# Nature of the beast? Complex drivers of prey choice, competition and resilience in Pleistocene wolves (*Canis lupus* L., 1754)

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## Abstract

The wolf (*Canis lupus* L., 1754) has been a major keystone predator in the Palaearctic since the late Middle Pleistocene. Today, wolves display considerable dietary plasticity over their range, characterised by their preferential consumption of large and medium-sized wild ungulates, supplemented by smaller prey, including small mammals, fish and plant foods. However, the origins of this dietary flexibility (arguably the key to the wolf's long persistence) are poorly understood in terms of responses to different drivers over the course of the Pleistocene, including changing climate, environment and competition from other large carnivores. Here, in the first study using direct palaeodietary measurements on British fossil wolves, carnivore competitors and potential prey species, we compare stable isotope ($\delta^{13}C$ and $\delta^{15}N$) evidence from three sites representing a late Middle Pleistocene interglacial (Marine Oxygen Isotope Stage [MIS] 7c-a, c.220-190kya), the early Devensian (last cold stage, MIS 5a, c.90-80kya) and the middle Devensian (MIS 3, c. 60-25kya). The results reveal clear patterns of changing wolf prey choice through time. Notwithstanding issues of collagen preservation obscuring some dietary choices in the oldest samples, both small and large prey (hare, horse) were taken by wolves in the MIS 7c-a interglacial, large prey only (reindeer, bison) during MIS 5a and a broader range of large prey items (horse, woolly rhinoceros, bison) during MIS 3. The results also reveal two further important aspects: (1) that where wolves and spotted hyaenas co-existed, they occupied the same dietary niche and the former was not outcompeted by the latter, and (2) that the stable isotope evidence indicates prey choices during MIS 7c-a and MIS 3 that are not in synchrony with palaeodietary reconstructions from previous studies based on wolf cranio-dental morphology. This establishes for the first time a likely lag between changing predatory behaviour and morphological response but is interestingly not seen in the wolves from MIS 5a, where the prey choices are echoed by the cranio-dental morphology.

**Keywords**: Wolves; *Canis lupus*; Pleistocene; stable isotopes; palaeodiet; morphology

## 1. Introduction

Wolves, *Canis lupus* L. 1754, are successful keystone predators of modern Palaearctic ecosystems. They are able to modulate their choice in prey, and hence diet, based on resource availability and regional environmental conditions. Extensive studies of wolf diet in North America (Voight et al. 1976; Fritts and Mech, 1981; Paquet, 1992; Boyd et al. 1994) and in Europe (e.g. Kojola et al. 2004; Nowak et al. 2011; Jedrzejewski et al. 2012; Wagner, 2012) have revealed that wolves typically predate large wild ungulates such as elk *Alces alces*, wapiti *Cervus canadensis*, reindeer *Rangifer tarandus*, and red deer *Cervus elaphus*, alongside medium sized species such as wild boar *Sus scrofa,* white-tailed deer *Odocoileus virginanus* and roe deer *Capreolus capreolus.* Of note is that consumption of livestock is generally low but is directly dependent on the abundance of wild ungulates, which are preferred as a more risk-free resource (Meriggi and Lovari, 1996; Imbert et al. 2016; Janeiro-Otero et al. 2020). Nevertheless, in some regions, seasonal resource availability, the selection of some prey types over others, and the demands of provisioning for young have allowed wolves to add berries (Homkes et al. 2020), smaller mammalian prey such as hare *Lepus* spp*.* and beaver *Castor fiber* (Mysłajek et al. 2019), spawning Pacific salmon *Oncorhyncus* spp*.* (Stanek et al. 2017) and even freshwater fish such as northern pike *Esox lucius* as an exceptional short-term prey item (Gable et al. 2018), into their dietary repertoire. It therefore appears that by having a wide menu of prey and other food types, wolves are afforded an unusually high level of foraging behavioural flexibility and dietary resilience, a factor that has undoubtedly facilitated their widespread geographical dispersal and presence in diverse habitats.

Yet, dietary flexibility and ecological resilience are not recent traits and a deeper understanding of the long-term evolution of these traits is therefore important for wolf conservation biology today. In Pleistocene wolf populations, morphological plasticity in the cranio-dental feeding apparatus provides clues as to how wolves were able to survive rapidly changing climatic and ecological conditions typical of this period (Fox-Dobbs et al. 2008; Leonard et al. 2007). In Britain, for example, palaeodietary-related morphological variation was characterised by temporal changes in jaw strength, molar crushing and carnassial slicing ability that implied differences in the proportion of flesh to non-flesh foods consumed and the ability to manipulate carcasses at different climatic periods (Flower, 2014; Flower and Schreve, 2014). When paired with concomitant changes in body mass (Flower, 2014; 2016), together these provide strong evidence for wolves adapting to variations in prey type. Hence, morphological plasticity and behavioural flexibility apparently enabled Pleistocene wolves to cope better with climatic and environmental change than many other competing large carnivores.

In general, flexible rather than specialist behaviour was an advantage during the early Middle Pleistocene (~500kya) when changes in ungulate diversity, driven by climatic and environmental change, led to the collapse of the once highly-diverse Early Pleistocene carnivore community, and the rise of the dominant wolf, lion and spotted hyaena group to become the top predators of the Late Pleistocene (Turner, 1992). Over time, wolves progressively became more adept at surviving Pleistocene climatic and environmental change, whereas in contrast, spotted hyaena (another social and very abundant large carnivore) became extirpated from north western Europe between 35-31ka (Stuart and Lister, 2014; Jones, 2019). Hence, morphological plasticity and behavioural flexibility also provided wolves with an advantage in the face of structural changes in the coeval carnivore community and inter-species competition.

Nevertheless, key questions remain over: i) the nature of these prey choices, ii) the impact competitive interactions with coeval carnivores had on wolf prey choice and iii) the extent to which cranio-dental morphology was in step with dietary behaviour, or whether a time lag existed between morphological and behavioural responses.

To address these questions, direct measurement of British Pleistocene wolf palaeodiet through time was undertaken using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from bone collagen, in combination with comparisons to established Pleistocene wolf morphometric data. Whilst dietary-specific cranio-dental morphology can provide indirect evidence of phenotypic variation over relatively longer timescales, analysis of stable isotope geochemistry from bone collagen can reveal dietary signatures in the years immediately prior to death. This is because bone collagen can reflect isotopic trends over shorter timescales as bone continuously remodels over several years of an animal’s life (Koch, 2008).

The composition of carbon and nitrogen in animal bone collagen is primarily derived from dietary protein, hence the $\delta^{13}C$ and $\delta^{15}N$ values of a consumer will reflect an average of what has been consumed. The use of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from bone collagen in Late Pleistocene (<60ka) palaeobiological studies is well established (for a review, see Bocherens, 2015), including, but not limited to, reconstructions of ungulate diet and derived inferences on local and more regional-scale palaeoecology (e.g. Richards & Hedges, 2003; Stevens and Hedges, 2004; Drucker et al. 2011; Drucker et al. 2012), whilst others have focused on trophic level reconstructions of biomes such as the Eurasian mammoth steppe and Beringia (e.g. Coltrain et al. 2004; Fox-Dobbs et al. 2008; Yeakel et al. 2013; Drucker et al. 2018). Key to this work, however, are studies with predators as their central focus, since these can spotlight prey choice and predator-prey interactions during the Pleistocene (e.g. Leonard et al. 2007; Bocherens et al. 2011, Bocherens, 2015; Baumann et al. 2020), thereby allowing the reconstruction of complex and changing food webs in the past.

In carnivore collagen, $\delta^{13}C$ and $\delta^{15}N$ values primarily reflect the $\delta^{13}C$ and $\delta^{15}N$ values of their herbivore prey and subsequent higher trophic level. However, this simplification is complicated by isotopic fractionation within their soft tissues, as well as a host of ecological, environmental and climatic factors. For instance, $^{13}C$ in herbivore collagen is driven by plant type, which in turn is controlled by C3 or C4 photosynthetic pathways related to environmental and climatic factors (for a review, see Bocherens, 2003), whilst $^{15}N$ is controlled by type of plant consumed, which is itself driven by factors such as temperature, aridity and moisture availability, as well as altitude and soil maturity (Drucker et al., 2011, 2012; Bocherens, 2015).

This is the first predator-centric stable isotope study for Pleistocene Britain using wolves as a lens to examine prey choice and competition. Previously, wolf specimens from a range of sites covering interglacial, interstadial and glacial conditions, and correlated respectively with Marine Oxygen Isotope Stage (MIS) 7c-a (c.220-190ka), MIS 5a (c. 90-80ka) and MIS 3 (c. 60-25ka) were found to exhibit high levels of palaeodietary and behavioural flexibility based on their cranio-dental morphology (Flower, 2014; Flower and Schreve, 2014). These different climatic stages thus provided 'snap shots' of divergent dietary behaviours that were thought to be driven by a combination of competition and environmental triggers. Crucially, these findings provided a unique opportunity to re-examine morphology in light of the new stable isotope data presented here.

Although most Pleistocene stable isotope studies relying on bone collagen remain firmly within the assumed 100kya limit for successful collagen retrieval (Hedges et al. 2005), viable collagen extraction in older skeletal material has occasionally been achieved for assemblages of 120kya (Scladina Cave, Bocherens et al., 1999 and Neumark-Nord 2, Britton et al., 2012) and c. 200ka (Stanton Harcourt, Jones et al. 2001). By including a much larger new dataset of wolf, other large carnivore and herbivore material from MIS 7, and supplementing this with additional stable isotope measurements from sites representing different parts of the last cold stage, the present study offers the first opportunity to examine changing wolf interactions with both the wider carnivore guild and prey spectrum over a significantly longer timescale.

## 1.2. Sites

Three faunal assemblages from cave sites in southwest Britain (Fig. 1) were selected for the dietary isotope study based on: i): prior knowledge of the wolf remains in the assemblage (Flower, 2014), ii) knowledge of the other fauna present (Schreve, 1997; Currant, 2004), iii) taphonomic comparability of the assemblages and iv) close geographical proximity of the sites in southwest Britain, thereby allowing more robust intercomparison.

The Hutton Cave faunal assemblage, interpreted as the vestiges of a wolf den (Currant, 2004), is characterised by an abundance of remains of horse (*Equus ferus*) and the presence of a late morphotype of steppe mammoth, *Mammuthus trogontherii*. Although no absolute dates are available from this locality, biostratigraphical comparison of the assemblage indicates that it is typical of the Sandy Lane Mammal Assemblage-Zone (MAZ) of Schreve (2001a), which has been dated elsewhere to the second half of the penultimate (MIS 7) interglacial (Candy and Schreve, 2007). Three temperate substages of comparable magnitude are recognised within MIS 7, most recently divided into two discrete interglacials: MIS 7e and MIS 7c-a (Berger et al. 2015), with the latter episode (with which the Hutton Cave assemblage is correlated) characterised by cool-temperate and predominantly open grassland conditions (Schreve, 2001b; Murton et al. 2016). Additional elements of the potential prey base available to wolves included mountain hare (*Lepus timidus*), wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) (Currant, 2004). Of the major predators, wolf, lion (*Panthera spelaea*) and spotted hyaena (*Crocuta crocuta*) are all present, with the mesocarnivores represented by red fox (*Vulpes vulpes*) and wild cat (*Felis silvestris*) (Schreve, 1997).

