressively from the occlusal surface to the root, and thus provide the opportunity to examine seasonally-resolved climate information (Bendrey *et al*. 2014; Hoppe *et al*. 2004; Sharp and Cerling, 1998). In mid-latitude environments horse enamel $\delta^{18}O$ reflects the $\delta^{18}O$ of meteoric water; variations in which are primarily driven by air temperature (Feranec *et al*. 2009; Rozanski *et al*., 1992). Under these environmental conditions, higher $\delta^{18}O$ values typically reflect warmer temperatures, and lower $\delta^{18}O$ values indicate colder temperatures. Enamel $\delta^{13}C$ reflects the vegetation in a horse's diet. In the context of the British Isles, where horses would have a diet composed exclusively of plants following the C_3 photosynthetic pathway, vegetation $\delta^{13}C$ is predominantly influenced by environmental factors such as water availability, temperature, and light and nutrient levels, with higher plant $\delta^{13}C$ values indicating more water- and/or nutritionally-stressed environments (Koch 1998; Kohn 2010).

MATERIALS AND METHODS

Four horse teeth from King Arthur's Cave and two from Sun Hole were selected for analysis (Table 1). Three of the King Arthur's Cave teeth (UPN-272, UPN-275, UPN-280) bear characteristic traverse fractures, produced by percussive blows and indicative of bone marrow extraction (Jacobi and Higham, 2011), while the fourth (UPN-276) was included in this study as it had previously been radiocarbon dated (OxA-6732 12150 ± 100 ^{14}C yr BP; Stevens and Hedges, 2004). UPN-272, UPN-275, and UPN-280 are likely to date to the same phase of activity at the site, coming from the 'mammoth layer' (Taylor, 1928), which corresponds to unit

Site	Sample code	Museum code	Species and element	Excavation context	^{14}C AMS lab code	^{14}C AMS date
Sun Hole	UPN-266	M5.2/14.1	*Equus ferus* left M^2	5th/6^{th} ft Pleistocene. C/6 under W wall		
Sun Hole	UPN-267	M5.2/30	*Equus ferus* right M^3	7th ft Pleistocene		
King Arthur's Cave	UPN-272	W.2.21/723	*Equus ferus* left M_1/M_2	?Mammoth layer. 7.9.27		
King Arthur's Cave	UPN-275	W2.21/1123	*Equus ferus* left M_3	?Mammoth layer. 23.6.29		
King Arthur's Cave	UPN-276	W2.21/285	*Equus ferus* ?left M^3	1st hearth	OxA-6732[1] OxA-V-2797-24[2]	12,150 ± 100 12,365 ± 55
Kngi Arthur's Cave	UPN-280	W2.21/726	*Equus ferus* left P_3/P_4	?Mammoth layer. 7.9.27	OxA-V-2754-50[2]	12,410 ± 50

Table 1. Equus ferus *teeth from Sun Hole Cave and King Arthur's Cave, analysed in this study. Date references:[1]Stevens and Hedges, 2004; [2]this study.*

3c in later excavations (ApSimon, 1992). We selected one of these teeth (UPN-280) for radiocarbon dating. UPN-276 comes from the '1st hearth' layer and has been dated to a later period at the site. However, there have been significant methodological improvements in sample preparation for radiocarbon dating since the OxA-6732 date was produced, which for Late Glacial samples often result in more precise, older dates than previous determinations (Jacobi and Higham, 2011). We therefore decided to re-date UPN-276, to test if it were comparable in age to the other King Arthur's Cave samples. Neither of the two samples (UPN-266, UPN-267) from Sun Hole Cave show evidence of human processing, but both come from the Late Glacial Pleistocene layers (Collcutt *et al*. 1981) at the site, from which the human ulna and culturally-modified fauna was excavated.

Of the six teeth selected for analysis three are third molars (M3), one is a third or fourth premolar (P3/P4), one is a second molar (M2), and one is a first or second molar (M1/M2) (Table 1). Horse tooth development and enamel mineralisation occurs sequentially; the M1 mineralises from around 0 to 24 months of age; M2 and M3 mineralisation occurs between approximately 9 and 35 months, and 24 and 52 months of age, respectively; P3 and P4 mineralise between approximately 15 and 34 months, and 21 and 48 months, respectively (Hoppe *et al*., 2004). As horses are typically fully weaned by the age of 9-12 months (Duncan, 1992) it is possible that our M1/M2 and M2 samples (UPN-266 and UPN-272) may at least partly be influenced by milk consumption, which would offset $\delta^{18}O$ and $\delta^{13}C$ relative to adult values (Wright and Schwarcz, 1998).

For stable isotope analysis, the surface of each tooth was cleaned via mechanical abrasion prior to sampling. Sequential enamel samples were then collected along the growth axis of each tooth at intervals of c.3mm. Samples were taken through the whole depth of the enamel, stopping as close to the enamel-dentine junction as possible. The enamel mineralisation process varies in duration across the tooth (Bendrey *et al*. 2015). Taking a sample through the entire depth of enamel at a given point along the tooth growth axis provides a homogenised sample; in horse this may represent several weeks to months (Higgins and MacFadden, 2004). Thus, while down-tooth $\delta^{18}O$ and $\delta^{13}C$ variations represent seasonal dietary/environmental variations, the original input signal may be dampened by the mineralisation process.

