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Multi-isotope zooarchaeological investigations at Abri du Maras: The paleoecological and paleoenvironmental context of Neanderthal subsistence strategies in the Rhône Valley during MIS 3

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Abstract

The exploitation of mid- and large-sized herbivores (ungulates) was central to hominin subsistence across Late Pleistocene Europe. Reconstructing the paleoecology of prey-taxa is key to better understanding procurement strategies, decisions and behaviors, and the isotope analysis of faunal bones and teeth found at archaeological sites represent a powerful means of accessing information about past faunal behaviors. These isotope zooarchaeological approaches also have a near-unique ability to reveal environmental conditions contemporary to the human activities that produced these remains. Here, we present the results of a multi-isotope, multi-tissue study of ungulate remains from the Middle Paleolithic site of Abri du Maras, southern France, providing new insights into the living landscapes of the Rhône Valley during MIS 3 (level 4.2 = 55 ± 2 to 42 ± 3 ka; level 4.1 = 46 ± 3 to 40 ± 3 ka. Isotope data (carbon, nitrogen) reveal the dietary niches of different ungulate taxa, including the now-extinct giant deer (*Megaloceros*). Oxygen isotope data are consistent with a mild seasonal climate during level 4.2, where horse (*Equus*), bison (*Bison*), and red deer (*Cervus elaphus*) were exploited year-round. Strontium and sulphur isotopes, provide new evidence for behavioral plasticity in Late Pleistocene European reindeer (*Rangifer*) between level 4.2 and level 4.1, indicating a change from the migratory to the sedentary ecotype. In level 4.1, the strong seasonal nature of reindeer exploitation, combined with their non-migratory behavior, are consistent with a seasonally-restricted use of the site by Neanderthals at that time or the preferential hunting of reindeer when in peak physical condition during the autumn.

Keywords: Middle Paleolithic; Collagen; Enamel; Dietary niche; Biogeography; Paleotemperatures

1. Introduction

1.1. Context

The exploitation of mid- and large-sized herbivores was a key adaptive behavior of both Neanderthal and early *H. sapiens* across north-west Europe throughout the Middle and Late Pleistocene (Discamps et al., 2011; Kuntz and Costamagno, 2011; Rendu et al., 2012; Marín et al., 2020). Reconstructing the paleoecology of prey-taxa is vital to better understanding hominin procurement strategies, decisions and behaviors. While the Last Glaciation (Marine Isotope Stage [MIS] 4–2; ~74–12 ka) was marked by climate fluctuations, MIS 3 (~57–29 ka) was a period of profound climatic instability, characterized by short-term and acute climatic oscillations (Voelker, 2002; Barron et al., 2003; Lisiecki and Raymo, 2005; Clement and Peterson, 2008; Kindler et al., 2014). While long-term species distribution and turnover is generally well characterized in the Late Pleistocene (Kahlke, 2014; Puzachenko et al., 2020), the impact contemporary climatic changes would have had on the behaviors of ungulate species is less well known, and the relationships between rapid climatic shifts and the dietary and migratory behaviors of ungulate species are poorly characterized. In turn, the interactions between changes in prey-species behavior and hominin subsistence strategies can be difficult to elucidate. There is a clear need for site-specific approaches, where the reconstruction of local environmental and paleoecological conditions can be contrasted to archaeological evidence in order to gain more nuanced interpretations of the inter-actions between environmental dynamism, the behaviors of prey-species and the subsistence strategies and landscape use of early human groups.

In recent decades, the stable isotope analysis of zooarchaeological assemblages has emerged as a leading means of reconstructing past faunal paleoecology, environments and paleotemperatures. Carbon and nitrogen isotope ratios of bone collagen derive from diet, and in modern ecosystems and recent-historic case studies have been shown to reflect both broad environmental conditions and also the niche feeding behaviors of different taxa of large herbivores over the period of tissue formation (e.g., Ben-David et al., 2001; Drucker et al., 2001, 2012; Feranec, 2007; Hofman-Kamińska et al., 2018). Sulphur isotope ratios measured in bone collagen can also prove useful in food web studies but when considering ungulate species are of most use as a tool for reconstructing geographical range use, with values corresponding to local soils and lithological unit, rainfall and coastal proximity (see review in Nehlich, 2015). As strontium isotope ratios of skeletal tissues relate directly to that of local lithology, soils and plants, these techniques can provide more direct evidence of movement histories (see Britton, 2020, for an overview). When combined with the serial-sampling of incrementally-developing tissues that do not undergo subsequent remodeling (Hillson 2005), such as tooth enamel, these can provide evidence of time-series (i.e., seasonal) movement information, as demonstrated in modern migratory North American caribou (Britton et al., 2009). Given the relationship between temperature and the δ^{18}O of local precipitation, and the near-linear relationship between the δ^{18}O of body water and that of mineralized tissues, the oxygen isotope analysis of mammalian skeletal tissues can provide valuable insights into past thermal conditions (see Pederzani and Britton, 2019, for an overview). When obligate drinking species, such as horses or bison, are targeted and sequential sampling approaches are employed (i.e., of molariform teeth), these approaches can provide evidence of local seasonal climatic conditions (Fricke et al., 1998; Kohn et al., 1998; Sharp and Cerling, 1998). These techniques have successfully been applied to European Middle and Late Pleistocene sites, reconstructing paleoclimate and paleoenvironmental change, faunal niche feeding behaviors and migratory habits, and through this better understanding hominin subsistence strategies (e.g., Bocherens, 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Pellegrini et al., 2008; Stevens et al., 2008; Bernard et al., 2009; Britton et al., 2011; Fabre et al., 2011; Britton et al., 2012; Price et al., 2017; Drucker et al., 2018; Jones et al., 2018; Britton et al., 2019; Jones et al., 2019; Schwartz-Narbonne et al., 2019; Drucker, 2022).

1.2. Reconstructing faunal paleoecology and paleoenvironmental conditions using isotope zooarchaeology

The isotopic compositions of preserved faunal tissues found at archaeological and paleontological sites, including dental enamel and collagen extracted from bones, are a complex product of isotopic inputs during life and the biological process that occur within an organism. Given the variation inherent in many different isotopic systems across landscapes and between (and within) biomes, isotopic inputs obtained through food and water ingested reflect feeding behaviors but also prevailing environmental conditions and geospatial histories, as well as an organism’s physiology. Understanding these issues, and the fundamental principles, assumptions and caveats inherent behind the application of these isotopic techniques to mammalian tissues, is essential in order to be able to interpret isotopic data from zooarchaeological and paleontological remains.

Carbon isotopes Carbon isotope techniques are based around the principle that animal body tissues (e.g., bone collagen) reflect the isotopic composition of the food ingested throughout life. The relative abundance of the stable isotopes of carbon, ^{13}C and ^{12}C ($\delta^{13}C$), varies characteristically between different biomes—e.g., between plants of different photosynthetic pathways (Smith and Epstein, 1971; DeNiro and Epstein, 1978) or between terrestrial and marine ecosystems (Schoeninger and DeNiro, 1984). Studies of resource partitioning and niche feeding ecology have generally focused on environments where both C_3 and C_4 plants can be found, such as sub-tropical Africa (e.g., Koch, et al., 1995; Cerling, et al., 1999) and North America (e.g., Gadbury, et al., 2000; MacFadden, 2008). These plants have different photosynthetic pathways, selecting against ^{13}C to different degrees, and therefore display large differences in their $\delta^{13}C$. However, studies have demonstrated the effectiveness of carbon isotope analysis to reveal resource partitioning among modern (e.g., Feranec et al., 2007; Hofman-Kamińska et al., 2018) and Late Pleistocene (e.g., Britton et al., 2012; Schwartz-Narbonne et al., 2019) ungulates in purely C_3 environments. Such variations stem from intra-ecosystems variations in carbon isotope values of different plant communities and reflect dietary choices of herbivores living within C_3 environments (see Bocherens, 2003; Drucker, 2022, for an overview). Lichens, for example, exhibit less negative $\delta^{13}C$ values than other terrestrial plants incorporated into the diet of Northern ungulates (Ben-David et al., 2001, Maguas and Brugnoli, 1996, Park and Epstein, 1960). This has been demonstrated to raise ^{13}C amounts in the blood and dentine of modern *Rangifer* (Ben-David, et al., 2001, Drucker, et al., 2001), and is often reflected in bone collagen $\delta^{13}C$ values of Late Pleistocene European *Rangifer* (e.g., Fizet et al., 1995). Closed forest systems, including temperate woodlands (Bonafini et al., 2013), can feature anomalously ^{13}C-depleted vegetation, a so-called 'canopy effect'. Anticipated differences between the bone collagen $\delta^{13}C$ of a species regularly feeding on lichens or in dense forest have therefore formed the basis of investigations in cervid feeding ecology in Late Pleistocene Europe, inferring both niche partitioning but also broader environmental conditons (e.g., Drucker et al., 2008; Immel et al., 2015). It should also be noted that the δ^{13}C of bodily proteins can also reflect physiological differences, such as ruminant digestion and methane production, which leads to tissue ^{13}C enrichment (e.g., Cerling and Harris, 1999).

While δ^{13}C values can also be obtained from the carbonate component of dental enamel, where preservation permits, bone collagen is often the favored analyte in studies of faunal dietary paleoecology as (due to remodeling and renewal) it reflects averaged dietary isotopic intake over a number of years (e.g., Hedges et al., 2007) and the preservation and isotopic integrity of bone collagen can be assessed by means of a number of quality indicators (DeNiro, 1985; van Klinken, 1999). Furthermore, analysis of bone collagen often permits the co-generation of nitrogen and, increasingly, also sulphur isotope data which can aid in the inference of other aspects of faunal paleoecology.