Banwell Bone Cave is the type site for the Banwell Bone Cave MAZ (Currant and Jacobi, 2001; 2011) and has been attributed to the Early Devensian (Weichselian), the early part of the last cold stage. Assemblages of this age have been correlated with MIS 5a (Gilmour et al. 2007; Currant and Jacobi, 2011; Stevens and Reade, 2021). The classic low diversity fauna of Britain at this time featured bison *Bison priscus,* reindeer *Rangifer tarandus* and mountain hare *Lepus timidus,* in addition to mesocarnivores including red fox, arctic fox *Alopex lagopus,* and wolverine *Gulo gulo.* Notably, brown bear *Ursus arctos* is the only other large carnivore present apart from wolf, with both *P. spelaea* and *C. crocuta* absent from Britain (Turner, 2009; Currant and Jacobi, 2001, 2011) at this time.

The final assemblage comes from the site of Sandford Hill and is largely the product of accumulation by spotted hyaenas (Currant, 2004). The presence of horse, woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) in association with spotted hyaena, bison and reindeer is considered typical of the Pin Hole MAZ of the Middle Devensian (Weichselian), correlated with MIS 3 (Currant and Jacobi, 2011). A radiocarbon date on *C. crocuta* yielded a corresponding age estimate of 36 ±1.9 ka (Burleigh et al. 1982), although given recent advances in collagen ultrafiltration methods, re-dating of this specimen would now be advised (Jacobi et al. 2006). Mountain hare and red deer make up the complement of herbivores known from the site, with wolf, red fox, lion and brown bear also present.

## 2. Material and Methods

### 2.1. Material

Permission for destructive sampling was granted from the South-West Heritage Trust, Taunton, UK, where the specimens are housed. The assemblages of Hutton Cave, Banwell Bone Cave and Sandford Hill are important sites for understanding the Pleistocene fauna and palaeoenvironment of the Mendip Hills in Somerset. Initially included in the wolf morphometric analyses of Flower (2014), knowledge of the faunal composition, chronology and palaeoenvironmental context of each assemblage (see Schreve, 1997; Currant, 2004) aided in choosing likely competitors and potential prey species from each assemblage. Understanding carnivore prey choice and competitive interactions relies on the ability to distinguish the $\delta^{13}C$ and $\delta^{15}N$ of their prey, and hence the inclusion, wherever possible, of all likely prey species present within these reconstructed communities is important (Bocherens, 2015). Based on this reasoning, the aim of this isotope study was to include the best possible range of likely wolf prey species, in addition to their coeval competitors, tempered by state of preservation and availability of specimens for sampling.

## 2.2. Methods

All sampling and analyses were undertaken at the National Environmental Isotope Facility (NEIF), British Geological Survey, Keyworth, Nottingham, UK. Samples were taken from compact areas of bone avoiding areas of morphological or taphonomic interest. Before sampling for collagen extraction, all samples were pre-screened in order to assess collagen preservation by taking ~1mg of whole bone powder from each specimen (Bocherens et al. 1997). The surface of each sample was lightly abraded using a diamond-tipped burr and dental drill to remove surface contamination.  1 mg of bone powder was then removed and %N measured using a Costech Elemental Analyser (EA) on-line to a VG TripleTrap and Optima duel-inlet mass spectrometer with %N calibrated against an Acetanilide standard. Specimens with %N <1.0 were not subject to further destructive sampling as bone nitrogen content <1.0 suggests poor collagen preservation and would necessitate the destruction of a significantly larger sample.  The sampling permit protocol required bone powder to be removed by abrading the surface of each bone, rather than cutting sections of bone in order to minimize damage. A 1.0%N was therefore used as the minimum requirement for sampling.

All specimens deemed viable were re-sampled prior to bone collagen extraction. The sampling area was lightly abraded using a diamond-tipped burr to remove surface contamination, with 20-100mg of whole bone powder removed for collagen extraction, using a modified Longin (1971) method, ahead of isotopic analysis. 7.5 ml of 0.5M HCL was added to bone powders and left for 24H at 5°C to demineralise. Samples were then centrifuged and washed with MilliQ water and the sample transferred to a hot block at 70 °C for 48H in pH3 solution to gelatinise.  Following this, samples were then filtered (8μm ezee-filter, Elkay, Basingstoke), frozen and freeze dried. All bone collagen samples are screened for collagen condition, through %N and %C content and atomic C/N ratios. Samples with C/N of ≤ 2.9 or ≥3.6 were excluded (DeNiro, 1985). For $\delta^{13}C/\delta^{15}N$ isotope analysis, 0.6mg of collagen was weighed in duplicate for each sample. Isotope ratios of carbon and nitrogen were measured by continuous flow-elemental analyser-isotope ratio mass spectrometry (CF-EA-IRMS). The instrumentation comprises a ThermoFinnigan EA IsoLink coupled to a Delta V Plus isotope ratio mass spectrometer via a ConFlo IV interface. Carbon and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{15}N$) are reported in per mil (‰) relative to VPDB and AIR respectively. Carbon isotope ratios were calibrated using a 2-point calibration against an in-house powdered gelatine standard (M1360P from British Drug Houses) calibrated to USGS 40 and 41 (-20.45 ‰) and USGS 40 (-26.39 ‰).

Nitrogen isotope ratios were calibrated using a 2-point calibration against M1360P calibrated to IAEA N-1 and IAEA N-2 (8.12 ‰) and a fish gelatin (Elemental microanalysis B2215, certified value +4.26 ‰). An additional check standard comprising a modern cow bone was also included. M1360P was used to calculate %N and %C (15% N and 42.4% C, calibrated against USGS 40 and USGS 41). Repeated measurements of M1360P gave a 1σ reproducibility of <0.2 for both elements. Duplicate sample 1σ reproducibility was <0.2 for both elements.

Trophic enrichment values, occurring between predator bone collagen and their assumed prey, were taken from Bocherens (2015) as 1.0 ±0.3‰ for $\delta^{13}C$ and 4.2 ±1.4‰ for $\delta^{15}N$, based on predators and prey being from archaeological rather than modern contexts.

All statistical analyses were conducted in SPSS (v.21).

## 3. Results

After screening all specimens, viable collagen was extracted from 67 samples, with 8 excluded from further interpretation based on ratios of C/N being outside the accepted range of 2.9 to 3.6 (DeNiro, 1985). Results are shown in Table 1. Of particular note are the number of successful samples from Hutton Cave (n=16), correlated with MIS 7c-a, and from the MIS 5a age deposits at Banwell Bone Cave (n=16). The MIS 3 assemblage from Sandford Hill further provided a rich set of dietary isotope data (n=35).

### 3.1. Hutton Cave

The overall isotopic range from the penultimate interglacial assemblage of Hutton Cave shows relative stability in $\delta^{13}C$ values, with a range of -2.1‰ between minimum and maximum values (Table 2a). In contrast, $\delta^{15}N$ values are much more variable, with a much larger range of 10.7‰

Out of a suite of herbivores sampled, only horse and hare provided viable collagen and in terms of $\delta^{13}C$ values, both show minimal variation in their ranges (Table 2b, Figure 2a), which is in contrast to their $\delta^{15}N$ values, which show a high level of variability. This is especially the case for hare, which exhibits a range of 2.1‰ to 6‰.

Although carnivore $\delta^{13}C$ values appear more variable than those of herbivores, they are consistent with each other; wolf and spotted hyaena share similar mean and maximum-minimum ranges, and the single lion $\delta^{13}C$ value also fits within these ranges at -19.8‰ (Table 2b). As expected, higher variation is present between herbivore and carnivore $\delta^{15}N$ values, consistent with differences in trophic level (Bocherens and Drucker, 2003). Again, wolves and spotted hyaena share similar $\delta^{15}N$ value ranges (Table 2), whilst the single lion is considerably elevated in comparison at 12.8‰.

When differences in trophic enrichment factors between carnivores and their herbivorous prey are considered (Figure 2b), two of the Hutton Cave wolves plot in close proximity to both hare and horse, whereas the third wolf plots more closely with the group of spotted hyaenas. As many of the prey species targeted did not yield viable collagen, it is likely that key prey resources are missing from this isospace; this is highlighted by the single lion specimen, which has much higher $\delta^{15}N$ values than all the other carnivores sampled.

## 3.2. Banwell Bone Cave

The overall isotopic range of the Early Devensian assemblage of Banwell Bone Cave shows minimal variation in $\delta^{13}$C values, with a range of -1.9‰ (Table 2a) that compares well with that of Hutton Cave. However, mean $\delta^{15}$N is higher at 10.7‰, with a much larger range of 12.2‰.

The low variability of $\delta^{13}$C values in herbivores and slightly more variable results from the carnivores, are similar to the pattern seen earlier at Hutton Cave. However, there is a marked elevation in $\delta^{15}$N values for all sampled fauna in comparison to the other sites (Table 1, Figure 2b, Figure 3a). These elevated values are also highly variable: reindeer ranges from 7.8‰ to 9.7‰, bison have slightly higher $\delta^{15}$N values ranging from 10.2‰ to 11.3‰, which overlaps with those of brown bear (11.3‰ to 14.0‰) (Table 2b). As the top predator, wolves have the highest $\delta^{15}$N values (mean 13.5‰), which are also comparatively the least variable ranging from 13.0‰ to 13.6‰ (Table 2b). Of note is the single hare sample with a low $\delta^{15}$N value of 1.8‰ (Table 2b). As a single sample only, although the difference between it and the other species sampled is stark and its isotopic similarity to other hares at Hutton Cave and Sandford is interesting, it may not fully be representative of all hares at Banwell.

When trophic enrichment factors are considered (Figure 3b), wolves are likely consuming bison, in addition to reindeer. One of the brown bears appears to follow a similar diet. However, the remaining four bears are either utilising a so-far unquantified resource (although it is difficult to see what this may be, given that no other ungulates are present in Britain at this time) or (perhaps more likely) other factors, such as seasonal torpor, are in effect.

### 3.3. Sandford Hill

The overall isotopic range of the assemblage at the Middle Devensian site of Sandford Hill, shows higher variation in $\delta^{13}C$ values than both the Hutton Cave or Banwell Bone Cave assemblages, with a range of 3.6‰ (Table 2a). In contrast, the overall range of $\delta^{15}N$ values is lower at 8.8‰ (Table 2a).

The large herbivores including bison, horse and woolly rhino produced similar $\delta^{13}C$ values ranging from -21.2‰ to -20.9‰ (Table 2b), clustering as a group (Figure 4a). Reindeer are comparatively more variable, ranging from -18.7‰ to -19.5‰, whilst hare is more variable still, ranging from -22.3‰ to -20.8‰ (Table 2b). Carnivore $\delta^{13}C$ values are more variable than the coeval herbivores, with brown bear and spotted hyaena being key examples (Table 2b).

It is notable that $\delta^{15}N$ values are relatively low in comparison to Banwell Bone Cave (Figure 4a) and are more comparable to those from Hutton Cave. In general, carnivore $\delta^{15}N$ values are lower (Tables 1, 2), with differences in trophic level between carnivores and herbivores much more pronounced (Figure 4a). Similar to Hutton Cave, wolf and spotted hyaena overlap in their $\delta^{13}C$ and $\delta^{15}N$ values, whereas lions are much more variable at Sandford Hill. Although brown bears are separated from the large carnivore cluster (Figure 4a) by lower $\delta^{13}C$ values, the range of their $\delta^{15}N$ values is similar to that of spotted hyaena. Variation in herbivore $\delta^{15}N$ values is relatively high, with woolly rhino, horse and hare being notable examples (Tables 1, 2).