For each tooth, enamel samples were taken from the cusp that showed the best level of preservation. Nonetheless, several of the teeth sampled were poorly preserved. Sample locations were measured relative to the enamel-root junction (ERJ), or the lowest preserved point of the tooth if the ERJ was absent, as was the case for the culturally fractured teeth. The absence of the ERJ in several samples means no common anchor point exists across the teeth and as such, the isotopic profiles cannot be used to infer the timing of any seasonal patterns (e.g. to assess season of birth). However, this does not prevent assessment of variations in the magnitude of seasonal differences. Further truncation of the isotope profiles may exist due to tooth wear of the occlusal surface.

Enamel samples (c. 5-7 mg) were treated with 0.1M acetic acid (0.1ml/mg) for 4 hours to remove potential diagenetic carbonates, and then thoroughly rinsed and freeze dried. Isotopic analysis was performed using a Gas Bench II coupled to a Delta Plus XP IRMS at the Bloomsbury Environmental Isotope Facility, UCL, with each sample being reacted with 100% orthophosphoric acid at 45°C for 4 hours in individual vessels. Results are reported relative to the international standard VPDB calibrated using the IAEA NBS19 standard, and long-term analytical precision is ±0.04‰ and ±0.08‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. A full list of all stable isotope results is available as a supplementary file from this link: https://ubss.org.uk/resources/procsupplement/28_2_221-238.xlsx.

Sample code	Collagen yield (%)	ä^{13}C (‰)	ä^{15}N (‰)	Atomic C/N	14C AMS lab code	^{14}C AMS date	Corrected age BP	Age calBP 68.2% probability	Age calBP 95.4% probability
UPN-276	not given	-20.4	1.3	3.3	OxA-6732	12,150 ± 100	n/a	14,142-13,846	14,388-13,747
	3.0	-20.4	1.6	3.3	OxA-V-2797-24	12,365 ± 55	12,410 ± 50	14,664-14,292	14,846-14,168
UPN-280	4.9	-21.3	0.3	3.2	OxA-V-2754-50	12,410 ± 50	12,450 ± 50	14,784-14,320	15,006-14,205

Table 2. *AMS radiocarbon data from UPN-276 and UPN-280.*
References: OxA-6732: Stevens and Hedges, 2004. All others :this study.

For radiocarbon dating, powdered dentine samples (c. 300 - 800 mg) were collected from samples UPN-276 and UPN-280. The dentine was processed at UCL following the Oxford Radiocarbon Accelerator Unit (ORAU) collagen extraction protocol (Brock *et al.* 2010). The sample was first demineralised in 0.5M HCl for 24 hours, then treated with 0.1M NaOH for 30 minutes to remove possible contaminating humic acids, followed by a further 0.5M HCl wash for 1 hour. The sample was then heated to 75°C in pH3 water for 48 hours, passed through a 9-um EeziTM filter and then through an ultrafilter (>30kD), and finally frozen and dried. The processed collagen was then submitted to ORAU for AMS analysis. Because the pre-treatment of the radiocarbon samples was done at UCL, it was necessary to correct for any potential contamination introduced into the samples during the pre-treatment process. Corrections were calculated through a series of measurements on known age samples to determine both the age and amount of carbon added to the sample during pre-treatment, following the method of Wood, *et al*. (2010).

RESULTS AND INTERPRETATION

UPN-280 was dated to 12,410 ± 50 ^{14}C yr BP (OxA-V-2754-50) giving a corrected date of 12,450 ± 50 14C yr BP, which corresponds to 15,006 – 14,205 cal. BP (Table 2). This date overlaps with the previously published radiocarbon dates on culturally modified horse remains from King Arthur's Cave (Jacobi and Higham, 2011), falling at the younger end of the range of dates. UPN-276 was dated to 12,365 ± 55 14C yr BP (OxA-V-2797-24) giving a corrected date of 12,410 ± 50 14C yr BP, which corresponds to 14,846 – 14,168 cal. BP (table 2). This date also overlaps with the radiocarbon dates on culturally-modified horse remains from the site and is around 450 years older than the previous date (OxA-6732) determination for this specimen (Stevens and Hedges, 2004). The overlap indicates the samples may come from the same phase of human activity at the site as the other dated specimens, although the possibility of more than one phase being represented within the range of dates cannot be ruled out.