Nitrogen isotopes The δ^{15}N value of ungulate bone collagen depends on a number of factors, most notably the δ^{15}N values of the plants at the base of the food chain. A range of variables can lead to depletion or enrichment in plant ^{15}N, which, in turn could affect the tissue δ^{15}N values of animal feeders. Plant δ^{15}N values depend on nitrogen availability, the source of nitrogen that is incorporated into the plant, the characteristics of nitrogen cycling in the soils at any given location, as well the plant's physiology in terms of how they uptake nitrogen (Högberg 1997; Amundson et al., 2003; Hobbie and Högberg, 2012). Plants which obtain their nitrogen with the assistance of mycorrhizae, for example, tend to have lower δ^{15}N values than plants that lack these symbionts (Högberg 1997). This means that in contemporary arctic and boreal ecosystems, grasses—which do not obtain their nitrogen with the assistance of these fungal associations—are normally ^{15}N enriched relative to shrubs and trees that do (see data collated in Bocherens, 2003: 61, Figure 3). In environments that are extremely nutrient-poor, such as tundra environments, competitive partitioning of the overall nitorgen pool by plants through a variety of mehanisms can lead to variations in δ^{15}N values of plant species (Nadelhoffer et al., 1996). In light of these variations, selective feeding on particular plant species, can lead to variation in bone collagen δ^{15}N amongst large herbivores, interpretted as evidence of niche partitioning in Late Pleistocene studies (e.g., Bocherens, 2003; Britton et al., 2012; Schwartz-Narbonne et al., 2019)

Large scale studies of soil δ^{15}N have observed trends in δ^{15}N with both temperature and precipitation (e.g., Amundson et al., 2003), and it is thought that these likely influence soil (and therefore plant) δ^{15}N values in nonagricultural (i.e., unmanaged) primarily through influencing the loss mechanisms which are part of the natural cycling of nitrogen within soils (Houlton and Bai, 2009). In contemporary ecosystems, cooler and wetter conditions influence nitrogen cycling in soils, leading to less ^{14}N being lost through leaching, denitrification, and ammonia volatilization, and thus decreasing plant δ^{15}N values (Amundson et al., 2003). Soil maturity has also been linked to ^{15}N enrichment in plants, and plants growing on pioneer soils may have lower δ^{15}N values due to the inhibition of microbial activity (e.g., Hobbie et al., 1998). It is largely on the basis of these broad relationships between climatic conditions and precipitation, and the pattern of glacial-interglacial successions in the Quaternary, that long-term changes in the δ^{15}N of archaeological herbivore collagen throughout the Late Pleistocene of north-west Europe have been explained (e.g., Richards and Hedges, 2003; Stevens and Hedges, 2004; Stevens, et al., 2008).

However, in modern ecosystems, while there are general trends with climate, correlations between soil/plant δ^{15}N and climate on a global level are poor (Hobbie and Högberg, 2012). It is likely that confounding factors, such as mycorrhizal association and type, along with precipitation are perhaps the most important influences (Hobbie and Högberg, 2012). Other extraneous influences are also known to influence soil $\delta^{15}N$, such as grazing pressure, which can serve to raise $\delta^{15}N$ values in soils and therefore plants, in a complex cycle of nitrogen transfer between herbivores and their forage (e.g., Sjögersten et al., 2010). Bone collagen $\delta^{15}N$ of large herbivores from the Late Pleistocene is therefore a product of multiple influences, from soil maturity and broad-scale climatic influences, to precipitation patterns, through to the individual plant communities and density of animals grazing regularly at a specific location. Furthermore, when considering the $\delta^{15}N$ of large herbivores, potential influences of their adaptive biology and physiology on tissue $\delta^{15}N$ must also be considered. For example, modern studies have demonstrated that ^{15}N-enrichment from diet to tissue is dependent on the protein content of graze and forage consumed, with low protein diets leading to lower diet-tissue offsets and thus (potentially) lower tissue $\delta^{15}N$ values (Sponheimer et al., 2003). Furthermore, physiological variations, such as pregnancy, lactation, and malnutrition have also been demonstrated to influence ^{15}N-enrichment in contemporary forming tissues (e.g., Fuller, et al., 2004; Fuller et al., 2005; Mekota, et al., 2006).

Sulphur isotope analysis Although data are also typically obtained from bone collagen in archaeological case studies, compared to carbon and nitrogen isotope studies there have been comparatively few applications of sulphur isotope analysis ($\delta^{34}S$) to Late Pleistocene materials, although applications are increasing. While useful in archaeology for exploring other aspects of personal life history, such as diet (see review in Nehlich 2015), when applied to Late Pleistocene ungulate remains, sulphur isotope analysis is perhaps most useful as a means of investigating geographical range use and, by inference, faunal spatial paleoecology and even the hunting territories of human groups (e.g., Jones et al., 2019).

At the base of the food-chain, the sulphur incorporated into food-webs originates from sulphates in groundwater and rain, as well as from atmospheric deposition, leading to variations in plant, and therefore herbivore, δ^{34}S. Other sources of sulphur also contribute to the bioavailable pool (that which is incorporated into biomolecules), however, notably due to the weathering of sulphur-bearing minerals into soils from different rock types which can introduce additional variation in terrestrial contexts (see discussion in Nehlich 2015: 4, Figure 3). Another major source of variability in sulphur 'isoscapes' is coastal proximity. Sea spray sulphates result in rain and aerosols with δ^{34}S values of ~20 ‰ (Nielsen, 1974), a uniform and relatively high value that is distinct from the more variable values found in terrestrial and freshwater ecosystems (Peterson and Fry, 1987; Nehlich 2015). The influence of these oceanic sulphates on the δ^{34}S of soils, plants and animals can extend tens of kilometers in land—the 'sea spray effect' (e.g., Richards et al., 2001; Zazzo et al., 2011). While there have been comparatively few applications (to either modern or ancient ecosystems), δ^{34}S has been applied to faunal tissues to explore migratory behavior. For example, given the distinctions between terrestrial and marine sulphates, δ^{34}S of otoliths has been used to differentiate between anadromous and non-anadromous ecotypes of fish (e.g., Godbout et al., 2010). The sampling of modern mammalian bodily proteins such as keratin has also demonstrated strong geographical trends, especially with coastal proximity, suggesting spatial variation in sulphur isotopes may prove a useful means of exploring past faunal spatial ecology in certain contexts (e.g., Zazzo et al., 2011). Few modern studies have incorporated the analysis of sulphur isotopes in bone collagen to explore the usefulness of this approach in inferring faunal movements, although limited work on modern North American *Rangifer* and *Bison* has demonstrated differences between migratory and non-migratory individuals, and correlations between δ^{34}S and strontium isotope ratios (Britton 2010).

Applications to Late Pleistocene faunal samples have indicated the potential of these techniques to infer (at least relative) differences in range use by different species in the same region (e.g., Wißing et al., 2019: 4, Figure 2) and possible changes in human hunting range utilized and/or the spatial paleoecology of prey-species through time (e.g., Jones et al., 2019). However, other studies of Late Pleistocene fauna have also indicated that faunal $\delta^{34}S$ values, via the $\delta^{34}S$ of soils and plants, may (like $\delta^{15}N$) be strongly influenced by prevailing climatic conditions. This includes temperature and the presence of permafrost, both of which may serve to influence the rate of mineralization and volatilization of sulphur in soils, altering soil $\delta^{34}S$ (e.g., Drucker et al., 2011; Reade et al., 2020). While work is required to characterize this relationship, variability in soil $\delta^{34}S$ induced by climatic change poses a challenge to the further development of this method as a tracer of past faunal spatial behaviors, especially in diachronic studies. The potential for baseline variability through time with climatic change, coupled with modern environmental sulphur contamination, also renders the production of the isoscapes necessary for the spatial assignment of sulphur isotope data in archaeological case studies difficult. Despite this, isoscapes built around archaeological datasets can provide useful approximations of anticipated geographical variability in environmental $\delta^{34}S$ (e.g., Bataille et al., 2021). Furthermore, at any given site, it is still possible to interpret $\delta^{34}S$ values of faunal bone collagen from broadly contemporary samples within a relative framework, allowing the identification of individuals or particular taxa/groups that may deviate from the range of $\delta^{34}S$ values typically measured in fauna at that site and therefore identifying them as having inhabited a distinct area or range during life. In studies seeking to directly reconstruct seasonal movement habits or identify the use of particular areas of the landscape, however, alternative methods such as strontium isotope analysis are required.

Strontium isotope analysis The $^{87}Sr/^{86}Sr$ ratio of herbivore enamel (bioapatite) is directly related to the $^{87}Sr/^{86}Sr$ ratio of ingested plants. This, in turn, is a product of the soils and water available to the plants and ultimately correlates with underlying lithologies, with the relative content of ^{87}Sr to ^{86}Sr being a function of the age of the rock as well as it's mineral composition and original chemical content (Capo et al., 1998; Bentley 2006). Generally, higher $^{87}Sr/^{86}Sr$ values are demonstrated in older rocks, and lower values in younger rocks. When combined with serial-sampling, the strontium isotope analysis of can permit the reconstruction of seasonal movements. A small number of archaeological studies have utilized these methods to explore the spatial paleoecology and migratory behavior of Late Pleistocene fauna, including members of the extinct genus *Mammut* (e.g., Hoppe et al., 2009; Wooller et al., 2021) and Late Pleistocene European *Rangifer* (e.g., Britton et al., 2011; Price et al., 2017). Significantly, the use of modern materials has recently allowed an assessment of the relationship between movement histories and the isotopic values exhibited in *Rangifer* enamel—confirming the relationship between environmental and geological conditions, known movements, and dental isotope chemistry (Britton et al., 2009; Britton 2010).