When trophic enrichment factors between carnivores and herbivores are accounted for (Figure 4b), the species cluster in the isospace. Two groups of carnivores appear: the two wolves, spotted hyaenas and one lion appear to consume overlapping resources including horse, woolly rhino, bison, with perhaps some reindeer increasing their $\delta^{13}C$ values. However, the four remaining lions cluster with comparatively lower $\delta^{15}N$ values, suggesting perhaps increased importance of reindeer in their diet as opposed to bison. Brown bear is separate from both carnivore groups, with lower $\delta^{13}C$ values. Two of the bears plot closely with bison and horse, however, showing some sharing of resources with the predominantly wolf and spotted hyaena group.

### 3.4. Wolf populations through time

These results record a chronologically distinct ‘snapshot’ of a wolf population, their competitors and potential prey, from MIS 7 at Hutton Cave, MIS 5a at Banwell Bone Cave and MIS 3 at Sandford Hill. Tests of significance between $\delta^{13}C$ and $\delta^{15}N$ values between these separate wolf populations were conducted. First, Levene’s Test for homogeneity of variance was found to be equal between wolf groups for $\delta^{13}C$ ($F_{2,5}$=01.906, $p$=0242) and $\delta^{15}N$ ($F_{2,5}$=1.699, $p$ = 0.274). A one way ANOVA was then undertaken, which indicated that differences in $\delta^{13}C$ between MIS 7, 5a and 3 for each assemblage were significant ($F_{2,5}$=7.338, $p$=0.033) with Tukey HSD post hoc tests further indicating significant differences relating to the Hutton Cave with Sandford Hill wolf populations ($p$=0.033). Although not meeting the significance level of 0.05, Hutton Cave with the Banwell population are close to significance ($p$=0.096).

With respect to differences in $\delta^{15}N$ between the three wolf populations, these were found to be significant ($F_{2,5}$=118.222, $p$=0.000), with Tukey HSD post hoc tests further indicating significant differences occurring between Banwell and Sandford Hill wolves ($p$=0.000), as well as Hutton Cave ($p$=0.000). No significant differences were found between Sandford and Hutton Cave wolf $\delta^{15}$N values ($p$=0.609).

### 3.5. Wolves and their competitors

The significance of the relationship between wolves and spotted hyaenas was investigated at Hutton Cave and Sandford Hill. Levene’s Tests for both groups were found to be equal and hence non-significant ($p$ = <0.05). Using independent T tests, differences between wolves and spotted hyaenas at Hutton Cave were found to not be significant: $\delta^{13}$C ($t_{4}$=-0.210, $p$=0.844) and $\delta^{15}$N ($t_{5,}$=-0.049, $p$ = 0.963), as well as at Sandford Hill: $\delta^{13}$C ($t_{5}$=-1.811, $p$=0.130) and $\delta^{15}$N ($t_{4,}$=-1.075, $p$ = 0.343).

## 4. Discussion

### 4.1. Hutton Cave

The separation between $\delta^{15}$N values of the herbivorous prey species (horse, hare) and carnivorous predators (wolf, spotted hyaena and lion) at Hutton Cave is consistent with expected differences in trophic level. For the predators, wolves and spotted hyaena plot similarly, whereas lion is positioned in a higher trophic level than the other carnivores present. High $\delta^{15}$N in carnivores can be related to the amount of meat consumed (Bocherens, 2003), however, $^{15}$N composition of herbivore prey collagen is complicated by type of plants consumed and how they are affected by environmental factors, in addition to ambient temperature, moisture availability, soil maturity and metabolic processes (Britton et al., 2012).

The $\delta^{13}$C values in hare and horse at Hutton Cave are consistent with a grassland environment (Bocherens et al. 2015). Not only does this correspond well with the chronological attribution of the assemblage to the Sandy Lane MAZ and the MIS 7c-a interglacial (Schreve, 2001a, b) but these findings also provide the first insight into the past vegetation history around the locality, since no direct palaeobotanical proxies were present at the site. As a highly mobile and open environment indicator species, horses provide a regional environmental picture, whereas hares deliver a local signal based on their small home ranges, shorter lifespans and more generalised diets, making them an effective proxy for palaeoenvironmental reconstructions (Somerville et al. 2018).

The relatively low variation between herbivore and carnivore $\delta^{13}C$ values at Hutton Cave is consistent with trophic level differences between predators and their prey (Bocherens and Drucker, 2003). When trophic enrichment factors are considered (Figure 2a), two of the three wolves are inferred to be predominantly consuming horse and hare. However, the remaining wolf plots closely with the spotted hyaena group and, based on their comparatively higher $\delta^{13}C$ and $\delta^{15}N$ values, it seems this group are integrating an additional food source into their diet that is presently not accounted for by the herbivore data. Nevertheless, differences in isotopic values for both wolves and spotted hyaena were found not to be significant, thus reflecting the overall similarity of their diets. The aforementioned higher values are likely driven by consumption of herbivores from open environments (Bocherens et al. 1999). In the context of Hutton Cave, this is most likely to be from a medium-sized mixed-feeder prey species such as red deer (as opposed to the more woodland-adapted wild boar), although unfortunately this cannot be tested further because of the problem of collagen preservation.  Although the steppe mammoth sampled from Hutton Cave equally did not produce sufficient collagen for analysis, the frequently-observed elevated $\delta^{15}N$ values in mammoths (eg. Jones et al. 2001) suggests that these megaherbivores did not form part of the diet of either the wolves or the hyaenas from Hutton Cave.

This overlapping of wolf and spotted hyaena raises the question of competitive interaction. Although spotted hyaena were seemingly rarer during MIS 7c-a in comparison to lion (Schreve, 1997) and certainly less abundant than during both the Last Interglacial and Last Cold Stage in Britain, evidence here suggests their interactions with wolves in the vicinity were important and that similar prey selection from the same area was occurring.

In terms of wolf-hyaena interactions, the only known comparison is with last cold stage populations, for example in Belgium ~40kya, where wolves were apparently outcompeted by spotted hyaena for access to prey with high $\delta^{15}$N values, including mammoth, woolly rhino and horse (Bocherens et al. 2011). There, overlap in prey choice was more common between wolves and lone individuals of cave lion *Panthera spelaea* (Bocherens et al. 2011). It is therefore interesting that the opposite is true for Hutton Cave, during an interglacial, with wolves and spotted hyaenas on ‘equal footing’ and neither excluded from the two prey species sampled. A possible explanation for this may be the character of the MIS 7c-a interglacial, which has been identified as the most species-rich temperate-climate periods in the last c.400,000 years, attributed to its unique combination of high insolation variability, moderate temperatures and dry, open landscapes (Schreve, 2019). High herbivore diversity and concomitant biomass may thus have reduced inter-specific competition between these two major predators at this time.

Notwithstanding the fact that one of the Hutton Cave wolves was clearly consuming something not currently registered in the palaeodietary isospace (perhaps red deer), the new isotopic evidence presented here for a diet (at least partly) consisting of small prey (between 10-50kg) corroborates previous analysis of the cranio-dental morphology of MIS 7 wolves by Flower and Schreve (2014). That study highlighted an increased ability of wolves at this time to crush rather than slice foods, combined with reduced jaw strength characterised by shallower, narrower jaws. These morphological attributes led Flower and Schreve (2014) to conclude that wolves during the penultimate interglacial were focused primarily on small to medium-sized prey, likely constrained by competition with lions, and had increasingly generalised diets. The increased proportion of non-meat foods in the diet would be consistent with an interglacial period where plant and insect resources would be relatively more abundant than in cold-climate episodes. However, the isotopic evidence presented here reveals that MIS 7 wolves were also consuming large-sized prey (c.100-1000kg) such as horse. This was not predicted by the cranio-dental morphological study of Flower and Schreve (2014) and suggests that there is a lack of correspondence or lag between, on the one hand, some aspects of feeding behaviour and, on the other, the rate of morphological response. A possible reason for this might be the relatively rapid climatic and environmental turnover in MIS 7 and the short duration of each interglacial, with an early, forest-dominated temperate episode (MIS 7e) replaced by predominantly open conditions in MIS 7c-a (Schreve, 2019). This may have left wolf morphology lagging the change in hunting behaviour required, as landscape and vegetation changed.

It also raises the question of whether the relationship between wolves and spotted hyaena is an artefact of the latter’s apparently lower density in the landscape; were hyaena scavenging from wolf kills? However, although they were in competition for resources, as stated above, prey biomass in the vicinity was likely rich enough to sustain both predators, while both were equally competitively excluded from megaherbivore (>1000kg) prey by lions. Lions during MIS 7 would have inhabited a savannah context similar to their modern African counterparts, in addition to being comparatively much larger in size (Schreve, 1997), thereby giving them a competitive advantage over other carnivores.

At the co-eval site of Stanton Harcourt, Oxfordshire, Jones et al. (2001) reported high $\delta^{15}N$ values for straight-tusked elephant ($\delta^{13}C$ -20.8, $\delta^{15}N$ 10.7‰ and $\delta^{13}C$ -21.6 and $\delta^{15}N$ 13.2‰), steppe mammoth ($\delta^{13}C$ -21.1, $\delta^{15}N$ 10.9‰) and bison ($\delta^{13}C$ -20.9, $\delta^{15}N$ 11.0‰). However, there is difficulty in comparing these results to those in the present study from Hutton Cave. Although regional differences between southwest and central Britain at this time may be in play, perhaps underlined by the difference in $\delta^{15}N$ from horse at Hutton versus bison from Stanton Harcourt, which one would normally expect to be closely comparable, it is important to note that Jones et al. obtained collagen from molar dentine, which forms during the period of lactation (Bocherens et al. 1994). The high $\delta^{15}N$ values at Stanton Harcourt could thus potentially represent a suckling rather than a palaeoenvironmental signal. Furthermore, Jones et al. (2001) ruled out aridity as a driver of $^{15}N$ elevation based on apparent incompatibility with palaeoenvironmental evidence indicating fully interglacial conditions at the site. However, this contradicts current understanding of the palaeoenvironmental and palaeoclimatic characteristics of MIS 7c-a, which indicate a relatively cool interglacial with mean summer temperatures of +15 to +16°C (de Rouffignac et al., 1995; Murton et al., 2001) and higher magnitude insolation variability than any other interglacial of the Middle and Late Pleistocene (Berger et al., 2015). These factors produced a landscape of dry, predominantly open vegetation conditions with abundant grasses, sedges and dry ground herbs (e.g. Murton et al., 2001), with intensive grazing by large herbivores further increasing evapotranspiration and reducing surface water infiltration (Schreve, 2019). Dry conditions are therefore a strong feature of this interglacial (*contra* Jones et al., 2001) and may thus be a key influence on high δ$^{15}$N values, particularly for assemblages from central England.

## 4.2. Banwell Bone Cave

Separation between herbivore and carnivore trophic levels is less pronounced at Banwell than at either Hutton Cave or Sandford Hill, with overall elevated δ$^{15}$N values for most members, excluding the single hare sample that may not be representative of conditions at the site (see above). The overall higher δ$^{15}$N values for the Banwell Bone Cave wolf population were also found to be significantly different from those at either Hutton Cave or Sandford Hill, further highlighting the particularity of the Banwell Bone Cave assemblage.

However, δ$^{13}$C values are much more similar to those in the other two study assemblages, although a low level of significance was found between Hutton Cave and Banwell Bone Cave wolf populations in δ$^{13}$C values. One of the noticeable differences in δ$^{13}$C values is exhibited by reindeer, which at Banwell Bone Cave display lower than expected δ$^{13}$C values (Bocherens, 2003). Reindeer are lichen consumers, commonly resulting in bone collagen δ$^{13}$C values between -16 to -19‰ (Bocherens et al. 2015). However, at Banwell, lower δ$^{13}$C values suggest that, as with modern reindeer, these animals supplemented their lichen-based diet with other herbs or graminoids (Drucker et al., 2010).