Carbon stable isotopes results vary between different teeth, but no site-based differences are apparent (Table 3, Figure 3). Tooth-averaged δ^{13}C values range from 12.3‰ to 10.9‰, while overall variability in the samples analysed ranged from 12.6‰ to 10.6‰. Modern large herbivore tooth enamel δ^{13}C is typically enriched relative to the dietary intake by approximately 14.1 ± 0.5 ‰ (Cerling and Harris, 1999). Using this enrichment factor, an estimation of δ^{13}C dietary intake of 26.7 ± 0.5 to -24.7 ± 0.5 ‰ can be made, which is similar to the δ^{13}C values recorded for fossil seeds dating to the Late Glacial Interstadial from the Llanilid sedimentary sequence, South Wales (Lowe *et al*., 1999). Accounting for the influence of changing atmospheric CO^2 δ^{13}C these estimated Late Glacial δ^{13}C vegetation values are moderately higher than δ^{13}C values observed in a modern British grassland environment (Dungait *et al.,* 2008), and higher still than δ^{13}C values observed in a modern British woodland environment (Lockhead *et al*., 2008). Horse are primarily grazers, feeding on grasses and sedges in a range of habitats including open grasslands, meadows and woodland environments (Salter and Hudson, 1979; Crane *et al*., 1997; Pozdnyakova δ^{13}C., 2011). A range of habitats would have been available to horse at the time of the Late Upper Palaeolithic occupation of King Arthur's Cave and Sun Hole; pollen records are dominated by open-environment taxa such as grasses, sedges and herbs, but also contain evidence of limited juniper scrub, willow and birch (Walker *et al*., 2003; Hill *et al*., 2008). The higher δ^{13}C dietary estimates, when compared to δ^{13}C values measured in both modern British grassland and woodland vegetation,

Sample code	**Sampled enamel length (mm)**	**n**	**Tooth ŭ^{18}O (‰) average**	**Tooth ŭ^{18}O (‰) maximum**	**Tooth δ^{18}O (‰) minimum**	**Tooth δ^{18}O (‰) range**	**Tooth δ^{13}C (‰) average**	**Tooth δ^{13}C (‰) maximum**	**Tooth δ^{13}C (‰) minimum**	**Tooth δ^{13}C (‰) range**
UPN-266	61.0	11	-5.3	-4.4	-6.0	1.5	-11.3	-10.6	-11.9	1.4
UPN-267	56.6	11	-5.4	-4.3	-6.1	1.8	-11.3	-10.8	-11.6	0.8
UPN-272	51.5	7	-5.9	-5.5	-6.3	0.8	-12.3	-12.1	-12.6	0.6
UPN-275	43.2	13	-5.6	-4.7	-6.6	1.9	-11.4	-11.1	-11.7	0.6
UPN-276	35.7	10	-5.4	-4.7	-6.1	1.4	-10.9	-10.6	-11.2	0.7
UPN-280	35.6	8	-5.7	-5.2	-6.7	1.6	-11.5	-11.0	-11.8	0.8

Table 3. *Summary of $\delta^{18}O$ and $\delta^{13}C$* Equus ferus *tooth enamel results.*

suggest that growing conditions may have been less favourable than today, possibly due to lower nutrient or water availability. This could be due to lower precipitation amounts, higher temperatures, and/or less developed soils. The species composition of local flora inferred from pollen assemblages has also been used to infer limited soil development at this time (Walker *et al*., 2003).