There are, however, a number of caveats and considerations related to the use of strontium isotope analysis in inferring animal movements. The careful selection of samples is imperative, requiring teeth that form over a period sufficient to capture at least a year of isotopic inputs. This may, in some cases, mean multiple teeth are required from the same animals, for example in *Rangifer* (Britton et al., 2009). Data is typically then obtained via the sequential sampling of enamel as horizontal bands down the crown followed by ion-exchange column chemistry to isolate the strontium in the sample, prior to mass spectrometry (e.g., Britton et al., 2011; Funck et al., 2020), or via the direct laser ablation of the enamel (e.g., Wooller et al., 2021). The selection of which technique has implications for data precision, sample destruction, and the resolution achievable (see discussion in Boethius et al., 2022 for a recent summary), but studies of modern animals of known movements have established both techniques as an effective means of reconstructing movements during the period of tooth formation (e.g., wild migratory *Rangifer,* Britton et al., 2009; domestic sheep, Lazzerini et al., 2021). The analysis of different individuals from the same herd in both these modern cases has also allowed an assessment of the expected level of intra-herd variability.

Finally, in order to interpret intra-tooth strontium data and assess mobility patterns, the establishing of local predicted environmental bioavailable strontium is required, ideally within the framework of a wider isoscape. The deviations between ^{87}Sr/^{86}Sr variability predicted purely from geological maps, and 'bioavailable' strontium found in soils has been discussed extensively in the literature (see reviews in Capo et al., 1998; Bentley 2006; Britton 2020). Instead of relying on geological maps, isoscapes of 'bioavailable' strontium are typically developed through the determination of ^{87}Sr/^{86}Sr in modern rock or soil leachates, local waters, plant or faunal samples to generate source data, with the selection of analyte potentially influencing the isoscape produced (see discussion in Britton et al., 2020). These source data are then combined to produce spatial maps of strontium isotopic variation across landscapes using a variety of GIS-based or spatial aggregation techniques (see review in Holt et al., 2021). The inference of movement can then be made through visual comparison of variation in data with variation within those isoscapes, or with the assistance of spatial assignment software tools (e.g., Ma et al., 2020).

Oxygen isotope analysis There a number of different applications for oxygen isotope analysis in archaeology and paleoecology, all based on the relationship between the oxygen isotope composition (δ^{18}O) of an animal's body tissues and that of water consumed (Iacumin et al., 1996; Kohn, 1996; Longinelli, 1984; Luz et al., 1984). The oxygen isotope composition of environmental water is closely related to the δ^{18}O values of precipitation, reflecting local temperatures and other factors (Clark and Fritz, 1997; Dansgaard, 1964; Gat, 1980; Yurtsever, 1975). Although hydrological processes such as water movement, water mixing, groundwater recharge and the formation (and evaporation) of surface water bodies can all influence the oxygen isotope composition of local environmental water (and, by inference, drinking water), broad correlations between groundwater, mean annual precipitation, and climate at specific locales are universally apparent (see review in Pederzani and Britton, 2019). In obligate drinking mammals, where local environmental waters are the primary source of fluids imbibed, the relationship between the $\delta^{18}O$ of local environmental water and the $\delta^{18}O$ of an animal's body tissues is mediated by the $\delta^{18}O$ of body water. Homeothermic mammals have a metabolically-controlled, relatively constant body temperature (~37°C), and therefore the bioapatite (a carbonated hydroxyapatite) in their mineralized tissues precipitates in oxygen isotope equilibrium with body water at this temperature (Levinson et al., 1987; Longinelli, 1984; Luz et al., 1984). There is, therefore, a roughly linear relationship between the $\delta^{18}O$ of ingested water, body water, and bioapatite and this relationship has led to the application of $\delta^{18}O$ to archaeological and paleontological remains as a means of reconstructing past climatic conditions. While some variation in this relationship has been noted between species, fractionation factors have been established for a number of different taxa based on modern experimental studies (e.g., Delgado Huertas et al., 1995 [horses]), allowing the development of these techniques on faunal remains from archaeological sites as a means of reconstructing past paleotemperatures.

Paleothermic reconstructions using the oxygen isotope analysis of faunal remains from European Late Pleistocene sites have focused on a range of different mammalian species, and have employed analyses of both the carbonate (CO_3) and phosphate (PO_4) components of tooth enamel, using a range of different Pleistocene mammals (e.g., Delgado Huertas et al., 1997; Fabre et al., 2011; Skrzypek et al., 2011; Kovács et al., 2012). As obligate drinkers with significant daily water requirements, and taxa found in both glacial and interglacial faunal assemblages, equids and large bovids are particularly useful for mapping past $\delta^{18}O$ precipitation patterns and paleoclimate conditions. The analyses of these taxa from anthropogenically-derived (archaeofaunal) assemblages have the potential to generate terrestrial paleoclimate proxy data near-synchronous to human site-use, enabling estimates of mean annual temperatures when dental tissues are bulk sampled (e.g., Britton et al., 2019) and of seasonal paleotemperatures when hypsodont teeth are incrementally sampled (e.g., Pederzani et al., 2021).

In addition to the in-built assumptions inherent in the reconstruction of paleotemperatures detailed above, a number of other factors can influence data produced and thus paleotemperature estimates. For example, the choice of tooth sampled is important. Early forming teeth, in general, should be avoided due to a known enrichment in ^{18}O in the body water (and thus tissues) of juvenile animals during nursing compared to adult individuals (see review in Pederzani and Britton 2019). Sampling strategy therefore must incorporate knowledge of likely age-at-weaning for species targeted. As well as tooth selected, method of sampling can influence data generated (Reade et al., 2015). In the determination of bioapatite $\delta^{18}O$ different moieties can be targeted, influencing data obtained. In paleotemperature reconstructions using older Paleolithic materials, the phosphate is often the favored analyte as it is generally considered to be more resistant to post-depositional alteration compared to the carbonate component (Iacumin et al., 1996; Zazzo et al., 2004). Furthermore, the vast majority of modern calibration data for converting bioapatite $\delta^{18}O$ to predicted $\delta^{18}O$ drinking water has so far been generated from phosphate data and the use of carbonate $\delta^{18}O$ ($\delta^{18}O_{CO3}$) for paleotemperature estimation would therefore require an additional conversion step to predicted $\delta^{18}O$ of bioapatite phosphate ($\delta^{18}O_{PO4}$) prior to paleotemperature calculations, which can increase uncertainty. Conversion equations themselves, which are required to convert $\delta^{18}O_{PO4}$

to estimates of the $\delta^{18}O$ of drinking water ($\delta^{18}O_{dw}$) and then to estimates of temperature, also include inherent assumptions and introduce (often large) compound uncertainties (Pryor et al., 2014). These conversions, and the uncertainties introduced, are discussed at length in a number of papers (e.g., Pryor et al., 2014) and are detailed here in the Supplementary Online Material (SOM) S3.

1.3. The site of Abri du Maras

The site of Abri du Maras is located on the west bank of the Rhône River, in a small valley at the confluence of the Ardèche River (Fig. 1). The site is all that remains of a vast southeast facing rock shelter, situated today 70 m above the river itself at the outer edge of the gorge. The Rhône Valley lies between mountainous regions—the Massif Central to the west and the foothills of the Alps to the east—with the valley itself connecting more northerly parts of France to the Mediterranean. Many tributaries, including the Ardèche River, connect the Rhône River to the Massif Central. Archaeological and zooarchaeological evidence from the region's caves and rock shelters suggest a farsighted circulating subsistence model closely associated with the regional micro-topography, interactions with non-human carnivores and the estimated availability of (seasonal) resources including prey-species, biotopes and raw material outcrops (Daujeard and Moncel 2010; Daujeard et al., 2016). Monospecific prey assemblages, characterized by the high dominance of remains of a single species represented by a large (minimum) number of individuals (Gaudzinski, 2006), are found at some Middle Paleolithic sites in the region, including at Abri du Maras with *Rangifer* (Daujeard and Moncel, 2010; Daujeard et al., 2012; Moncel and Daujeard, 2012; Daujeard et al., 2019; Marin et al., 2020; Moncel et al., 2021). Monospecific faunal assemblages increase significantly all over Europe from MIS 5 onwards, and when involving animals that live in large herds, such as reindeer, are often linked to cooperative and planned mass hunting strategies, and flexible resource utilization against a background of increasing climatic instability (Gaudzinkski, 2006). In such contexts, understanding the spatial paleoecology of the prey taxa can be key to interpreting these human hunting practices (e.g., interception hunting; Britton et al., 2011).