When trophic enrichment factors are accounted for, the central position of wolves between reindeer and bison (Figures 3a, b) indicates they were consuming both species. As the only two large herbivores present in Britain at this time (Currant and Jacobi, 2001), this is not surprising. A recent study of Banwell Bone Cave by Stevens and Reade (2021) further underlines this trophic position (Figures 5a, b).

Previous analysis of the cranio-dental morphological of MIS 5a wolves highlighted this wolf population as being better adapted to fast carnassial slicing, paired with deeper and stronger jaws (Flower and Schreve, 2014). It was inferred that these morphological differences, in comparison to wolves of MIS 7 and 3, enabled them to better hunt and subdue large-sized prey and consume carcasses faster, which combined with high incidences of tooth breakage and heavy tooth wear, implied high levels of dietary stress in a competitive environment (Flower and Schreve, 2014).

These inferences on prey size are borne out in the new isotope data here, since wolves appear to be actively hunting both reindeer and bison. However, evidence for intense competition with brown bears is lacking, notwithstanding that one brown bear does plot with the other sampled wolves. As it is commonplace for brown bears to scavenge wolf kills (e.g. Ordiz et al. 2020; Prugh and Sivy, 2020), it is possible that this scenario was occurring at Banwell. Indeed, the aforementioned wolf morphological differences, in combination with tooth breakage and wear data from Flower and Schreve (2014), indicates that Banwell wolves were adept at consuming carcasses as quickly as possible, which may relate to the threat of kleptoparisitism. This finding, where dietary behaviour and morphology are synchronous, is in clear contrast to the situation reported from Hutton (4.1). Although MIS 5a is an interstadial, it is thought that the cold-adapted reindeer and bison arrived in Britain across the continental landbridge to the European mainland during MIS 5b, but were then stranded through MIS 5a by a rise in sea level (Currant, 2004). If so, this would give any wolves present in Britain a longer period of time (around 20ka) for their morphology to come fully in line with predatory choices.

However, the range in both $\delta^{15}N$ and $\delta^{13}C$ values for brown bear suggests that other factors may be at play. During the Pleistocene, brown bears were more carnivorous than either their modern counterparts or cave bears *Ursus spelaeus*, especially when inhabiting the same landscape as the latter (Munzel et al., 2008; Bocherens et al. 2011). Although cave bear is missing from the Late Pleistocene record in Britain, the high $\delta^{15}N$ values of some of the Banwell brown bears (similar to those of wolves) is suggestive of carnivory; and the consumption of bison and reindeer. However, the range of both $^{15}N$ and $^{13}C$ also suggests a level of dietary flexibility: omnivory, with the inclusion of reindeer or resources not discernible from this study. Dietary flexibility in Late Pleistocene brown bear has been established (Munzel et al. 2008; Bocherens et al. 2011) and could similarly be invoked for the Banwell brown bears.

Another reason for the range in brown bear $^{15}N$ values may be in their response to environmental conditions, with colder periods eliciting a longer dormancy period and thus leading to higher $\delta^{15}N$ values (Fernàndez-Mosquera et al., 2001). Although Fernàndez-Mosquera et al. found that $\delta^{13}C$ values did not follow an environmental trend, Pérez-Rama et al. (2011) found that torpor reduced $\delta^{13}C$ values due to utilisation of fat stores, which corroborated with higher $\delta^{15}N$ values driven by longer torpor in colder climates, and were both recorded in bone collagen.

Nonetheless, the overall high $\delta^{15}N$ values in more than one species present at Banwell, in addition to the relative elevation in $^{15}N$ in most fauna in comparison to Hutton Cave, is intriguing. As noted previously, $^{15}N$ composition of herbivore collagen is controlled by a range of different factors, including soil maturity (e.g. Drucker et al., 2011, 2012), with high $\delta^{15}N$ values linked to mature soils with increased microbial activity, warmer conditions and closed habitats, and low $\delta^{15}N$ values attributed to immature soils with low activity, colder conditions and open habitats (Drucker et al. 2011, 2012).

However, herbivore $\delta^{13}C$ values at Banwell Bone Cave are indicative of open environmental conditions (cf. Bocherens et al. 2015), and in conjunction with palaeoecological evidence from deposits of similar age at Cassington, Oxfordshire (Maddy et al. 1998), linking high $\delta^{15}N$ values with aforementioned factors of closed environments and climatic warmth is complex.

Although MIS 5a is an interstadial, pollen evidence and Coleopteran MCR reconstructions from Cassington suggest relatively cool continental conditions in southern Britain that deteriorated towards the end of the interstadial. Pollen spectra from Cassington are predominantly herbaceous indicating a largely open steppe/tundra environment, with variable coverage of open aspect pine and spruce forests that characterise southern Scandinavia today (Maddy et al. 1998). When combined with evidence from Coleoptera, temperatures gradually cooled over time from a mean of 17 to 18°C for the warmest month and -4 to 4°C for the coldest month, further declining to maximum summer temperatures of 14°C and the notably cold temperatures of 7 to 11°C during the warmest month and -10 to -30°C during the coldest at the end of MIS 5a/transition to MIS 4 (Maddy et al. 1998). It therefore seems unlikely that high $\delta^{15}N$ values here were driven by long established warm conditions and closed habitats that would be more characteristic of a warm interglacial rather than a cool interstadial.

Higher $\delta^{15}N$ values in fauna have also been linked to aridity (Heaton et al. 1986; Bocherens et al. 1994; Grocke et al, 1997), with arid conditions at the end of the Late Glacial proposed as a driver for elevated horse $\delta^{15}N$ values seen at this time (Stevens and Hedges, 2004). Increasingly open environmental conditions are linked to drier conditions, and it is therefore possible that the predominantly open conditions and dry grassland communities (with xerophile beetles also present) as seen at Cassington (Maddy et al. 1998) could be linked to drier climatic conditions in southern Britain. These could be largely responsible for the elevated $\delta^{15}N$ values of Banwell Bone Cave. This theory is also supported by Stevens and Reade (2021), who attributed similarly high $\delta^{15}N$ values in bison and reindeer to arid conditions. These authors ruled out nutritional stress as a driving factor due to the lack of evidence of starvation in either species, their abundance in the assemblage and proposed long-term coexistence in the area.

It is also worth noting the comparably low $\delta^{15}N$ values of the hare sampled. Although a single specimen, it is suggestive of a more complex scenario than an overall picture of higher $\delta^{15}N$ at the site**.** Hare from Hutton and Banwell share lower $\delta^{15}N$ values (Hutton 2.1-6‰, Banwell 1.8‰) than coeval large herbivores. This difference may relate to leporids being caeco-colic hindgut fermenters, a process responsible for lower $\delta^{15}N$ values in bone tissue (Sponheimer et al. 2003), however, the effects of coprophagy on isotopic composition are as yet not well understood (Somerville et al. 2018). Nevertheless, as mentioned previously, leporids provide a localised environmental signal. Even with the effects of caeco-colic hindgut fermentation lowering $\delta^{15}N$ values, it would still be expected to reflect the overall elevated $^{15}N$ signal identified in the other fauna present and be higher than at Hutton Cave or Sandford Hill.

### 4.3. Sandford Hill

As with Hutton Cave, trophic levels between carnivores and herbivores are clear at Sandford Hill (Figure 4a), and in contrast to Banwell Bone Cave, $\delta^{15}N$ values have returned to a lower environmental baseline (Table 2a). Differences in wolf $\delta^{15}N$ values are also not significant between Sandford Hill and Banwell. However, in contrast to Hutton Cave, herbivore niches at Sandford Hill are more compressed, with isotopic values similarly clustered for horse, bison and woolly rhino (Figure 4a), as frequently observed from Late Pleistocene contexts (Bocherens et al., 2011). Of note are the higher reindeer $\delta^{13}C$ values here, in contrast to those from Banwell Bone Cave, indicating a diet perhaps richer in lichen (Bocherens, 2015). Additionally, $\delta^{13}C$ values for the wolf population were also found to be significant in comparison to those at Hutton Cave.

Three carnivore groupings are recognised at Sandford Hill: (1) wolves and spotted hyaenas, (2) lions, and (3) brown bears, with the addition of a single lion in the 'wolf-hyaena' group, and a spotted hyaena in the 'bear' cluster. Focussing on the wolves first, and taking into consideration trophic enrichment factors (Figure 4b), consumption of horse, in addition to woolly rhino and bison is indicated. Comparable studies have been obtained from Late Pleistocene Beringia (>50-23ka BP), where wolf prey values overlap with horse, bison and reindeer and similarly occupy a central position in the isospace amongst most large prey types (Leonard et al. 2007).

As with Hutton Cave, wolves and spotted hyaenas once again overlap in their prey consumption and are in competition for resources, with no significant difference found between their isotopic values. Similarly, this apparently did not result in competitive exclusion from certain prey items, rather both carnivores were able to sustain comparable diets, likely aided by the presence of a rich prey base present in the vicinity of the cave.

The pattern seen at Sandford Hill is compared in Figures 6a and 6b from the aforementioned evidence from the middle part of the last cold stage in Belgium, where wolves were apparently competitively excluded by cave hyaenas from larger prey species with high $\delta^{15}N$ values, such as woolly rhino, horse and woolly mammoth (Bocherens et al. 2011). At Sandford Hill, wolves apparently share the isospace with hyaenas and the dietary influence of horse and woolly rhino is clearly present within the wolves (Figures 6a and 6b). Whether this is the result of wolves engaging in direct hunting of rhinos themselves, or the result of scavenging carcasses accumulated by hyaenas (or even lion) cannot, however, be determined. The presence of visible characteristic hyaena gnawing on the rhino remains from Sandford Hill attests to their exploitation of the bones.

Analysis of cranio-dental morphology in MIS 3 wolves by Flower and Schreve (2014) revealed similar results to those from MIS 7, namely an increased ability to crush rather than slice foods, paired with shallower, narrower jaws. This suggested they were hunters of small to medium-sized prey, with more generalist diets, and that they were likely excluded from the largest prey by lion, brown bear and particularly spotted hyaena. As with Hutton Cave, however, the new isotopic evidence from Sandford Hill does not tally entirely with these conclusions, since it indicates that wolves were also taking large prey, such as horse and bison, and potentially scavenging very large prey such as woolly rhino. This may again reveal an intriguing lag between a change in dietary behaviour and a morphological response in the cranio-dental apparatus, possibly the result of very rapid stadial-interstadial oscillations during MIS 3 (Rasmussen et al., 2014). Furthermore, just as at Hutton Cave, wolves again appear to have shared resources with spotted hyaenas rather than been competitively excluded by them.

The wolf-hyaena grouping dominates the large herbivores of bison, horse and woolly rhino (Figure 4b), whereas lions apparently preferentially consumed reindeer, explaining their lower $\delta^{15}N$ values in comparison to the other carnivores present. However, their similar $\delta^{13}C$ values implies some reliance on prey with comparatively lower $\delta^{13}C$ values, such as horse. This corroborates the findings of Yeakel et al. (2003) who equally identified lions as consuming a large proportion of reindeer in the Swabian Jura. After the Last Glacial Maximum in mainland Europe, and with the extirpation of hyaena from the region, wolves became the dominant predators with access to a larger suite of herbivorous prey, leading to the suggestion that lions then adopted the role of reindeer specialists (Bocherens et al. 2011, 2015). The situation presented by Sandford Hill, which occurs prior to the Last Glacial Maximum, perhaps foreshadows this niche partitioning.