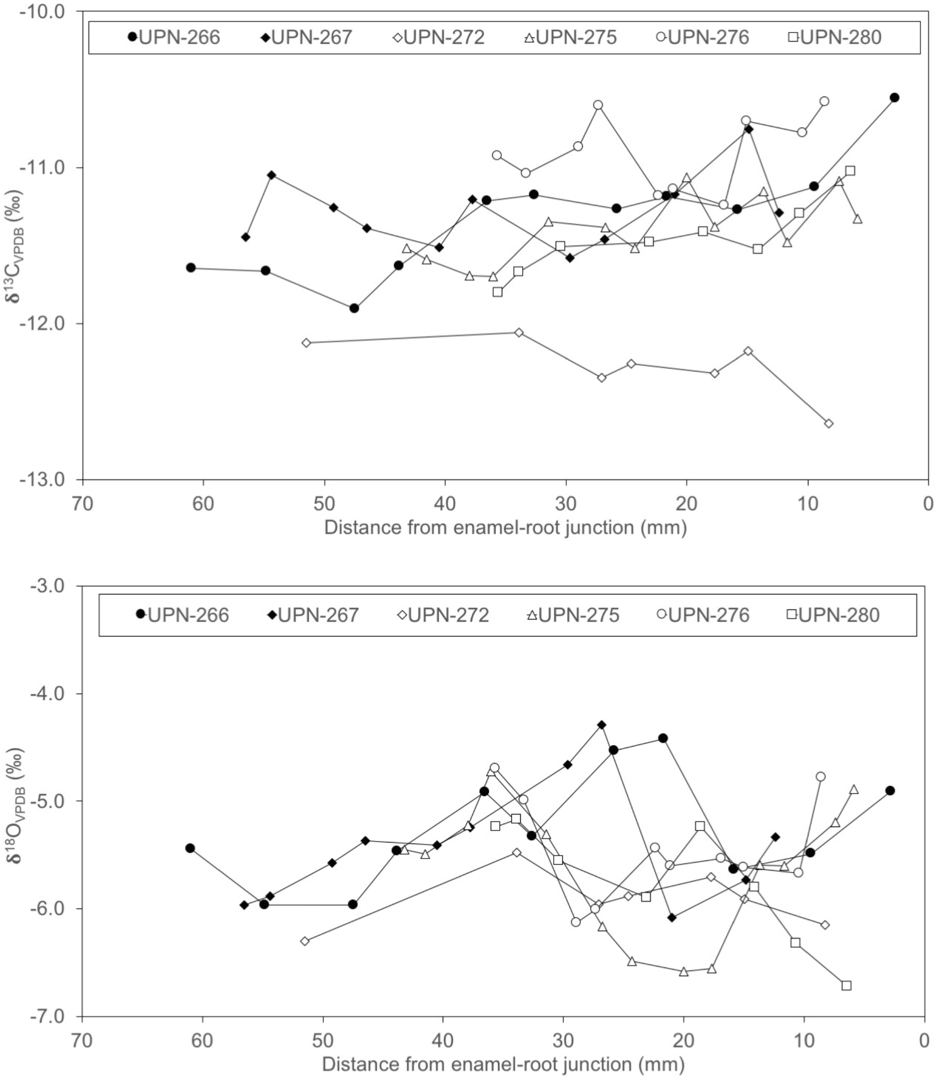

Figure 3. *$\delta^{13}C$ and $\delta^{18}O$ intra-tooth profiles for each* Equus ferus *tooth sampled. Open symbols indicate samples from King Arthur's Cave, filled symbols indicate samples from Sun Hole.*

The difference in $\delta^{13}C$ between different animals, particularly between UPN-272 and the other samples, represents variations in the $\delta^{13}C$ of diet between the animals. UPN-272 is one of the teeth (the other being UPN-266) we identified as potentially containing a milk signature. In humans, breastfeeding results in higher tooth enamel $\delta^{18}O$, while $\delta^{13}C$ is lower in infants prior to the introduction of solid foods (Wright and Schwarcz, 1998). While the $\delta^{13}C$ results from UPN-272 are indeed lower than the other samples, we argue that this is not due to a milk influence. Horses begin grazing from birth, steadily increasing the proportion of vegetation in the diet and decreasing rates of suckling throughout the first 6-12 months of life (Crowell-Davis *et al.*, 1985). This would produce a down-tooth $\delta^{13}C$ profile that steadily increased in value; this is not the pattern we observe for UPN-272 (Figure 3). Further, if suckling were influencing this sample, its $\delta^{18}O$ values could be expected to be higher than the other samples; results show this is not the case (Table 3, Figure 3). There is also no evidence of a suckling signal in UPN-266 (table 3, fig. 3). As such, we maintain that the $\delta^{13}C$ results reflect an environmentally-derived dietary signature for all teeth sampled. Differences between intra-tooth $\delta^{13}C$ profiles could be produced by animals exploiting different micro-habitats within the landscape or could represent short-term variability in environmental conditions, as each tooth is very unlikely to have formed during the exact same two-year period.

No clear pattern of down-tooth $\delta^{13}C$ variation is apparent in the data. There are various possible interpretations; the response of vegetation to seasonal climate extremes may not have been sufficient to influence its $\delta^{13}C$ to any great degree; or horses may have consumed different vegetation in different seasons, effectively over-writing any climate induced seasonal variation in vegetation $\delta^{13}C$ or animal physiological and tooth mineralisation processes have dampened the enamel $\delta^{13}C$ relative to the dietary input.

Average oxygen stable isotope results are similar across all analysed teeth. Tooth averaged values range from 5.9‰ to 5.3‰; the overall variability in recorded values ranges from 6.7‰ to 4.3‰ (Table 3). While not statistically significant, minimum $\delta^{18}O$ values from King Arthur's Cave for UPN-272, -275, and -280 are lower than for the Sun Hole samples (Figure 4). This may be noteworthy as it suggests that these animals at King Arthur's lived under colder climatic conditions, an interpretation that appears to support King Arthur's Cave being occupied during a slightly earlier time period than Sun Hole. UPN-276 from King Arthur's Cave displays higher $\delta^{18}O$, comparable to the Sun Hole data (Figure 4). While its date (OxA-V-2797-24) overlaps with the other King Arthur's Cave horse dates, it falls at the younger end of the date range. Again, this could be indicative of a slightly later, warmer climate period, although no firm conclusions can be drawn from the available data.

The magnitude of down-tooth $\delta^{18}O$ variation, which indicates seasonal climate variations, ranges from 1.4‰ to 1.9‰, with the exception of UPN-272, which displays a considerably lower magnitude of within tooth variation (0.8‰). Notably, this is the tooth that is also the outlier in the $\delta^{13}C$ data. While the overall variation recorded in the enamel $\delta^{18}O$ is much lower than the variability observed in present day precipitation $\delta^{18}O$ in the British Isles, intra-tooth variation does approximate the modern day long-term average difference between summer and winter precipitation $\delta^{18}O$ (c. 1.5‰, Darling *et al*, 2003). The relatively consistent magnitude of down-tooth variation thus likely indicates seasonal variations in drinking water $\delta^{18}O$, dampened by tooth mineralisation processes, which are most likely linked to the seasonal temperature cycle.