Since 2009, excavations of the site have focused on Middle Paleolithic deposits, including stratigraphic unit 5 (bottom of the currently documented sequence at the site, dating to the end of MIS 5) and overlying unit 4, which contains two archaeological levels in its upper part (levels 4.1 and 4.2) which both date to MIS 3. The site has been dated by electron spin resonance (ESR) and Uranium-Thorium (U-Th) methods, with level 4.1 dating to between 46 ± 3 ka and 40 ± 3 ka and level 4.2 yielding dates ranging between 55 ± 2 to 42 ± 3 ka (Richard et al., 2015). Further analyses of two enamel hydroxyapatite samples from level 4.2 using these same methods have yielded ages of 42 ± 3 and 42 ± 6, which together with an infrared stimulated luminescence (IRSL) age of 46 ± 4 ka confirm the attribution of this site to MIS 3 (Richard et al., 2021). Both of these levels contain the well-preserved evidence of hominin occupation, including abundant lithic artefacts, rare cordage remains, traces of combustion and diffuse ash lenses, and anthropogenically-modified faunal remains. The lithic assemblage comprises Levallois products and other core technologies, and includes retouched flakes, blades projectile tips and points largely made of local and semi-local flint (Hardy et al., 2013; Moncel et al., 2014; Daujeard et al., 2019; Hardy et al., 2020; Ruebens et al., 2022). Despite being close in date (or even sub-contemporaneous), levels 4.1 and 4.2 have yielded very different faunal and seasonality-indicator data, along with slightly different patterns of butchery which may suggest site use by two distinct groups with contrasting traditions (Vettese et al., 2022). The faunal spectrum in 4.2 is varied and comprises, in order of abundance, *Rangifer tarandus, Equus ferus* cf. *germanicus, Bison priscus, Cervus elaphus* and *Megaloceros giganteus*, with spring-summer and autumn human occupations. Level 4.1 is largely dominated by *Rangifer* which, combined with indicators of selective butchery and autumn season of death mortality profile, is suggestive of seasonally-restricted, cooperative and planned mass *Rangifer* hunting strategy and short-term occupations (Daujeard et al., 2019; Moncel et al., 2021; Vignes, 2021; SOM Table S1). Understanding potential differences in the paleoecology of species exploited, particularly the spatial ecology of *Rangifer*, would be an important step in better understanding Neanderthal subsistence strategies in these different levels.

Aside from the (macro-) faunal remains, paleoenvironmental studies have been limited for levels 4.1 and 4.2 of the site. Micromammals are scarce, largely due to poor preservation, although the presence of a single sample of *Microtus* ex gr. *arvalis-agrestis* found in level 4.1 is consistent with a rather open environment (Daujeard et al., 2019). Dental microwear analysis of reindeer from level 4.1 has indicated grass-dominated mixed feeding, which is also consistent with an open environment, complementing the results of a small isotopic pilot study on faunal material from the same level indicating a lack of dense forest cover (Daujeard et al., 2019). Charcoal identified in both levels 4.1 and 4.2, however, suggest the presence of at least some woodland and taxonomic analyses has identified *Pinus sylvestris* type in both levels 4.1 and 4.2, along with *Betula* in level 4.1 only (Daujeard et al., 2019). While *Pinus sylvestris* grow in dry and cold conditions, *Betula* require higher soil humidity rates, which may indicate that, in level 4.1 at least, conditions may have been relatively humid/milder (which is in agreement with the results of sedimentological analysis for the site, see Daujeard et al., 2019; Moncel et al., 2021). These data may seem somewhat contradictory to the presence of *Rangifer*, which are often considered a cold-adapted species and therefore inferring a harsh or steppic environment. However, it should be noted that there are multiple ecotypes of *Rangifer* today (Festa-Bianchet et al., 2011) and the behaviors and habitat preferences of Late Pleistocene European *Rangifer* (and variation therein) should not be assumed. Furthermore, it has long been recognized that the environments of northern Europe during MIS 3 (and at other phases of the Late Pleistocene) were non-analogous to any modern environment, that is, characterized by combinations of animals (and plants) living together that are not found in sympatry today (see Stewart 2005 for discussion of Europe as a whole, and Foury et al., 2016 for discussion of the Rhône valley specifically). Therefore, given the limited paleoenvironmental data available from Abri du Maras, the diversity of species present (i.e., *Rangifer* with two other cervids, including the extinct *Megaloceros*) at the site, and the differences in prey-selection and seasonality of site use indicated from past zooarchaeogical studies between levels 4.1 and 4.2, elucidating further information about the paleoecology of the species exploited, or the broader paleoenvironmental suite, using isotope zooarchaeological approaches is of key interest.

Here, we present the results of a multi-isotope, multi-tissue study of herbivore remains from level 4.1 (46 ± 3 to 40 ± 3 ka) and level 4.2 (55 ± 2 to 42 ± 3 ka) at the Middle Paleolithic site of Abri du Maras (Ardèche, France), with the goal of providing new insights into the paleoenvironmental and paleoecological context of Neanderthal activity in the Rhône Valley during MIS 3. The specific aims of this study are: 1) to provide evidence of local paleothermic conditions; 2) to assess niche feeding behaviors and landscape use by key subsistence species; 3) to examine potential relationships between herbivore ecology and/or seasonal biogeography at the site, the paleoenvironment, and the subsistence behaviors of contemporary hominin groups.

2. Materials and methods

2.1. Sample selection

Ungulate bone and teeth from the recent excavations at Abri du Maras (levels 4.1 and 4.2) were selected for destructive sampling and isotope analysis, including teeth of *Equus* and *Rangifer* for oxygen and strontium isotope analysis respectively, and *Bison*, *Cervus*, *Equus*, *Megaloceros* and *Rangifer* bone for carbon, nitrogen and sulphur isotope analysis (see Table 1 for all samples involved in this study). These samples are part of collections currently housed at the Institut de Paléontologie Humaine (IPH), Paris, for their ongoing study following taxonomic identification.

Due to sample availability, two complete *Equus* mandibular second premolars were sampled and analyzed for oxygen ($\delta^{18}O$) isotope analyses for climate reconstruction from level 4.2 only. Depending on the extent of tooth wear, horse second premolar enamel mineralizes between the ages of ~13 and 31 months, allowing the inference of more than a year of isotopic inputs (Hoppe et al., 2004). Weaning in horses generally takes place before the start of second premolar development, meaning that any nursing effects on $\delta^{18}O$ are avoided by choosing this tooth type (Hoppe et al., 2004). A third *Equus* tooth, a third molar, suitable for analyses was recovered from level 4.1, but was only analyzed for $^{87}Sr/^{86}Sr$ (see below) but not $\delta^{18}O$. As different tooth positions exhibit different enamel mineralization rates throughout tooth growth, they are not exactly comparable in their seasonal $\delta^{18}O$ patterns, a concern particularly in horses (Bendrey et al., 2015). As this M3 was the only available *Equus* tooth specimen from level 4.1 any inter-level difference in $\delta^{18}O$ could not be securely assigned to environmental differences but could also be an artefact from comparing different tooth positions. For this reason, we decided not to sample this tooth for $\delta^{18}O$. No bone was sampled from these individuals due to them being loose teeth.

In order to explore the seasonal mobility of *Rangifer*, two mandibular teeth (second and third molars) were selected from four *Rangifer* for strontium ($^{87}Sr/^{86}Sr$) isotope analyses. Due to the availability of material, samples included three individuals from level 4.1, but only a single individual from level 4.2. While intra-tooth $\delta^{18}O$ can be helpful in 'anchoring' $^{87}Sr/^{86}Sr$ within a seasonal context, given that *Rangifer* are non-obligate drinkers and long-distance and/or altitudinal migrations can cause intra-tooth $\delta^{18}O$ profiles to deviate substantially from a classic seasonal sinusoid (Britton et al., 2009), coupled with the need for minimally-destructive intra-tooth sampling, the decision was made not to sample the *Rangifer* teeth for oxygen isotope analysis. However, in the absence of oxygen isotope data, the periodicity of *Rangifer* tooth crown formation and mineralization, and thus the seasonality of intra-tooth $^{87}Sr/^{86}Sr$ can still be approximated based on previous studies, including a single radiograph study (Wu et al., 2012) and from comparable datasets from other cervid species. For example, Brown and Chapman (1991: 373) determined that formation of the second and third molar crowns of *Dama dama* commence at <3.5 and 9 months of age and complete at 9 and <18 months respectively. While intra-tooth oxygen isotope studies on *Rangifer* are not straight forward for the reasons stated above, the scant intra-tooth oxygen isotope data from modern migratory and non-migratory individuals (Britton et al., 2009; Britton 2010) suggest these estimates of enamel mineralization time are appropriate. Therefore, sampling of the se second and third molars can (depending on extent of wear) provide evidence of calving grounds, summer and winter range during the first year of life, and summer/autumn range during the second year of life (Britton et al., 2009). It must be noted, however, that any intra-tooth isotope study using archaeological materials has unavoidable assumptions inbuilt with regards to both the growth rate/mineralization time and birth seasonality of ancestral species being similar to extant individuals today. Anticipated to be a likely non-migratory species, an *Equus* third molar was selected from level 4.1 for strontium isotope analyses as a comparator to the *Rangifer*.