The lack of overlap between wolves and brown bears in the Sandford Hill isospace suggests that some level of dietary differentiation is taking place. Although the ranges of both $\delta^{13}C$ and $\delta^{15}N$ values in bears are smaller than seen earlier at Banwell, clustering based on their $\delta^{13}C$ and $\delta^{15}N$ values is apparent with two bears consuming horse. The remaining two are either supplementing their diets with bison, or their isotopic signatures are affected by torpor, as previously discussed with the Banwell brown bears.

As part of the Pin Hole MAZ, the Sandford Hill assemblage is characteristic of the ‘Mammoth steppe’ conditions of MIS 3. Although the calcareous limestone of

Sandford Hill has not favoured preservation of plant or insect proxies, information on the climate and environment can be gleaned from open sites of this age in central England. Plant macrofossil evidence from the site of Lynford in Norfolk, reveals a cool open grassland of herbaceous plants (Schreve, 2006; Boismier et al., 2012), correlating well with the beetle assemblage present with inferred mean July temperatures of 12-14°C and mean winter month temperatures at or below -10°C (Boismier et al. 2003). Palaeotemperature reconstructions at Whitemoor Haye in Staffordshire corroborate these fndings, with cooler mean July temperatures of 8-11°C and mean December temperatures of -22 and -16°C (Schreve et al., 2013). It is therefore likely that similar environmental and climatic conditions were present at Sandford Hill.

## 5. Conclusions

This is the first predator-centric stable isotope study for Pleistocene Britain using wolves as a lens to examine prey choice and competition. The study was designed to allow comparison of the predator-prey dynamics from an interglacial (MIS 7c-a), the early part of the last cold stage (MIS 5a) and the middle part of the last cold stage (MIS 3), by examining the prey choices of a range of large carnivores under contrasting climatic and environmental scenarios. The results from the stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analyses presented here also enabled comparison with a previous study by Flower and Schreve (2014), which used changes in wolf cranio-dental apparatus to reconstruct changing diet over the same period and thus enables a direct comparison of proxy indicators of dietary flexibility.

Although collagen preservation potential declines with age, the results are notable for the successful retrieval of viable collagen back to c.200ka (MIS 7c-a), one of very few studies to have this (cf. Jones et al., 2001). The isotopic measurements provide clear evidence for changing prey consumption and the interaction of wolves with other potential competitors. With respect to prevailing environmental and climatic parameters, the $\delta^{13}C$ values in herbivores from all three sites are consistent with predominantly open, grassland environments, although occurring under different climatic regimes. High $\delta^{15}N$ values from most of the Banwell Bone Cave specimens, however, are likely to reflect a notable signal of aridity.

In terms of prey choice, MIS 7 c-a interglacial wolves were consuming both small and large prey (hare and horse) respectively, although there is evidence for an additional food source presently not accounted for (likely the result of collagen preservation, since a wide range of taxa were originally sampled). During MIS 5a, wolves were consuming reindeer and bison at Banwell Bone Cave and during MIS 3, when herbivores niches were apparently more compressed, horse, bison and woolly rhino were being predated. The results reveal that wolves were apparently competing on an equal footing with spotted hyaenas, sharing the same dietary isospace. They were therefore not pushed into taking smaller prey or lower choice food items and were able to consume a wide range of large herbivores during both periods when the two species coexisted, MIS 7 and MIS 3, no doubt facilitated by the richness of the environment and accompanying herbivore biomass. This is in contrast, however, to the evidence from other parts of north-west Europe such as Belgium, where wolves were apparently out-competed by hyaenas during the last cold stage (Bocherens et al., 2011). Over the three study sites presented here, competition between wolves and brown bear is variable, with overlaps noted during

MIS 5a for consumption of bison, but only partially for MIS 3, where there is more differentiation except for the consumption of horse. With regards to lion, however, there is no evidence of any dietary overlap with wolves or any other large carnivore during MIS 7; lion is positioned on a higher trophic level and although the dietary source could not be identified in the present study, it may well have involved predation of megaherbivores such as rhinos or elephants. During MIS 3, lions appear to have occupied a much narrower niche than the wolves, adopting the role of reindeer specialists. This behaviour has been noted in sites post-dating the Last Glacial Maximum in northern Europe (Bocherens et al. 2011, 2015) but the evidence from Sandford Hill indicates that this behaviour can now be traced back further into the middle part of the last cold stage.

Finally, the results from the present study offer a tantalising insight into the tempo and mode of evolution within the wolf lineage, namely the morphological responses of the cranium, jaws and dentition to changing diet. While the palaeodietary evidence from Banwell (MIS 5a) indicates close correspondence between prey selection, carnassial tooth morphology and deeper and stronger jaws in wolves, suggesting adaptations for subduing large prey and rapid consumption of carcasses (Flower and Schreve, 2014), the same degree of synchrony is not seen at Hutton Cave (MIS 7c-a) nor at Sandford Hill (MIS 3). At both those sites, the cranio-dental morphology of the wolves, notably enhanced crushing capacity of the teeth, combined with shallower, narrower jaws, suggested a more generalist diet (including non-meat foods) and a focus on small to medium-sized prey (Flower and Schreve, 2014). This contrasts with the evidence from the present study, which reveals that wolves were also taking large prey during MIS 7c-a and 3. This demonstrates for the first time that during both these periods, predatory behaviour and morphology were not in step. A possible reason for the offset may be the abrupt nature of the climatic and vegetation oscillations at these times. These may have precipitated rapid changes in hunting behaviour as wolves responded flexibly to their changing circumstances but caused morphological adaptations in the wolves' cranio-dental apparatus to fall out of step with the shifting prey choices.

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Figure 1: Map of British study sites. Half column width.

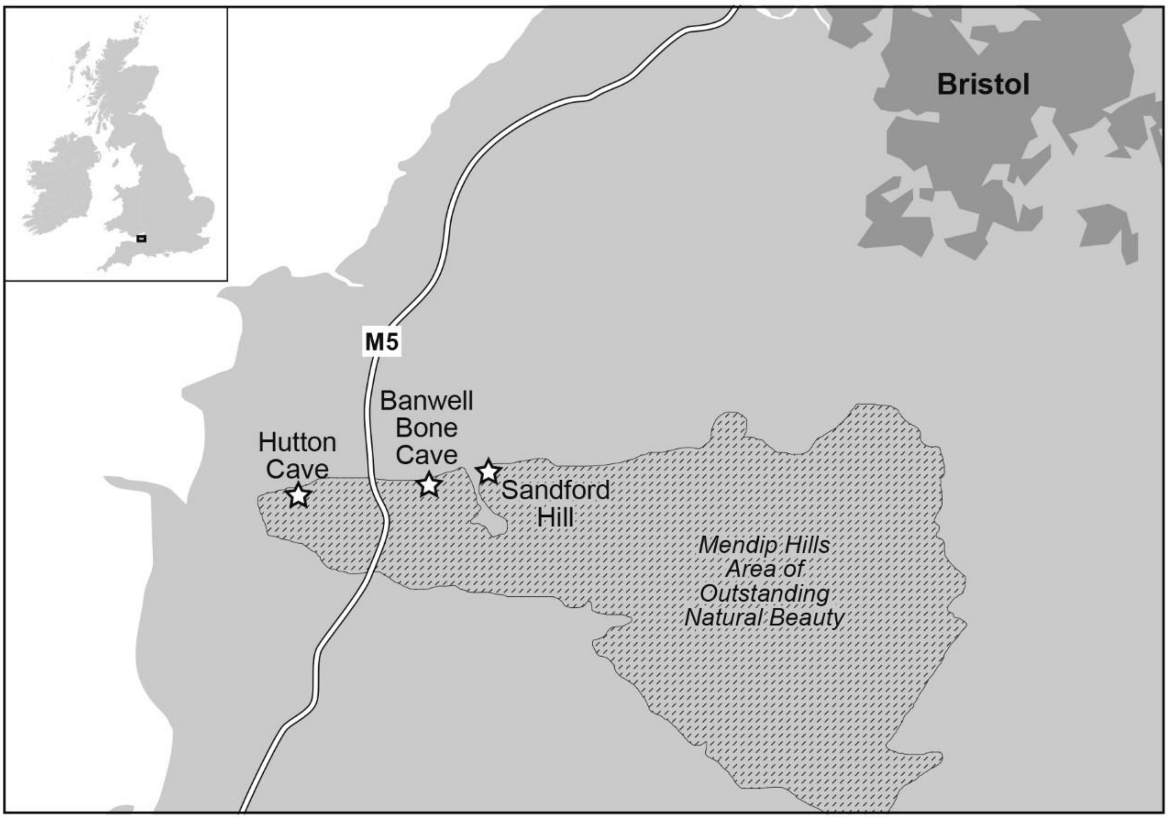

Figure 2a: δ$^{13}$C and δ$^{15}$N values of carnivores and herbivores from Hutton Cave. Figure 2b: Trophic enrichment factor applied to carnivores following Bocherens (2015). Mean herbivore δ$^{13}$C and δ$^{15}$N values shown to 1 standard deviation.

Double column width.

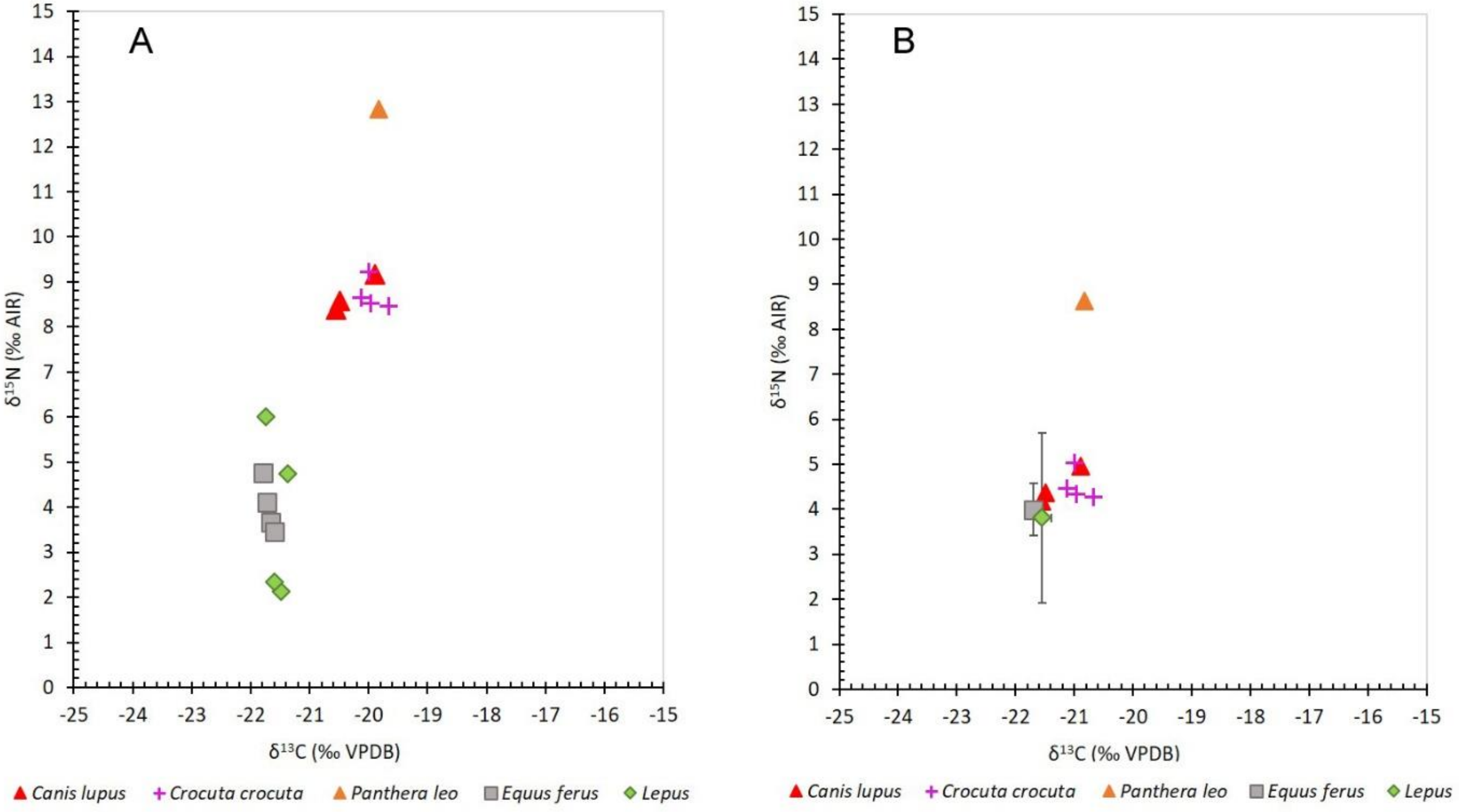

Figure 3a: δ$^{13}$C and δ$^{15}$N values of carnivores and herbivores from Banwell Bone Cave. Figure 3b: Trophic enrichment factor applied to carnivores following Bocherens (2015). Mean herbivore δ$^{13}$C and δ$^{15}$N values shown to 1 standard deviation. Double column width.