Estimates of drinking water $\delta^{18}O$ and palaeotemperatures can be made through a series of known quantitative relationships between enamel $\delta^{18}O$ and meteoric $\delta^{18}O$, and meteoric $\delta^{18}O$ and air temperature, with corrections applied for glacial-interglacial changes in ocean $\delta^{18}O$ and geographical gradients in meteoric $\delta^{18}O$(Arppe and Karhu, 2010; Bryant *et al.*, 1996; Coplen *et* *al*., 2002; Darling *et al*., 1997; Degaldo Heurtas *et al*., 1995; Pryor *et al*., 2014; Rozanski *et al*., 1992). However, it should be recognised that with each data conversion, associated uncertainties increase (Pryor *et al*., 2014). Further, there is no single standardised method to relate meteoric $\delta^{18}O$ to air temperature (see Pryor *et al*., 2014 for discussion), and no consensus on the most appropriate way to account for potential differences between modern and past meteoric $\delta^{18}O$–temperature relationships. As such, while geographical gradients in meteoric $\delta^{18}O$–temperature appear to have remained remarkably similar since the Late Pleistocene for the British Isles (Darling *et al*., 2003), all estimates should be treated with a degree of caution.

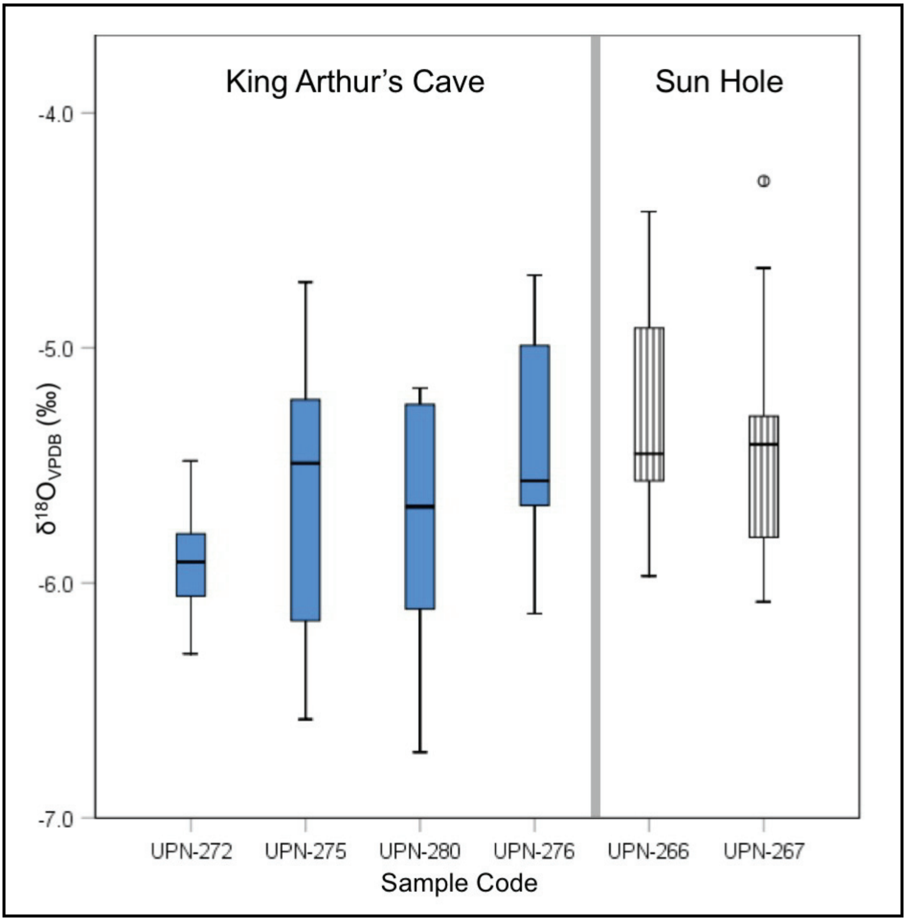

Figure 4. *Boxplot of $\delta^{18}O$ values for each tooth*.

Our data estimates drinking water $\delta^{18}O$ for the horses from King Arthur's Cave and Sun Hole to have averaged -8.4 ± 0.7‰, which may have ranged on a seasonal basis from around -10.2 ± 2.5‰ to -6.7 ± 2.5‰ (see supplementary data file for full details: https://ubss.org.uk/resources/procsupplement/28_2_221-238.xlsx.). A high degree of uncertainty is associated with the seasonal estimations, and it is likely the true variation in seasonal values has been altered by the enamel mineralisation process (Hoppe et al., 2004). Groundwater

$\delta^{18}O$ in southwest England at the end of the Late Pleistocene has been estimated to be around -8‰, in contrast to present day measurements of around -7‰ (Darling *et al.*, 2003; 1997). Within the British Isles, where evaporative enrichment of surface water is low, long term precipitation and groundwater $\delta^{18}O$ have been shown to be reasonable approximations of one another (Darling *et al.*, 2003). We therefore suggest that our data represents surface water $\delta^{18}O$ during the period of human activity at Kings Arthur's Cave and Sun Hole. Based on this, average air temperatures can be estimated. Depending on the method used (see supplementary file for details) temperature estimates range from 7.6 ± 2.2 °C to 10.1 ± 1.4 °C (Arppe and Karhu, 2010; Pryor *et al.*, 2014; Rozanski *et al.*, 1992). While there is a high degree of uncertainty around these estimates, all are lower than the current (1961-1990) average annual temperature of 12.8°C for southwest England and Wales (Met Office, 2017).