Following on from a previous pilot study of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic niche variability in *Equus* (*n* = 3), *Megaloceros* (*n* = 2) and *Rangifer* (*n* = 3) from level 4.1 (Daujeard et al., 2019), further bone samples from five ungulate taxa were selected for collagen extraction and analyses from level 4.2, including *Equus* (*n* = 5), *Megaloceros* (*n* = 2), *Rangifer* (*n* = 1), *Bison* (*n* = 2) and *Cervus elaphus* (*n* = 5). It should be noted that, with the exception of the *Rangifer* sample from level 4.2 (M10-121) from which both mandibular teeth and bone were sampled, bone samples and the teeth sampled for strontium and oxygen described did not (to our knowledge) originate from the same individuals. While, ideally, these different isotope analyses would be undertaken from the same individuals, the horse teeth were all loose and it was not possible to sample the mandibles from the reindeer from which teeth were selected in level 4.1 due to their poor preservation/friability. Conversely, while bone was successfully sampled from other *Rangifer* mandibles in level 4.1, their teeth were insufficient for strontium isotope analyses (e.g., lacking in a complete and relatively unworn second and/or third molar, both of which are required to reconstruct a full year of movement history).

2.2. Tooth and bone sampling protocols

For all teeth, the buccal face of the anterior loph was selected for sampling as it tends to have thicker enamel than the lingual side. The whole face was abraded (using air abrasion) to remove superficial enamel. Each complete tooth was then ultrasonicated in Milli-Q ultrapure water for 5 mins. Incremental enamel samples were taken as horizontal bands, perpendicular to the tooth growth axis, using a diamond-coated tungsten carbide cutter point (NTI-Kahla) from the enamel-root junction (ERJ) to the occlusal surface. Sampling increments were 1–2 mm, measured as distances from the ERJ in each specimen using digital calipers. For the *Equus* from level 4.2, between 25 and 28 samples of fine enamel powder, ranging in weight from ∼5 to ∼15 mg, were collected from each tooth. For the *Rangifer*, between 5 and 10 serial samples of fine enamel powder, ranging in weight between ~3 and ~8 mg (albeit with a single sample, SEVA32976IX, weighing ~1mg) were collected from each tooth depending on crown height available to sample/extend of wear. A single sample of dentine, presumed to be diagenetically altered and therefore reflecting of local soil values, was taken from the molar roots of each of the *Rangifer* teeth samples in order to provide a secondary indicator of local environmental strontium ^{87}Sr/^{86}Sr at the site. For the single *Equus* tooth from level 4.1, three samples, spaced evenly down the crown (~12–14 mm apart), were taken in a similar way. Bone (~1–2 g) was sampled for collagen extraction using rotary stainless-steel cutting implements and cleaned using air abrasion.

2.3. Oxygen isotope analysis

Silver phosphate precipitations and mass spectrometry Serial samples of *Equus* tooth enamel (~10 mg) were prepared for phosphate oxygen isotope analysis in the Archaeological Chemistry Laboratories, Department of Archaeology, University of Aberdeen following methods described in Britton et al. (2019) using a rapid precipitation method, after Tütken et al. (2006) and based on O'Neil et al. (1994) and Dettmann et al. (2001: Appendix, GSA Data Repository item 20018), with minor modifications.

Phosphate $\delta^{18}O$ values were determined by continuous flow isotope ratio mass spectrometry (CF-IRMS), measured with a Thermo-Fisher thermal conversion elemental analyzer (TC-EA) connected to a Finnigan Delta Plus XL mass spectrometer, at the Department of Geochemistry, University of Tübingen, Germany. Mean values and standard deviations (1 SD) were provided by the analyzing laboratory, calculated from the analysis of each sample in triplicate (SOM Table S2). In some instances, mean values were provided from duplicate measurements, due to small sample size, sample loss, loss of sample integrity or through internal data quality control checks in Tübingen (SOM Table S2). Long-term laboratory reproducibility was reported as ± 0.3‰ (1 SD), while mean reproducibility for the samples analyzed in this study was ± 0.2‰ (1 SD) or better. A detailed description of silver phosphate precipitation, and the calibration of mass spectrometry data and standards can be found in SOM S1.

Modelling of intra-tooth oxygen isotope data, conversion equations and air temperature estimations The extended process of tooth enamel growth and mineralization of ungulate teeth causes a predictable damping of the seasonal amplitude of oxygen isotopic change expressed tooth enamel compared to the seasonal amplitude in consumed environmental water (Kohn et al., 1996; Passey and Cerling, 2002; Kohn, 2004; Blumenthal et al., 2014; Green et al., 2017; Trayler and Kohn, 2017). Therefore, a correction procedure is necessary in order to obtain faithful paleotemperature reconstructions on a seasonal time scale, which can be achieved using an inverse model (Passey et al., 2005; Green et al., 2018). Such models take into account the sampling geometry and species-specific characteristics of tooth enamel formation to estimate the original $\delta^{18}O$ input. In this study, horse tooth enamel $\delta^{18}O$ seasonal curves were inverse modelled following methods in Passey et al. (2005) using R v.4.1.2 (R Core Team, 2021) and an R code translation of the originally published MATLAB code. Details of the modelling procedure are described in SOM S2 and we provide all code and data necessary to reproduce this step in the SOM File S1.

Corrected summer peak and winter trough $\delta^{18}O$ values were extracted from the most likely model solutions and used to estimate summer and winter paleotemperatures following methods in Pryor et al. (2014), and are described in more detail in SOM S2. Mean $\delta^{18}O$ values were computed as the mean of unmodeled summer peak and winter trough values, rather than as annual averages, following comparisons in Pederzani et al. (2021) showing that summer/winter means and year-long averages of modelled or unmodeled $\delta^{18}O$ sinusoidal curves yield essentially identical results. However, to indicate that these values don’t represent averages of complete annual cycles, we refer to them as ‘midpoints’ to avoid confusion. Details of the temperature estimation procedure are provided in SOM S2, and we provide the spreadsheets that were used for all estimations in SOM File S1.

2.4. Bone collagen extraction and analysis

Collagen was extracted using the Longin (1971) method, with modifications based on the recommendations of Collins and Galley (1998), and with the addition of an ultrafiltration step

(Brown, et al., 1988), as described in Britton et al. (2012). Collagen samples were analyzed (in duplicate) for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (MPI-EVA, Leipzig, Germany), on a Delta XP mass spectrometer coupled to a Flash EA 2112 elemental analyzer, with an analytical precision of ± 0.3‰ (1 SD) or better based on replicate analyses of an in-house methionine standard. See SOM S3 for details of data normalization and standards (in-house and international).

An additional aliquot of collagen was analyzed for stable sulphur ($\delta^{34}S$) isotopes at the Scottish Universities Research Centre (SUERC) for all collagen extracts, including those from which $\delta^{13}C$ and $\delta^{15}N$ data have been previously presented (Table 1; Daujeard et al., 2019). This was conducted on a Delta V Advantage continuous-flow isotope ratio mass spectrometer coupled via a ConfloIV to an IsoLink elemental analyzer (Thermo Scientific, Bremen), a system which enables the co-measurement of carbon, nitrogen and sulphur stable isotope ratios (Sayle et al., 2019), generating additional $\delta^{13}C$ and $\delta^{15}N$ measurements as well as $\delta^{34}S$ with an analytical precision of ± 0.3‰ (1 SD) or better for each isotope (see SOM S2 for method statement and details of normalization of data and standards). As multiple sets of $\delta^{13}C$ and $\delta^{15}N$ measurements were obtained from each sample (see SOM Table S3 and Table S4 for MPI-EVA and SUERC data, respectively), for the purposes of this study the calculated mean of all measurements is used for each sample (SOM Table S5), which slightly modifies the values reported for some of the same samples from level 4.1 previously reported in Daujeard et al. (2019). However, across the two laboratories, the average standard deviation (1 SD) about the mean for the measurement of all individual aliquots was lower than the largest long-term reproducibility/analytical error reported by either laboratory. Thus, the data are considered comparable. No subsequent statistical treatments were applied to the carbon and nitrogen isotope data, beyond the descriptive statistics in the text below (mean, standard deviation, etc.). However, we explored the partition of the samples according to their $\delta^{34}S$ values using hierarchical clustering (‘hclust’ base function, R v.4.1.2). We used the ‘average’ agglomeration method to define the clusters as it provided the highest cophenetic correlation coefficient for our dataset (c = 0.896) among the different agglomeration methods (Legendre and Legendre 1998).

2.5. Strontium isotope analysis

Sample preparation and mass spectrometry All samples of *Rangifer* tooth enamel (plus the dentine, and three sub-samples of *Equus* tooth enamel from level 4.1) were analyzed for strontium isotope ratios using the ion-exchange solution method described in Copeland et al. (2008) and Britton et al. 2009, a modification of the method from Deniel and Pin (2001). $^{87}Sr/^{86}Sr$ ratios were determined using a Thermo Fisher (Thermo Fisher Scientific, Bremen, Germany) Neptune multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) in the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology. Strontium concentrations of the enamel samples were determined using the method described in Copeland et al. (2008), which is accurate to within ± 31 ppm. Analytical precision was ± 0.00003 (2 SD) or better, based on the repeat analysis of external and in-house standards. For detailed descriptions of sample preparation, correction of mass spectrometry data and details of standards and blanks see SOM S5.