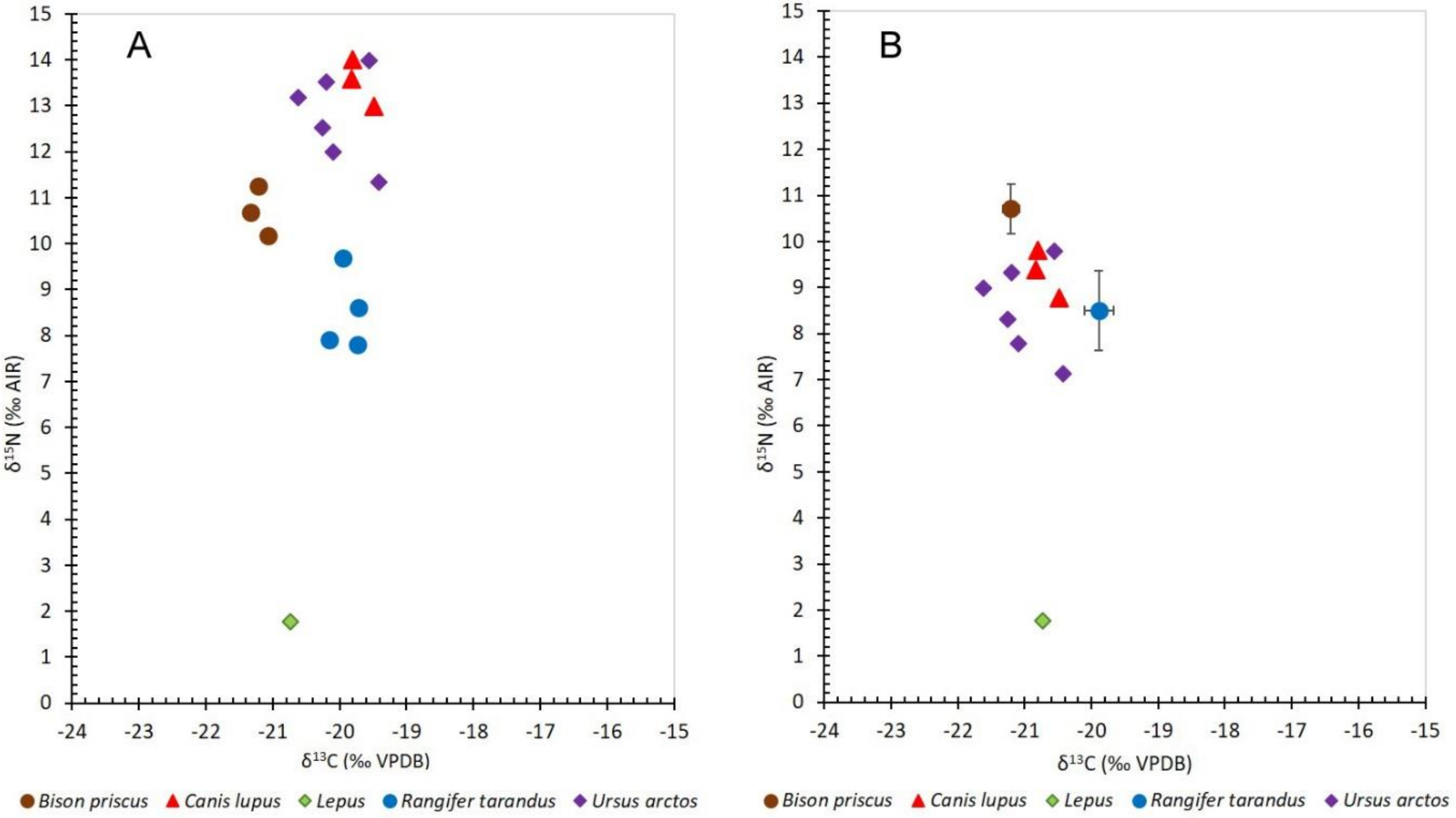

Figure 4a: δ$^{13}$C and δ$^{15}$N values of carnivores and herbivores from Sandford Hill. Figure 4b: Trophic enrichment factor applied to carnivores following Bocherens (2015). Mean herbivore δ$^{13}$C and δ$^{15}$N values shown to 1 standard deviation. Double column width.

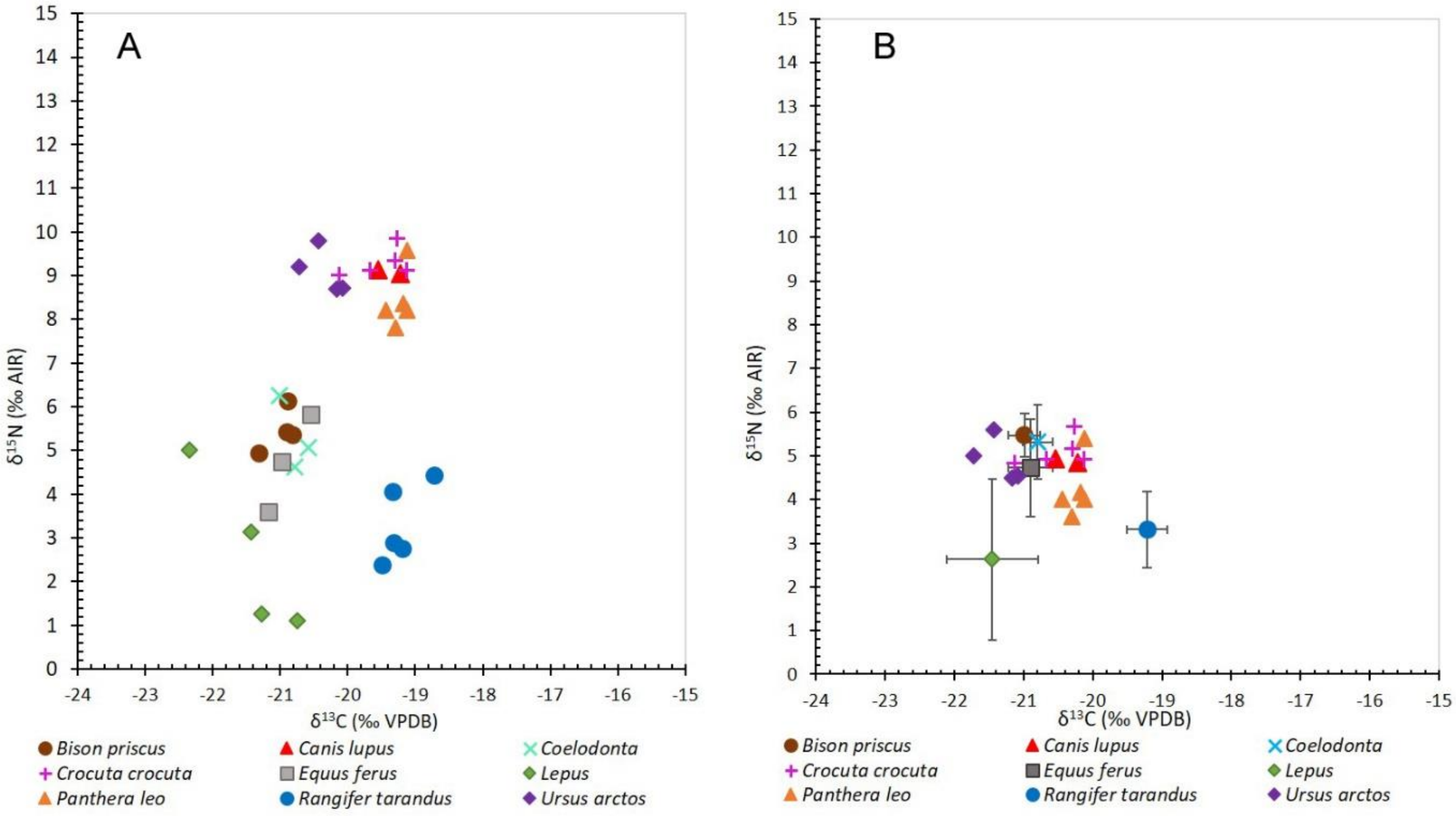

Figure 5a: δ$^{13}$C and δ$^{15}$N values from Banwell from this study (closed symbols) compared to those from Stevens and Reade (2021) (open symbols). Figure 5b: Trophic enrichment factor applied to carnivores following Bocherens (2015). Mean herbivore δ$^{13}$C and δ$^{15}$N values shown to 1 standard deviation. Double column width.