Overall, our results suggest that local to King Arthur's Cave and Sun Hole, at the time of the post-LGM recolonisation of the British Isles, temperatures had increased significantly from their low during the LGM at least at an annual average scale. Temperatures were approaching, but were still lower than, modern annual averages. We cannot reliably assess seasonal temperature variability based on our results, due to the dampening introduced by the enamel mineralisation process and the large uncertainties associated with enamel-based palaeotemperature estimates (Arppe and Karhu 2010; Hoppe *et al.*, 2004; Pryor *et al.*, 2014). The elevated carbon isotope values in the vegetation signal, relative to the present day, likely indicate a nutrient and/or water limited growing environment within the habitats the horse were feeding. The oxygen isotope results indicate that this was unlikely to have been caused by temperature extremes, and therefore may indicate more arid environmental conditions, or less developed/more minerogenic soils. The variability observed between different teeth suggests that year to year conditions were variable, with fluctuations in temperatures and moisture levels apparent.

ENVIRONMENTAL AND ARCHAEOLOGICAL CONCLUSIONS

The occupation of the British Isles after the LGM is largely considered as a northwestward expansion of Magdalenian people from potential areas such as the Paris Basin, the Belgium Ardennes, and the German Rhineland. These were mobile groups who utilised seasonal hunting camps, and whose settlement and subsistence strategies appear to have been determined by resource availability, particularly of large prey such as horse and reindeer (Enloe and Audouze 2010; Leesch *et al*. 2012; Miller, 2012). As King Arthur's Cave and Sun Hole are situated in valleys, it is conceivable that their function may have been as temporary bases for targeting nearby wild horse populations. The environmental conditions would have been of great importance to the behavioural ecology of horse in these landscapes and therefore a factor in human resource exploitation decisions.

Overall, the climate and environment local to King Arthur's Cave and Sun Hole at 15.2 – 14.6 ka was relatively mild, although most probably still cooler than present day. The vegetation appears to have been experiencing some degree of environmental stress, which we believe most likely relates to nutrient- and water- limiting conditions. Based on our results, it appears temperatures rose earlier in southwest Britain than in Greenland (c. 14.7ka), which corroborates findings from other palaeoenvironmental studies (e.g. Walker *et al.*, 2003). However, this is the first study to directly link such palaeoenvironmental inferences with the human reoccupation of the British Isles after the LGM. Our data indicates King Arthur's Cave was occupied under colder climate conditions than Sun Hole, which could support the interpretation that King Arthur's Cave was occupied at a slightly earlier time than at Sun Hole Cave.

Regardless of the possible chronological differences between the two sites, the presence of horse in both areas indicates that vegetation was sufficiently developed to support large herbivore populations. The climatic warming associated with the Late Glacial Interstadial has been linked to the gradual replacement of pioneer steppic plants by more shrub and woodland species (Pettit and White, 2012; Walker *et al*., 1994). However, the dominance of horse in the faunal assemblages, who have a dietary preference for vegetation types typically found in open landscapes, combined with the environmental stress we interpret from our data, suggests a still relatively marginal landscape, lacking in ecological maturity.

ACKNOWLEDGEMENTS

We are very grateful to the UBSS Museum for supporting this project and granting permission to work on the specimens analysed in this study. In particular, we would like to thank Linda Wilson for her help with the sampling application process and in facilitating sample collection at the Museum, as well as Allan Summerfield and Wendy Russ for their assistance during our sample collection visit to the Museum. This work was funded by a European Research Council Consolidator Grant to RS (UP-NORTH, ID: 617777).

REFERENCES

ApSimon, A.M., Smart, P.L., Macphail, R., Scott, K. and Taylor, H., 1992. King Arthur's Cave, Whitchurch, Herefordshire: reassessment of a Middle and Upper Palaeolithic, Mesolithic and Beaker site. *Proceedings of the University of Bristol Spelaeological Society.* **19.** 2. 183-249.

Arppe, L. and Karhu, J.A. 2010. Oxygen isotope values of precipitation and the thermal climate in Europe during the middle to late Weichselian ice age. *Quaternary Science Reviews.* **29.** 9–10. 1263-1275.

Barton, R.N.E. 1997. Fifth interim report on the survey and excavations in the Wye Valley, 1997 and new AMS Radiocarbon dating results from Madawg Rockshelter. *Proceedings of the University of Bristol Spelaeological Society.* **21.** 1. 99-108.

Bendrey, R., Vella, D., Zazzo, A., Balasse, M. and Lepetz, S., 2015. Exponentially decreasing tooth growth rate in horse teeth: implications for isotopic analyses. *Archaeometry.* **57.** 6. 1104-1124.

Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., Kaplan, J.O., Andreev, A., Bezrukova, E., Blyakharchuk, T., Jankovska, V. and Khazina, I., 2017. Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quaternary Science Reviews.* **157**. 80-97.

Brock, F., Higham, T., Ditchfield, P., and Bronk Ramsey, C. 2010. Current pretreatment methods for AMS radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). *Radiocarbon.* **52.** 1. 103-112.

Brooks, S.J. and Langdon, P.G., 2014. Summer temperature gradients in northwest Europe during the Lateglacial to early Holocene transition (15–8 ka BP) inferred from chironomid assemblages. *Quaternary International.* **341.** 80-90.

Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., and Genna, B.J. 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. *Geochimica et Cosmochimica Acta.* **60.** 24. 5145-5148.

Cerling, T. E., and 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.