Spatial assignment For the four *Rangifer*, in addition to the generation of individual intra-tooth profiles (see below, ‘Results’), and one *Equus*, spatial assignment of strontium isotope data from three points during tooth growth in each individual tooth-pair was undertaken using the ‘assignR’ package v.2.2.0 in R (Ma et al., 2020). Assignment of the *Equus* samples were done as a reference for a (presumably) local, non-migratory species. The ‘assignR’ package permits the inference of geographical origin from isotope data, with assignments in the case of $^{87}Sr/^{86}Sr$

based on variability of environmental $^{87}Sr/^{86}Sr$ across the landscape (the strontium isoscape; Fig. 2). We used the global bioavailable $^{87}Sr/^{86}Sr$ isoscape, and the associated spatial error raster produced by Bataille et al. (2020). The three sample locations in each *Rangifer* sampled selected for spatial assignment include: 1) the sample closest to the occlusal surface of the second molar (the earliest forming section of the intra-tooth profiles obtained, expected to broadly correspond with location during the first summer of life); 2) the sample closest to the ERJ of the second molar (broadly corresponding to location during the first winter of life); and 3) the sample closest to the ERJ of the third molar (broadly corresponding to location during the second summer/autumn of life). For *Equus*, the three samples were taken from the M3, close to the occlusal surface, at the midpoint, and close to the ERJ. For each sample, treated as sample of unknown origin, we generated the posterior probability surface of origin rescaled to 1, then we extracted the area corresponding to 80% of the posterior probability density. R code is provided in SOM File 2.

3. Results

3.1 Intra-tooth enamel oxygen isotope data from level 4.2 Equus

Oxygen isotope data generated from two *Equus* teeth (lower second premolars) from level 4.2 demonstrate sinusoidal intra-tooth patterns, with values ranging from 16.3 to 19.3‰ with a midpoint (mean of summer and winter extremes) of 17.8‰ (N6-767) and 15.2 to 18.9‰ with a midpoint of 17.1‰ (N6-687; Fig. 3, and full data in SOM Table S2 and summary of seasonal extrema in SOM Table S6). This results in a seasonal $\delta^{18}O$ amplitude of ~ 3‰. Given the well documented linear relationship between *Equus* sp. enamel $\delta^{18}O$ and drinking water $\delta^{18}O$ (Bryant et al., 1994; Sánchez Chillón et al., 1994; Delgado Huertas et al., 1995), we take the characteristic sinusoidal $\delta^{18}O$ curves seen here in sequentially sampled tooth enamel to be reflective of seasonal changes in $\delta^{18}O$ of environmental water consumed by these individuals, that most likely in turn reflect seasonal temperature changes. Based on the linear relationship between $\delta^{18}O$ of enamel ($\delta^{18}O_{enamel}$) and $\delta^{18}O$ of drinking water ($\delta^{18}O_{dw}$) and in turn with $\delta^{18}O$ of precipitation, as described in SOM S3, we estimated $\delta^{18}O_{dw}$ and paleotemperatures in order to facilitate comparisons with other paleoclimate information and with modern climates. This approach relies on some inherent assumptions including a certain degree of physiological similarity between modern and Pleistocene animals, a broadly comparable system of atmospheric circulation, and that drinking water sources of the studied animals isotopically reflect precipitation inputs. These are mostly thought to be justified for European Late Pleistocene settings, although local hydrotopography and drinking water sources need to be studied on a case-by-case basis. Additionally, it should be noted that they introduce a certain unavoidable (and mathematically not fully captured) degree of uncertainty to paleotemperature estimations (see Pryor et al., 2014 and SOM S2 for details on error sources that are accounted for).

An overview of unmodelled summer, mean and winter $\delta^{18}O_{enamel}$, inverse modelled summer and winter $\delta^{18}O$, and corresponding $\delta^{18}O_{dw}$ and paleotemperature estimates is provided in SOM Table S6. Drinking water $\delta^{18}O$ estimates fall at -0.6 ± 2.1‰ for summer, -7.6 ± 2.1‰ for annual means, and at -16.2 ± 2.2‰ for winter (Fig. 4). In comparison, interpolated estimates of modern precipitation $\delta^{18}O$ indicate that current precipitation at the site exhibits $\delta^{18}O$ values of -1.5‰ in July and -9.9‰ in January and mean annual $\delta^{18}O$ of -6.3 ± 0.1‰ (95% CI; Bowen and Revenaugh, 2003; Bowen et al., 2005; Bowen, 2022), Paleotemperature conversions for the two individuals from level 4.2 indicate summer temperatures of 31 ± 4.8°C, winter temperatures of -10 ± 4.3°C and mean annual temperatures of 12 ± 4.0°C (Fig. 4), where error ranges indicate the compound error of the paleotemperature estimation as described in Pryor et al. (2014). This compares to modern day (1981-2009) temperatures of 4.3 ± 1.6°C in January, 23.3 ± 1.1°C in July and an annual average of 13.4 ± 0.5°C estimated for the site using the ClimateEU model (Marchi et al., 2020).

3.2. Bone collagen carbon, nitrogen and sulphur isotope data of ungulates from level 4.1 and 4.2

Full results of the faunal bone collagen extracted and analyzed from Abri du Maras can be found in the SOM (SOM Table S3 [Leipzig], SOM Table S4 [SUERC], and SOM Table S5 [means]), including all quality (%C ,%N, %S, C:N, C:S and N:S) data. δ^{13}C and δ^{15}N of all specimens are shown in Figure 5, and corresponding δ^{34}S data of all samples with sufficient remaining collagen for that analysis are shown in Figure 6. Although approximately half of the samples have %C and %N marginally lower than that of modern collagen (i.e. less than ~35 ± 8.8 wt% for C, and 11–16 wt% for N; van Klinken 1999), their atomic C:N ratios are between 3.2 and 3.5, and are therefore within the expected range for well-preserved bone (DeNiro, 1985; Ambrose, 1990; van Klinken, 1999; Dobberstein et al., 2009). Furthermore, δ^{13}C and δ^{15}N values are not significantly correlated with %C or %N respectively, or with C:N ratios (see SOM Figs. S1–S4). The atomic C:S ratios range from 545 to 827 and the N:S ratios range from 157 to 250, and are therefore within the range expected for modern mammalian bone collagen (C:S = 600 ± 300 and N:S = 200 ± 100; Nehlich and Richards, 2009).

Mean δ^{13}C and δ^{15}N values (± 1 SD) for horses (*n* = 8) are -20.3 ± 0.2‰ and 3.3 ± 0.8‰, and values are similar within both levels. Mean values from the *Bison* samples (*n* = 2), both level 4.2, are elevated relative to the horses with being -19.7 ± 0.0‰ and 5.6 ± 0.0‰ for carbon and nitrogen respectively. The three cervid taxa all have similar mean δ^{13}C (*Megaloceros*: -19.5 ± 0.1‰ [*n* = 4]; *Rangifer*: -19.9 ± 0.2‰ [*n* = 4]; *Cervus elaphus*: -19.8 ± 0.2‰ [*n* = 5]), but differ in their δ^{15}N, with *Cervus elaphus* (all from level 4.2) having the lowest values (3.9 ± 0.4‰), *Megaloceros* have the most elevated values (5.5 ± 0.1‰) and *Rangifer* displaying the greatest range of values from 3.9 to 6.0‰ (mean = 4.8 ± 0.9‰).

Of the 23 bone collagen extractions, 19 yielded sufficient material for the measurement of sulphur isotope ratios. While species δ^{34}S means (± 1 SD) are similar in some species (e.g., *Megaloceros*: 5.2 ± 0.6‰ [*n* = 3]; *Bison*: 5.5 ± 0.2‰ [*n* = 2]; as well as between *Rangifer*: 3.7 ± 2.8‰ [*n* = 4] and *Cervus elaphus*: 3.3 ± 1.2‰ [*n* = 4]), there are notable differences between species and, in some cases, between levels. *Rangifer* and *Cervus elaphus* display a greater range of values than other species, including an outlier value of 0‰ in the single *Rangifer* sampled from level 4.2 (Fig. 6). Of the samples that have sulphur data, both *Cervus elaphus* (*n* = 4; level 4.2 only) and *Equus* (*n* = 6) have a fairly wide range of δ^{34}S values (from 2.0‰ to 4.9‰; and 2.3‰ to 6.8‰ respectively), although not as large as the range of sulphur isotope ratios shown in the *Rangifer* (which varies from 0.0‰ to 6.0‰). With the exception of the single *Rangifer* sample from level 4.2, according to the hierarchical cluster analysis, the animals at Abri du Maras fall into two broad groups with regards to sulphur: group 1) 4.8–6.8‰ and group 2) ~2–3.2‰ (SOM Fig. S3). All species analyzed are present in group 1, and *Equus*, *Rangifer* and *Cervus* can be found in group 2, with animals from both levels found in each of the groups. A recently produced sulphur isoscape for the region (based on bone collagen data from the Mesolithic to the modern day) suggests that δ^{34}S values around Abri du Maras could be expected to range from 4 to 7‰ (SOM Fig. S4, based on data from Bataille et al., 2021). Thus, individuals from sulphur group 1 are consistent with this local range, but those in group 2 are comparatively low, and not consistent with values found within the immediate region.

3.3. Intra-tooth strontium isotope data from Rangifer *and* Equus *from level 4.1 and 4.2*

Tooth enamel strontium (Sr) concentrations of archaeological *Rangifer* samples ranged from 86–200 ppm (SOM Table S7), which are similar to those measured in modern caribou (Britton et al., 2009) and in domestic cattle (Evans et al., 2007). Strontium concentrations of *Equus* enamel were higher (~250 ppm), but also in line with values expected from archaeological herbivore teeth (Evans et al., 2007; Groot et al., 2020). Data from the M_2 and M_3 of intra-tooth samples of all three individual *Rangifer* sampled from level 4.1 bear similar isotope values (Fig. 7; SOM Table S7), ranging from 0.7085 to 0.7101 with a mean of 0.7089 ± 0.0003. This average is a little higher than the mean of three samples of horse tooth enamel sampled from a single horse from the same level, close to the occlusal surface, mid-crown and at the enamel root junction (0.7086 ± 0.0001). The strontium isotope values measured in all dentine samples from *Rangifer* from both level 4.1 and level 4.2 range from 0.7086 and 0.7092 (mean = 0.7088 ± 0.0003), are a secondary confirmation of the expected range of local values (see Fig. 2 for a predicted strontium isoscape of the region). In contrast, the intra-tooth values of the single reindeer individual sampled from level 4.2 shows a different trend to the reindeer from level 4.1, with a higher degree of intra-tooth variability, the values ranging from 0.7090 to 0.7125 (mean = 0.7112 ± 0.0012).