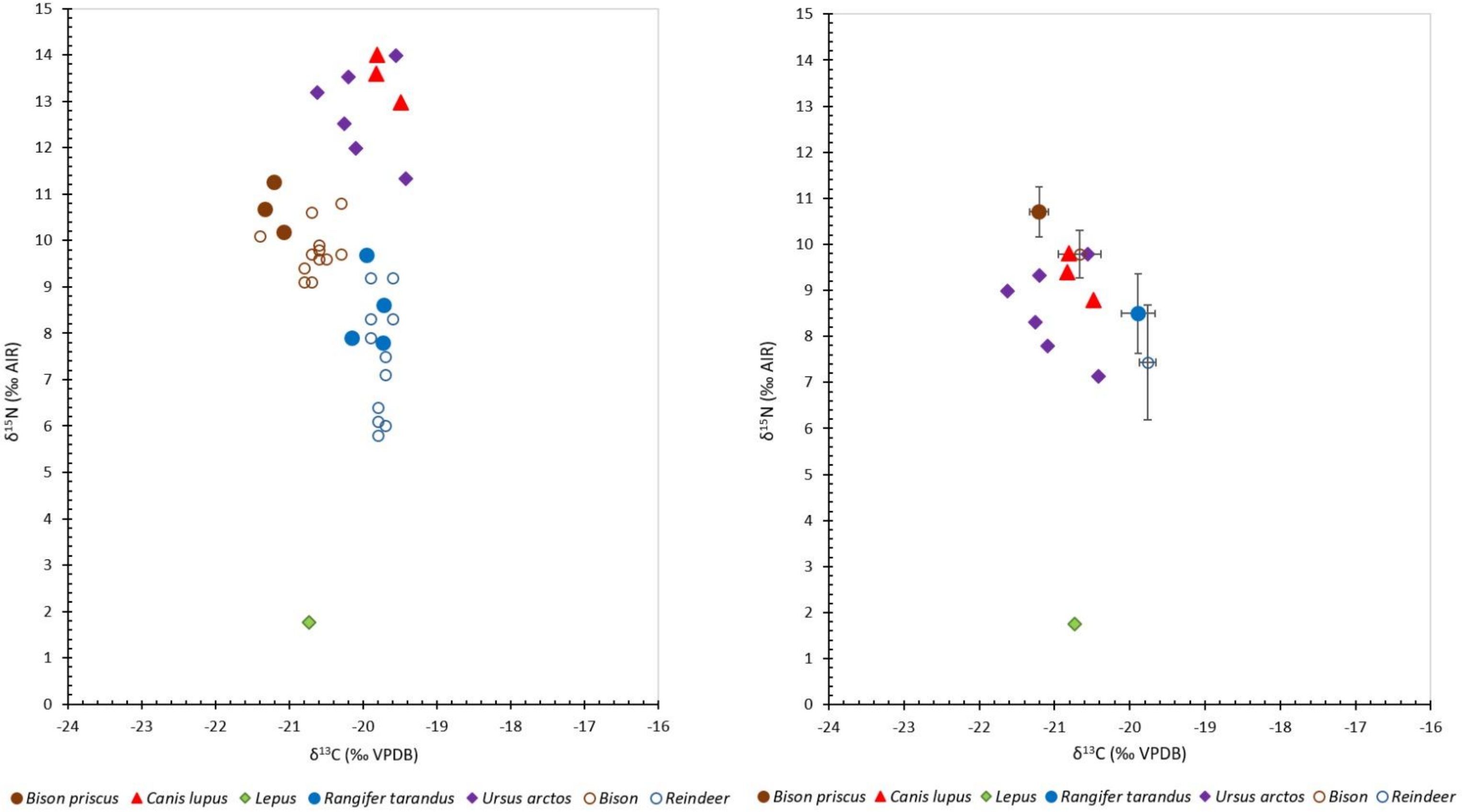

Figure 6a: Sandford Hill data from this study (symbols in legend followed by SH), compared with data from Goyet, published by Bocherens et al. (2011). Figure 6b: Trophic enrichment factor applied to carnivores following Bocherens (2015). Mean herbivore $\delta^{13}$C and $\delta^{15}$N values shown to 1 standard deviation.

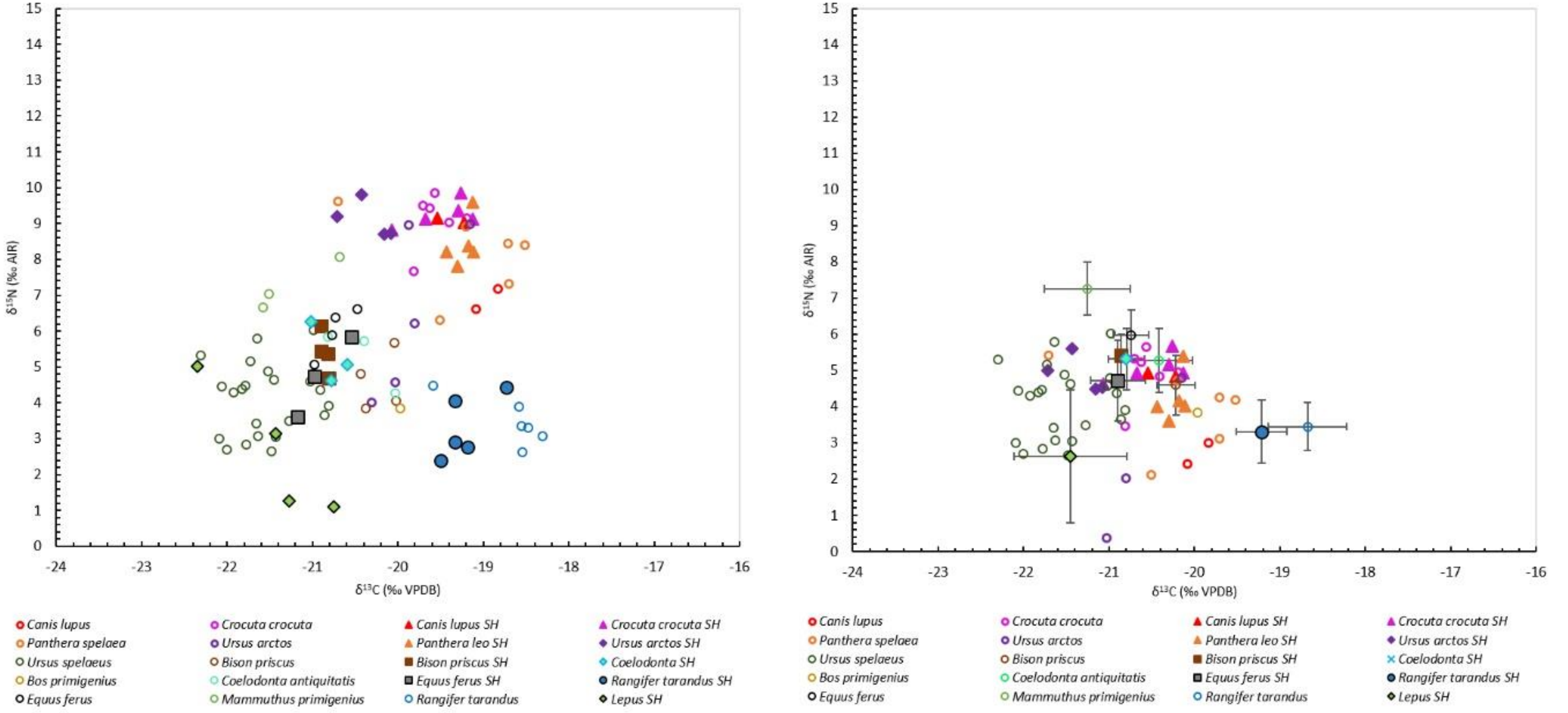

Table 1: Results from isotopic analyses conducted during this study.