Collcutt, S.N., Currant, A.P., and Hawkes, C.J. 1981. A further report on the excavations at Sun Hole, Cheddar. *Proceedings of the University of Bristol Spelaeological Society.* **16.** 1. 21-38.

Coope, G.R. and Lemdahl, G. 1995. Regional differences in the Lateglacial climate of northern Europe based on coleopteran analysis. *Journal of Quaternary Science.* **10.** 4. 391-395.

Coplen, T.B., Hopple. J.A., Böhlke, J.K., Peiser, H.S., Rieder, S.E., Krouse, H.R., Rosman, K.J.R., Ding, T., Vocke Jr, R.D., Révész, K.M., Lamberty, A., Taylor, P., and De Bièvre, P. 2002. *Compilation of Minimum and Maximum Isotope Ratios of Selected Elements in Naturally Occurring Terrestrial Materials and Reagents.* Water-Resources Investigations Report 01-4222.

Crane, K.K., Smith, M.A., and Reynold, D. 1997. Habitat selection patterns of feral horses in southcentral Wyoming. *Journal of Range Management*. **50.** 374-380.

Crowell-Davis, S.L., Houpt, K.A., and Carnevale, J. 1985. Feeding and drinking behavior of mares and foals with free access to pasture and water. *Journal of Animal Science*. **60**. 883-889.

Darling, W.G., Edmunds W.M., and Smedley, P.L. 1997. Isotopic evidence for palaeowaters in the British Isles. *Applied Geochemistry.* **12.** 6. 813-829.

Darling, W.G., Bath, A.H., and Talbot, J.C. 2003. The O & H stable isotopic composition of fresh waters in the British Isles. 2. Surface waters and groundwater. *Hydrology and Earth System Sciences*. **7.** 183-193.

Degaldo Heurtas, A., Iacumin, P., Stenni, B., Sánchez Chillón, B., and Longinelli, A. 1995. Oxygen isotope variation of phosphate in mammalian bone and tooth enamel. *Geochemica et Cosmochimica Acta.* **59.** 20. 4299-4305.

Duncan, P. 1992. *Horses and grasses, the nutritional ecology of equids and their impact on the Camargue*. Ecological Studies 87. London. Springer.

Dungait J.A.J., Docherty G., Straker V., and Evershed R.P. 2008. Interspecific variation in bulk tissue, fatty acid and monosaccharide $\delta^{13}C$ values of leaves from a mesotrophic grassland plant community. *Phytochemistry.* **69.** 2041–2051.

Elias, S.A., and Matthews, I.P., 2014. A comparison of reconstructions based on aquatic and terrestrial beetle assemblages: Late glacial–Early Holocene temperature reconstructions for the British Isles. Quaternary International 341, 69-79.

Enloe, J.G., and Audouze, F. 2010. The Magdalenian Site of Verberie (Le Buisson Campin). In: Zubrow, E. B.W., Audouze, F. and Enloe J.G. (Eds) *The Magdalenian Household: Unraveling Domesticity*. Albany. State University of New York Press.

Feranec, R.S., Hadly, E.A., and Paytan, A. 2009. Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **271**. 1. 153-160.

Higgins, P. and MacFadden, B.J., 2004. “Amount Effect” recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **206.** 3. 337-353.

Hill, T.C.B, Woodland, W.A., Spencer, C.D., Marriott, S.B., Case, D.J. and Catt, J.A., 2008. Devensian Late-glacial environmental change in the Gordano Valley, North Somerset, England: a rare archive for southwest Britain. *Jounral of Paleolimnology.* **40.** 431-444.

Hoppe, K.A., Stover, S.M., Pascoe, J.R. and Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **206.** 3. 355-365.

Jacobi, R.M. and Higham, T.F.G., 2009. The early Lateglacial re-colonization of Britain: new radiocarbon evidence from Gough’s Cave, southwest England. *Quaternary Science Reviews.* **28.** 19. 1895-1913.

Jacobi, R. and Higham, T., 2011. The Later Upper Palaeolithic recolonisation of Britain: new results from AMS radiocarbon dating. In: Ashton, N., Lewis, S, Stringer, C., (Eds.), *The ancient human occupation of Britain.* Developments in Quaternary Science. **14.** 223-247.

Kindler, P., Guillevic, M., Baumgartner, M., Schwander, J., Landais, A., Leuenberger, M. 2014. Temperature reconstruction from 10 to 120 kyr b2k from the NGRIP ice core. *Climate of the Past.* **10.** 887-902

King, S.R.B. 2002. Home range and habitat use of free-ranging Przewalski horses at Hustai National Park, Mongolia. *Applied Animal Behaviour Science.* **78.** 2-4. 103-113.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences.* **26.** 1. 573-613.

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 Sciences.* **107.** 46. 19691-19695.

Leesch, D., Müller, W., Nielsen, E. and Bullinger, J., 2012. The Magdalenian in Switzerland: re-colonization of a newly accessible landscape. *Quaternary International.* **272.** 191-208.

Lister, A.M. and Stuart, A.J. 2008. The impact of climate change on large mammal distribution and extinction: Evidence from the last glacial/interglacial transition. *Comptes Rendus Geoscience.* **340.** 9–10. 615-620.