The raw posterior probability distribution maps assessed from the $^{87}Sr/^{86}Sr$ spatial assignment from the three different locations on the crowns of four *Rangifer* and one *Equus* are provided in SOM Figures S7, S8, and S9. Based on the spatial assignment of the samples closest to the occlusal surface of both the M_2 and the M_3, we determined the areas where the samples have an 80% chance of originating, and considered these areas respectively as the winter and summer areas potentially used by each *Rangifer* (Fig. 8). For the *Equus* we determined the potential areas corresponding to the highest and the lowest $^{87}Sr/^{86}Sr$ values of its profile, respectively the sample closest to the M_3 ERJ (0.7086) and the sample closest to the occlusal surface (0.7085), which are almost entirely overlapping (91.8% of overlap; Fig. 8). The three *Rangifer* from level 4.1, as well as the *Equus*, show potential use of areas within of ~50 km of Abri du Maras in both winter and summer but also areas on the eastern side of the Rhône Valley or southwest of Abri du Maras (Fig. 8). Summer and winter ranges of *Rangifer* J6-306 almost overlap entirely (88.4% of overlap) and show a strong agreement with the *Equus*' range. A similar pattern is observed for *Rangifer* 80/133 while the overlap between potential summer and winter ranges is less pronounced (48.6%). *Rangifer* N6-178 seems to show a higher segregation in its seasonal range use (21.4% of overlap) but both potential summer and winter ranges can still be found close to Abri du Maras. Spatial assignment also highlighted for this individual potential areas in summer slightly further north of Abri du Maras (Fig. 8). *Rangifer* M10-121 from level 4.2, shows a complete separation between the potential summer and winter areas (0% of overlap, Fig. 8). Summer assignment highlights areas similar to the ones used by the *Equus* and the *Rangifer* from level 4.1, in the vicinity of Abri du Maras. However, winter assignment suggests the use of areas away from Abri du Maras with potential areas located 150-200 km from the site, in the northern most parts of the Rhône valley or further to the east, or even more distant, in the southwest direction (Fig. 8).

4. Discussion

4.1. Paleoclimatic context

<u>Seasonal paleotemperatures at Abri du Maras</u> Based on the oxygen isotope data from level 4.2, and compared to modern day temperatures at the study site (Fig. 4), the MIS 3 climate at Abri du Maras seems to have been similar, if perhaps slightly colder to modern day conditions in terms of mean annual averages, but substantially more seasonal than today (i.e. with warmer summers, and cooler winters). It should be noted that seasonal paleotemperature reconstructions are substantially less reliable than mean annual paleotemperature estimates, due to the necessity of using an inverse model in order to try and remove the effect of time averaging from the tooth enamel mineralization process. While we believe seasonal temperatures to be particularly relevant to reconstructing environments and human-climate

interactions, this limitation means that temperature seasonality can at most be discussed in relatively broad terms, or when supported by direct isotopic comparisons, and we discuss this in more detail below (section 4.2).

The number of individuals analyzed here is relatively small, which increases the uncertainty around paleotemperature estimates. However, both individuals are remarkably similar in their $\delta^{18}O$ seasonal curves, indicating a consistent reflection of environmental parameters across individuals. At the same time, sinusoidal $\delta^{18}O$ curves with a pronounced seasonal amplitude in both individuals indicates that they were unlikely to have obtained much drinking water from a seasonally buffered water source such as large rivers or springs fed from groundwater. This further indicates that *Equus* at Abri du Maras most likely reflect climatic impacts on $\delta^{18}O$ of local environmental water sourced from precipitation. Impacts of slight differences in habitat and water source use on enamel $\delta^{18}O$ between animals drinking water from the Rhône River compared to those drinking precipitation-fed water sources on the local limestone plateaus have been suggested for the data set from Payre (Ecker et al., 2013; Bocherens et al., 2016), a site located on a similar hydrotopographic setting in close proximity to the Rhône ~50 km upstream of Abri du Maras. A similar scenario could potentially also be envisaged for Abri du Maras, which is also situated only a few hundred of meters from the Rhône River. However, the seasonally pronounced $\delta^{18}O$ variation in the level 4.2 horses does not support this. As larger rivers generally exhibit low seasonal $\delta^{18}O$ variability due to higher water residence times, and incorporate snow melt and mixing of water from different locations/altitudes (Rank et al., 2018), a year-round consumption of Rhône River water would most likely result in a lack of seasonal variation in $\delta^{18}O$, which is not observed here. Indeed, estimates of $\delta^{18}O_{dw}$ show stronger seasonal differences than expected from local precipitation, rather than an attenuated amplitude that could be expected if animals were sourcing from a strongly buffered water source. A substantial contribution of river water to the drinking water of the Abri du Maras

Equus sampled here therefore seems unlikely, and we instead suggest that their δ^{18}O values reflect local climatic conditions. This also means that comparatively low winter $\delta^{18}O_{dw}$ values observed in the archaeological specimens compared to modern δ^{18}O values of precipitation are in our view unlikely to be related to wintertime drinking from low δ^{18}O river water. Instead, winter may have exhibited more cold/wet conditions compared to today.

Finally, one aspect of the local paleoenvironment that remains unknown and may have had the potential to influence faunal δ^{18}O values is aridity. High aridity induces ^{18}O-enrichment compared to local precipitation in plants and stagnant open water bodies and therefore in some herbivores, with leaf water or open water signatures superimposing (and therefore obscuring) relationships with precipitation δ^{18}O (e.g., Ayliffe and Chivas, 1990; Cormie et al., 1994; Levin et al., 2006). However, in contrast to evaporation sensitive species (including cervids and caprines), obligate drinkers, such as equids and large bovids, are considered evaporation insensitive and the δ^{18}O of their body tissues are unlikely to be strongly influenced by leaf water changes given their dependency on drinking for meeting their water requirements (Levin et al., 2006). At the same time, drinking from evaporatively enriched water bodies such as large lakes, similarly to larger rivers, would result in a lack of seasonal δ^{18}O variation in animal teeth, which is not observed. It is therefore unlikely the phosphate δ^{18}O of the horses included in this study, and the seasonal enrichment observed, is reflecting high aridity. There are few other site-specific indicators of paleoenvironment beyond the faunal suite and isotopic data generated in this study, with the exception of charcoal analysis which has identified wood species include *Pinus sylvestris* type and *Betula*, the latter of which has been found in level 4.1 (Daujeard et al., 2019; Moncel et al., 2021). While *Pinus sylvestris* grow in dry and cold conditions, *Betula* require higher soil humidity rates. This may indicate that, in level 4.1 at least, conditions were not overly arid. Future studies at the site could incorporate the oxygen isotope analysis of non-obligate drinking species, such as *Cervus elaphus*, as a comparison to the obligate drinking species in order to establish water deficiency and, through this, establish an aridity index for the site (e.g., Levin et al., 2006). Future paleoclimatic studies using oxygen isotopes would ideally incorporate strontium isotope analyses, at the very least for serial-samples corresponding to seasonal δ^{18}O peaks and troughs. Although studies of Late Pleistocene European horses have not indicated migratory behavior (e.g., Pellegrini et al., 2008), and the ^{87}Sr/^{86}Sr data from the level 4.1 horse analyzed here is also consistent with sedentary behavior, conservation of this behavior in all phases of the Late Pleistocene cannot be assumed. Furthermore, other species, such as red deer, which could be useful comparators in calculating aridity index, may undertake seasonal movements.