| Site | Age (MIS) | Species | Specimen Number | NEIF Lab Number | %C | %N | C/N | $\delta^{13}C$ (VPDB) | $\delta^{15}N$ (AIR) | Sample date |
|---|---|---|---|---|---|---|---|---|---|---|
| Hutton | 7 | *Canis lupus* | 42/95/129-10 | 10 | 41.5 | 14.1 | 3.4 | -20.6 | 8.4 | 2018 |
| Hutton | 7 | *Canis lupus* | 42/1995/145 | 145 | 36.2 | 12.1 | 3.5 | -20.5 | 8.6 | 2015 |
| Hutton | 7 | *Canis lupus* | 42/1995/738 | 738 | 40.7 | 14.1 | 3.4 | -19.9 | 9.2 | 2015 |
| Hutton | 7 | *Crocuta crocuta* | 42/95/212-11 | 11 | 40.4 | 14.4 | 3.3 | -20.0 | 9.2 | 2018 |
| Hutton | 7 | *Crocuta crocuta* | 42/95/223-12 | 12 | 41.4 | 14.5 | 3.3 | -20.1 | 8.7 | 2018 |
| Hutton | 7 | *Crocuta crocuta* | 42/1995/218 | 218 | 42.1 | 14.6 | 3.4 | -19.7 | 8.5 | 2015 |
| Hutton | 7 | *Crocuta crocuta* | 42/1995/255 | 255 | 42.5 | 14.1 | 3.5 | -20.0 | 8.5 | 2015 |
| Hutton | 7 | *Equus ferus* | 42/95/536-14 | 14 | 40.6 | 14.4 | 3.3 | -21.7 | 3.7 | 2018 |
| Hutton | 7 | *Equus ferus* | 42/95/534-15 | 15 | 41.0 | 14.7 | 3.3 | -21.7 | 4.1 | 2018 |
| Hutton | 7 | *Equus ferus* | 42/1995/440 | 440 | 41.8 | 14.6 | 3.3 | -21.8 | 4.8 | 2015 |
| Hutton | 7 | *Equus ferus* | 42/1995/535 | 535 | 39.9 | 13.7 | 3.4 | -21.6 | 3.4 | 2015 |
| Hutton | 7 | *Lepus* | 42/1995/4/1-2 | 2 | 40.4 | 14.3 | 3.3 | -21.4 | 4.7 | 2018 |
| Hutton | 7 | *Lepus* | 42/1995/4/-3 | 3 | 40.8 | 14.4 | 3.3 | -21.5 | 2.1 | 2018 |
| Hutton | 7 | *Lepus* | 42/1995/8/1-7 | 7 | 41.9 | 14.4 | 3.4 | -21.7 | 6.0 | 2018 |
| Hutton | 7 | *Lepus* | 42/1995/8/2-8 | 8 | 42.9 | 14.3 | 3.5 | -21.6 | 2.3 | 2018 |
| Hutton | 7 | *Panthera spelaea* | 42/1995/260 | 260 | 39.1 | 13.3 | 3.4 | -19.8 | 12.8 | 2015 |
| Banwell | 5a | *Bison priscus* | 185/02/151-116 | 116 | 36.5 | 13.1 | 3.3 | -21.3 | 10.7 | 2018 |
| Banwell | 5a | *Bison priscus* | Banwell | 10-B | 32.4 | 11.2 | 3.4 | -21.1 | 10.2 | 2015 |
| Banwell | 5a | *Bison priscus* | Banwell | 10-J | 33.6 | 11.5 | 3.4 | -21.2 | 11.3 | 2015 |
| Banwell | 5a | *Canis lupus* | 40/1995/50-103 | 103 | 38.2 | 12.4 | 3.6 | -19.8 | 13.6 | 2018 |
| Banwell | 5a | *Canis lupus* | 40/1995/52-104 | 104 | 34.3 | 11.1 | 3.6 | -19.8 | 14.0 | 2018 |
| Banwell | 5a | *Canis lupus* | Banwell | 10-O | 29.6 | 10.2 | 3.4 | -19.5 | 13.0 | 2015 |
| Banwell | 5a | *Lepus* | 40/1995/1-101 | 101 | 36.3 | 11.9 | 3.6 | -20.7 | 1.8 | 2018 |
| Banwell | 5a | *Rangifer tarandus* | 40/1995/382-113 | 113 | 34.9 | 12.0 | 3.4 | -19.7 | 7.8 | 2018 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Banwell | 5a | *Rangifer tarandus* | SCHREVE COLLECTION-118 | 118 | 37.3 | 13.4 | 3.3 | -19.7 | 8.6 | 2018 |
| Banwell | 5a | *Rangifer tarandus* | 40/1995/321 | 321 | 28.7 | 9.3 | 3.6 | -20.2 | 7.9 | 2015 |
| Banwell | 5a | *Rangifer tarandus* | 40/1995/372 | 372 | 39.5 | 13.6 | 3.4 | -19.9 | 9.7 | 2015 |
| Banwell | 5a | *Ursus arctos* | 40/1995/229-107 | 107 | 31.2 | 10.9 | 3.3 | -19.4 | 11.3 | 2018 |
| Banwell | 5a | *Ursus arctos* | 40/1995/227-109 | 109 | 34.8 | 11.4 | 3.6 | -20.1 | 13.4 | 2018 |
| Banwell | 5a | *Ursus arctos* | 40/1995/230-110 | 110 | 35.5 | 12.4 | 3.3 | -20.3 | 12.5 | 2018 |
| Banwell | 5a | *Ursus arctos* | 40/1995/220 | 220 | 32.7 | 11.2 | 3.4 | -19.6 | 14.0 | 2015 |
| Banwell | 5a | *Ursus arctos* | Banwell | 21-22 | 35.4 | 12.4 | 3.3 | -20.1 | 12.0 | 2015 |
| Sandford | 3 | *Bison priscus* | 44/1995/637-92 | 92 | 41.3 | 14.3 | 3.4 | -20.9 | 5.4 | 2018 |
| Sandford | 3 | *Bison priscus* | 44/1995/638-93 | 93 | 38.6 | 13.3 | 3.4 | -20.9 | 6.1 | 2018 |
| Sandford | 3 | *Bison priscus* | 44/1995/639-94 | 94 | 39.7 | 13.1 | 3.6 | -20.8 | 4.7 | 2018 |
| Sandford | 3 | *Bison priscus* | 44/1995/641-96 | 96 | 40.5 | 14.2 | 3.3 | -20.8 | 5.4 | 2018 |
| Sandford | 3 | *Canis lupus* | 44/1995/61/16 | 61-16 | 43.2 | 14.9 | 3.4 | -19.5 | 9.1 | 2015 |
| Sandford | 3 | *Canis lupus* | 44/1995/61/3 | 61-3 | 41.1 | 14.2 | 3.4 | -19.2 | 9.0 | 2015 |
| Sandford | 3 | *Coelodonta* | 44/1995/471-88 | 88 | 42.2 | 14.7 | 3.4 | -21.0 | 6.3 | 2018 |
| Sandford | 3 | *Coelodonta* | 44/1995/477-89 | 89 | 42.6 | 14.8 | 3.4 | -20.6 | 5.1 | 2018 |
| Sandford | 3 | *Coelodonta* | 44/1995/478-90 | 90 | 41.3 | 14.6 | 3.3 | -20.8 | 4.6 | 2018 |
| Sandford | 3 | *Crocuta crocuta* | 44/95/286-73 | 73 | 41.7 | 14.4 | 3.4 | -19.3 | 9.4 | 2018 |
| Sandford | 3 | *Crocuta crocuta* | 44/95/288-74 | 74 | 37.8 | 13.4 | 3.3 | -19.7 | 9.1 | 2018 |
| Sandford | 3 | *Crocuta crocuta* | 44/95/289-75 | 75 | 37.7 | 13.8 | 3.2 | -19.3 | 9.9 | 2018 |
| Sandford | 3 | *Crocuta crocuta* | 44/1995/290-76 | 76 | 35.6 | 11.2 | 3.6 | -20.1 | 8.8 | 2018 |
| Sandford | 3 | *Crocuta crocuta* | 44/1995/291-77 | 77 | 35.3 | 13.0 | 3.2 | -19.1 | 9.1 | 2018 |
| Sandford | 3 | *Equus ferus* | 44/1995/429-84 | 84 | 40.3 | 13.6 | 3.5 | -21.0 | 4.7 | 2018 |
| Sandford | 3 | *Equus ferus* | 44/1995/430-85 | 85 | 41.3 | 14.2 | 3.4 | -21.2 | 3.6 | 2018 |
| Sandford | 3 | *Equus ferus* | 44/1995/428 | 428 | 32.5 | 11.2 | 3.4 | -20.5 | 5.8 | 2015 |
| Sandford | 3 | *Lepus* | 41/95/40-65 | 65 | 38.0 | 13.0 | 3.4 | -20.8 | 1.1 | 2018 |
| Sandford | 3 | *Lepus* | 44/95/42-67 | 67 | 38.3 | 13.0 | 3.5 | -22.3 | 5.0 | 2018 |
| Sandford | 3 | *Lepus* | 44/95/44-68 | 68 | 38.6 | 13.1 | 3.5 | -21.4 | 3.1 | 2018 |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| Sandford | 3 | *Lepus* | 44/95/45-69 | 69 | 42.5 | 13.7 | 3.6 | -21.3 | 1.3 | 2018 |
| Sandford | 3 | *Panthera spelaea* | 44/95/385-78 | 78 | 44.9 | 15.5 | 3.4 | -19.2 | 8.4 | 2018 |
| Sandford | 3 | *Panthera spelaea* | 44/1995/386-79 | 79 | 43.8 | 15.2 | 3.4 | -19.3 | 7.8 | 2018 |
| Sandford | 3 | *Panthera spelaea* | 44/95/397-80 | 80 | 43.1 | 14.9 | 3.4 | -19.1 | 9.6 | 2018 |
| Sandford | 3 | *Panthera spelaea* | 44/1995/404-81 | 81 | 42.1 | 14.4 | 3.4 | -19.4 | 8.2 | 2018 |
| Sandford | 3 | *Panthera spelaea* | 44/1995/415-82 | 82 | 41.1 | 14.4 | 3.3 | -19.1 | 8.2 | 2018 |
| Sandford | 3 | *Rangifer tarandus* | 44/1995/839-97 | 97 | 39.3 | 14.0 | 3.3 | -19.3 | 2.9 | 2018 |
| Sandford | 3 | *Rangifer tarandus* | 44/1995/840-98 | 98 | 37.5 | 13.0 | 3.4 | -19.5 | 2.4 | 2018 |
| Sandford | 3 | *Rangifer tarandus* | 44/95/841-99 | 99 | 39.2 | 13.4 | 3.4 | -19.3 | 4.1 | 2018 |
| Sandford | 3 | *Rangifer tarandus* | 44/1995/1120 | 20 | 40.7 | 13.9 | 3.4 | -18.7 | 4.4 | 2015 |
| Sandford | 3 | *Rangifer tarandus* | 44/1995/800 | 800 | 38.8 | 13.1 | 3.5 | -19.2 | 2.8 | 2015 |
| Sandford | 3 | *Ursus arctos* | 44/1995/67-70 | 70 | 32.9 | 10.8 | 3.6 | -20.7 | 9.2 | 2018 |
| Sandford | 3 | *Ursus arctos* | 44/95/93-72 | 72 | 35.7 | 11.8 | 3.5 | -20.4 | 9.8 | 2018 |
| Sandford | 3 | *Ursus arctos* | 44/1995/68 | 68 | 37.1 | 12.8 | 3.4 | -20.2 | 8.7 | 2015 |
| Sandford | 3 | *Ursus arctos* | 44/1995/76 | 76 | 39.4 | 13.5 | 3.4 | -20.1 | 8.7 | 2015 |

Table 2a and b: Mean, maximum and minimum, and ranges of isotopic values for each site (a) and for each species (b). Note that for Hutton lion and Banwell hare samples, n=1 with no maximum, minimum or ranges shown.

| **TABLE 2A** | | | | |
|---|---|---|---|---|
| **Assemblage** | **Mean** | **MAX** | **MIN** | **RANGE** |
| Hutton δ$^{13}$C | -20.8 | -19.7 | -21.8 | -2.1 |
| Hutton δ$^{15}$N | 6.6 | 12.8 | 2.1 | 10.7 |
| Banwell δ$^{13}$C | -20.2 | -19.4 | -21.3 | -1.9 |
| Banwell δ$^{15}$N | 10.7 | 14.0 | 1.8 | 12.2 |
| Sandford Hill δ$^{13}$C | -20.1 | -18.7 | -22.3 | -3.6 |
| Sandford Hill δ$^{15}$N | 6.3 | 9.9 | 1.1 | 8.8 |

| **TABLE 2B** | | | | |
|---|---|---|---|---|
| **Species** | **Mean** | **MAX** | **MIN** | **RANGE** |
| Hutton wolf δ$^{13}$C | -20.3 | -19.9 | -20.6 | -0.7 |
| Hutton wolf δ$^{15}$N | 8.7 | 9.2 | 8.4 | 0.8 |
| Hutton Hyaena δ$^{13}$C | -19.9 | -19.7 | -20.1 | -0.5 |
| Hutton Hyaena δ$^{15}$N | 8.7 | 9.2 | 8.5 | 0.8 |
| Hutton lion δ$^{13}$C | -19.8 | | | n=1 |
| Hutton lion δ$^{15}$N | 12.8 | | | n=1 |
| Hutton Horse δ$^{13}$C | -21.7 | -21.6 | -21.8 | -0.2 |
| Hutton Horse δ$^{15}$N | 4.0 | 4.8 | 3.4 | 1.3 |
| Hutton hare δ$^{13}$C | -21.5 | -21.4 | -21.7 | -0.4 |
| Hutton hare δ$^{15}$N | 3.8 | 6.0 | 2.1 | 3.9 |
| | | | | |
| Banwell wolf δ$^{13}$C | -19.7 | -19.5 | -19.8 | -0.3 |
| Banwell wolf δ$^{15}$N | 13.5 | 14.0 | 13.0 | 1.0 |
| Banwell bear δ$^{13}$C | -19.9 | -19.4 | -20.3 | -0.8 |
| Banwell bear δ$^{15}$N | 12.6 | 14.0 | 11.3 | 2.7 |
| Banwell bison δ13C | -21.2 | -21.1 | -21.3 | -0.3 |
| Banwell bison δ$^{15}$N | 10.7 | 11.3 | 10.2 | 1.1 |
| Banwell reindeer δ$^{13}$C | -19.9 | -19.7 | -20.2 | -0.4 |
| Banwell reindeer δ$^{15}$N | 8.5 | 9.7 | 7.8 | 1.9 |
| Banwell hare δ$^{13}$C | -20.7 | | | n=1 |
| Banwell hare δ$^{15}$N | 1.8 | | | n=1 |
| | | | | |
| Sandford Hill wolf δ$^{13}$C | -19.4 | -19.2 | -19.5 | -0.3 |
| Sandford Hill wolf δ$^{15}$N | 9.1 | 9.1 | 9.0 | 0.1 |
| Sandford Hill hyaena δ$^{13}$C | -19.5 | -19.1 | -20.1 | -0.9 |
| Sandford Hill hyaena δ$^{15}$N | 9.3 | 9.9 | 8.8 | 1.0 |

| | | | | |
|---|---|---|---|---|
| Sandford Hill lion $\delta^{13}C$ | -19.2 | -19.1 | -19.4 | -0.3 |
| Sandford Hill lion $\delta^{15}N$ | 8.4 | 9.6 | 7.8 | 1.8 |
| Sandford Hill bear $\delta^{13}C$ | -20.3 | -20.1 | -20.7 | -0.6 |
| Sandford Hill bear $\delta^{15}N$ | 9.1 | 9.8 | 8.7 | 1.1 |
| Sandford Hill bison $\delta^{13}C$ | -20.9 | -20.8 | -20.9 | -0.1 |
| Sandford Hill bison $\delta^{15}N$ | 5.4 | 6.1 | 4.7 | 1.4 |
| Sandford Hill woolly rhino $\delta^{13}C$ | -20.8 | -20.6 | -21.0 | -0.4 |
| Sandford Hill woolly rhino $\delta^{15}N$ | 5.3 | 6.3 | 4.6 | 1.6 |
| Sandford Hill horse $\delta^{13}C$ | -20.9 | -20.5 | -21.2 | -0.6 |
| Sandford Hill horse $\delta^{15}N$ | 4.7 | 5.8 | 3.6 | 2.2 |
| Sandford Hill reindeer $\delta^{13}C$ | -19.2 | -18.7 | -19.5 | -0.8 |
| Sandford Hill reindeer $\delta^{15}N$ | 3.3 | 4.4 | 2.4 | 2.0 |
| Sandford Hill hare $\delta^{13}C$ | -21.5 | -20.8 | -22.3 | -1.6 |
| Sandford Hill hare $\delta^{15}N$ | 2.6 | 5.0 | 1.1 | 3.9 |

**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT author statement

Lucy Flower: Conceptualization, Methodology, Validation, Formal Analysis, Investigation, Writing, Visualisation. Danielle Schreve: Conceptualization, Methodology, Resource, Writing, Supervision, Funding Acquisition. Angela Lamb: Conceptualization, Methodology, Validation, Formal Analysis, Investigation, Writing, Supervision.