Lockheart M.J., Van Bergen P.F., and Evershed R.P. 1997. Variations in the stable carbon isotope compositions of individual lipids from the leaves of modern angiosperms: Implications for the study of higher land plant-derived sedimentary matter. *Organic Geochemistry* **26.** 137–153.

Lowe, J.J., Birks, H.H., Brooks, S.J., Coope, G.R., Harkness, D.D., Mayle, F.E., Sheldrick, C., Turney, C.S.M. and Walker, M.J.C. 1999. The chronology of palaeoenviornmental changes during the Last Glacial-Holocene transition: towards an event stratigraphy for the British Isles. *Journal of the Geological Society, London*. **156.** 397-410.

Met Office. 2017. UKCP09: *Met Office gridded and regional land surface climate observation datasets*. Centre for Environmental Data Analysis. Accessed January 2019: http://catalogue.ceda.ac.uk/uuid/87f43af9d02e42f483351d79b3d6162a

Miller, R., 2012. Mapping the expansion of the Northwest Magdalenian. *Quaternary International.* **272.** 209-230.

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

Pettitt, P. and White, M., 2012. *The British Palaeolithic: human societies at the edge of the Pleistocene world*. London. Routledge.

Pozdynyakova, M.K., Zharkikh, T.L., Yasinetskaya, N.I., Kolesnikov, M.P. 2011. Quantitative assessment of feeding in a free-ranging group of Przewalski horses, *Equus przewalkii*, in a steppe habitat (the Askania Nova Biosphere Reserve). *Biology Bulletin*. **38.** 7. 726-734.

Pryor, A.J.E, Stevens, R.E., O'Connell, T.C., and 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.

Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H. and Gkinis, V., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews.* **106.** 14-28.

Rozanski, K., Araguás-Araguás, L., Gonfiantini, R. 1992. Relation between long-term trends of oxygen-18 isotope composition of precipitation and climate. *Science.* **258.** 981-985.

Salter, R.E. and Hudson, R.J. 1979. Feeding ecology of feral horses in western Alberta. *Journal of Range Management.* **32.** 3. 221-225.

Schrag, D.P., Adkins, J.F., McIntyre, K., Alexander, J.L., Hodell, D.A., Charles, C.D., and McManus, J.F. 2002. The oxygen isotopic composition of seawater during the Last Glacial Maximum. *Quaternary Science Reviews.* **22.** 331-342.

Sharp, Z.D. and Cerling, T.E., 1998. Fossil isotope records of seasonal climate and ecology: straight from the horse's mouth. *Geology.* **26.** 3. 219-222.

Stevens, R.E., and Hedges, R.E.M. 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.

Taylor, H., 1928. King Arthur's Cave, near Whitchurch, Ross-on-Wye [Gloucestershire] Second Report: excavations in 1926 and 1927. *Proceedings of the University of Bristol Spelaeological Society.* **3.** 2. 59-83.

Walker, M.J.C., Bohncke, S.J.P., Coope, G.R., O'Connell, M., Usinger, H., and Verbrugeen, C. 1994. The Devensian/Weichselian Late-glacial in northwest Europe (Ireland, Britain, north Belgium, The Netherlands, northwest Germany). *Journal of Quaternary Science*. **9.** 2. 109-118.

Walker, M.J.C., Coope, G.R., Sheldrick, C., Turney, C.S.M., Lowe, J.J., Blockley, S.P.E. and Harkness, D.D., 2003. Devensian Lateglacial environmental changes in Britain: a multi-proxy environmental record from Llanilid, South Wales, UK. *Quaternary Science Reviews.* **22.** 5. 475-520.

Wood, R, E., Bronk Ramsey, C., and Higham, T.F.G. 2010. Refining background corrections for radiocarbon dating of bone collagen at ORAU. *Radiocarbon.* **52.** 2. 600-611.

Wright, L.E. and Schwarcz, H.P. 1998. Stable carbon and oxygen isotopes in human tooth enamel: identifying breastfeeding and weaning in prehistory. *American Journal of Physical Anthropology*. **106.** 1-18.

Zickel, M., Becker, D., Verheul, J., Yener, Y., and Willmes, C. 2016. *Paleocoastlines GIS dataset*. CRC806-Database, doi: 10.5880/SFB806.20. Accessed January 2019: https://crc806db.uni-koeln.de/layer/show/327/

Hazel Reade
UCL Institute of Archaeology,
31-34 Gordon Square, London, WC1H 0PY, UK

Fiona Holloran
UCL Institute of Archaeology,
31-34 Gordon Square, London, WC1H 0PY, UK

Jennifer A. Tripp
UCL Institute of Archaeology,
31-34 Gordon Square, London, WC1H 0PY, UK
Department of Chemistry, University of San Francisco,
2130 Fulton Street, San Francisco, CA 94117, USA

Sophy Charlton
Department of Earth Sciences, Natural History Museum,
Cromwell Road, London SW7 5BD, UK
PalaeoBARN, School of Archaeology,
1 South Parks Road, Oxford, OX1 3TG, UK

Anne-Lise Jourdan
UCL Department of Earth Sciences,
Gower Street, London, WC1E 6BT, UK

Rhiannon E. Stevens
UCL Institute of Archaeology,
31-34 Gordon Square, London, WC1H 0PY, UK