<u>Comparison with other Late Pleistocene paleoclimate proxy datasets from France</u> Due to the uncertainty inherent in the conversion of oxygen isotope delta values of tooth enamel to drinking water isotope values and paleotemperature estimates, a direct comparison with other enamel δ^{18}O values of Pleistocene horses represents the most robust way of contextualizing these data (Pryor et al., 2014; Skrzypek et al., 2016). A limited amount of published δ^{18}O data from *Equus* tooth enamel is available for Late Pleistocene southern France, and not all of this data has been obtained as sequential samples. Out of the published data, results from Abri du Maras level 4.2 most closely resemble bulk sampled MIS 3 data from La Baume de Gigny Cave in the French Jura (Fabre et al., 2011) and Combe Grenal in the Dordogne (Richards et al., 2017; Fig. 9). La Baume de Gigny Cave is located approximately 280 km northeast of Abri du Maras, while Combe Grenal is located ~ 350 km west of Abri du Maras. At La Baume Gigny Cave, *Equus* tooth enamel from Level VIII exhibits a δ^{18}O value of 17.2‰, almost identical to the midpoint values from Abri du Maras, although these deposits are somewhat younger than Abri du Maras level 4.2 at ~33 ka (Fabre et al., 2011). Sequentially sampled δ^{18}O data from a single *Equus* tooth from the immediately underlying but undated Level IX shows

similar winter δ^{18}O values, but comparatively lower summer and mean annual δ^{18}O values than at Abri du Maras. δ^{18}O values from Combe Grenal were bulk sampled from tooth fragments of varying lengths from a variety of tooth types, which may contribute to a relatively large scatter of δ^{18}O values (Richards et al., 2017). Individuals that most closely resemble Abri du Maras level 4.2 stem from Layer 10 (18.1‰), Layer 12 (17.3‰) and Layer 14 (18.1‰), which have been tentatively assigned to early MIS 3. Based on these comparisons, the δ^{18}O results from Abri du Maras level 4.2 fall comparatively high in the range of published δ^{18}O values for MIS 3 southern France, with relatively high summer peak values and a comparatively pronounced seasonal summer/winter difference. This may indicate relatively warm mean annual climatic conditions with warm summers, compared to other sites from MIS 3. Oxygen isotope data from *Equus* teeth from the geographically closest site of Payre (Ecker et al., 2013; Bocherens et al., 2016) unfortunately predate the data from Abri du Maras that are discussed here making direct comparison difficult. Predicted phosphate δ^{18}O values (converted from carbonate δ^{18}O) from samples from Levels D, F and G at Payre fall noticeably below the results from Abri du Maras (Fig. 9). Given the close spatial proximity to Abri du Maras, it is likely that the *Equus* from Payre either experienced far colder climatic conditions in this region during MIS 6 and earlier (Richard et al., 2021) than those at Abri du Maras during MIS 3, or sourced a larger amount of drinking water from rivers of alpine origin, as was proposed by Ecker et al. (2013) and Bocherens et al. (2016).

In order to compare the Abri du Maras δ^{18}O results more extensively to other climatic data, the conversions to paleotemperature estimates have to be used, as δ^{18}O values themselves incorporate species specific offsets from drinking water (Iacumin et al., 1996; Kohn, 1996). Paleotemperature estimates for annual means are for instance similar to the mean annual temperature estimates of ~ 9-14°C generated from *Bison* δ^{18}O for Layer 5 of La Ferrassie in the Dordogne (Pederzani et al., 2021). However, summer temperature estimates from Abri du

Maras are ~5 °C higher and winter temperatures ~ 10 to 15°C lower than temperature estimates from La Ferrassie. As a consequence, the *Equus* δ^{18}O data from Abri du Maras seems to indicate stronger summer-winter differences in climate. La Ferrassie Layer 5 is similar in age to Abri du Maras level 4.2, but is located ~ 350 km west of Abri du Maras and closer to the Atlantic rather than the Mediterranean coast. Climatic differences between the two sites may also stem from slight differences in age, as chronometric dates for both deposits show a considerable uncertainty that is typical for this time period. On the other hand, geographic differences in climate and circulation may also play a role. Given that the modern-day climate at both locations is very comparable, this means that either age related climatic differences are a more likely explanation or that geographic climate gradient between the Dordogne and the Ardèche were more pronounced during MIS 3. While these options are difficult to distinguish based on available data, comparisons with both other Pleistocene data and modern-day climatic data indicates that the *Equus* from Abri du Maras level 4.2 lived in a relatively mild climate in terms of mean annual temperature but with a pronounced seasonal temperature difference. The latter is perhaps of most significance when considering past animal (and human) experience of climate in the region. Seasonal temperature extremes may have impacted the seasonality of Neanderthal landscape use, particularly of higher altitude areas in this region. Indeed, a framework of strong seasonal mobility that has been hypothesized on the basis of archaeological, zooarchaeological and material culture evidence for this region of southeastern France between the plains of the Rhone Valley and the mid-mountains of the Massif Central from MIS 7 to MIS 3 (Daujeard et al., 2012). However, it must be noted that the seasonal temperature estimations in the current study bear unavoidably large errors of between 4 and 5°C. Although the lower end of these estimations would still result in cooler winters and warmer summers than are found in the region today, these estimations (and conclusions drawn from them) must be considered with appropriate caution.

4.2. Faunal dietary ecology and broader paleoenvironment

Despite the modest size of the dataset, as shown in Figure 5, interspecies differences, particularly in δ^{15}N are clear. *Equus* exhibit both the lowest mean δ^{13}C and δ^{15}N values. While these values are typical of grazers living in temperate (C3) ecosystems (e.g., Fizet et al., 1995; Bocherens, 2003), given that grasses are normally ^{15}N enriched relative to shrubs in contemporary arctic and boreal ecosystems (see Bocherens, 2003: 61) it is interesting that the *Bison* are elevated in both δ^{15}N and δ^{13}C relative to *Equus*. These differences are similar to those measured in equids and bovids at the older Eemian site of Neumark-Nord 2, Germany (~126 ka; Britton et al., 2012) and the (broadly) contemporary French site of Marillac (45–40 ka; Fizet et al., 1995). Differences in δ^{13}C are likely attributable to differences in the production levels of methane between these different species. Ruminant methane has negative δ^{13}C values (Metges et al., 1990), potentially leading to tissue enrichment in ^{13}C (e.g., Cerling and Harris, 1999), and similar patterns have been determined in a range of isotopic studies of European Late Pleistocene fauna (see discussion and Britton et al., 2012: Figure 3). However, there is less compelling evidence for a consistent ‘offset’ in δ^{15}N between equids and bovids and the factors influencing δ^{15}N values in herbivores are complex. Given that modern European bison are mixed/intermediate feeders (Merceron et al., 2014) and shrubs are often depleted in ^{15}N relative to grasses, one may expect collagen δ^{15}N values of potential mixed feeders should also be lower. However, another factor known to influence collagen δ^{15}N values of herbivores is the protein content of the diet, with the consumption of higher protein plants leading to increased diet-tissue offsets and ^{15}N-enrichment (Sponheimer et al., 2003). Horses are generally considered to be adapted to live on high fiber, low quality forage (Duncan et al., 1990), which could influence diet-tissue offsets and lead to lower δ^{15}N tissue values. In contrast, the elevated δ^{15}N values of *Bison* seen here may indicate the incorporation of higher nutrient food such as short grasses, sedges, forbs and leaves. It should be noted, however, that lower δ^{15}N values are not always observed in European Pleistocene horses relative to other herbivore species, suggesting that the selection of low quality forage by horses is not necessarily habitual and may be plastic, shaped by local habitat structure (see discussion in Britton et al., 2012). At Abri du Maras, however, grazing on low quality forage may indeed account for the δ^{15}N determined in the equids, whereas *Bison* were likely able to feed more flexibly and here are occupying a similar isotopic niche to *Megaloceros*.

At Abri du Maras *Rangifer* δ^{13}C values are also similar to other intermediate/mixed feeders, including *Bison* and *Cervus elaphus*. This is unusual as elevated δ^{13}C values are commonly measured in Pleistocene *Rangifer* compared to other large herbivore taxa and this is often attributed to lichen consumption (e.g., Fizet et al., 1995; Bocherens, 2003), due to the higher δ^{13}C values observed in modern lichens (e.g., Park and Epstein, 1960; Teeri, 1981). In the Abri du Maras dataset, the most elevated δ^{13}C (and δ^{15}N) values are exhibited in the four *Megaloceros* samples, which are similar both within and between levels. Values exhibited differ from previous isotope studies of pre-LGM *Megaloceros* bone collagen from south-west France which have indicated that this species occupied a similar isotopic niche to *Cervus elaphus* (Immel et al., 2015), with both taxa exhibiting lower δ^{13}C (relative to *Rangifer*) which has been associated with leaf feeding in forested environments, a so-called ‘canopy effect’ (e.g., Drucker et al., 2008). However, at Abri du Maras differences in δ^{13}C between the different cervid species are not as pronounced. There is no indication of a canopy effect in the δ^{13}C for either *Cervus elaphus* or *Megaloceros,* and the similar δ^{13}C of the reindeer does not suggest lichen was a major dietary component. The slightly elevated δ^{13}C in *Megaloceros* may be related to the consumption of plants such as forb species or sedges, which typically exhibit less negative δ^{13}C values, as has been concluded for *Megaloceros* dental enamel samples from Ireland (Chritz et al., 2009: 142).

The isotope values exhibited in the different deer species at Abri du Maras perhaps reflect the contemporary environmental and ecological suite of this part of France at the time (i.e., that woodland environments may have been mosaic and not extensive/dense). This is consistent with other paleoenvironmental proxy evidence from the site, including charcoal evidence, which is consistent with open forests or forest groves and also with the characterization of mosaic environments in the Rhône valley and along its tributaries, and other parts of central and southern France, and northern Iberia, during MIS 3 (see discussion in Daujeard et al., 2019). The higher $\delta^{15}N$ values seen in *Megaloceros* at Abri du Maras could also be consistent with this, and the similarity between $\delta^{13}C$ in *Rangifer, Cervus* and *Megaloceros* may indicate that lichen did not comprise any significant part of *Rangifer* diet in this period and—by inference—that lichen coverage may have been lower during these mild phases (as indicated by the oxygen isotope data from level 4.2 at least). Lichen declines are common described in the context of modern global warming and long-term vegetation-specific studies in the Arctic have demonstrated that warmer, and especially more humid conditions, favor mosses and vascular plants and lead to the physiological impairment of lichens and their subsequent decline (Olthof et al., 2008).

When comparing the cervid data from Abri du Maras to that from cooler periods of the Late Pleistocene (e.g., Drucker, 2022), it may be that niche spacing between these species was reduced in this earlier phase of MIS 3. A similar pattern has been seen in deer species during the Lateglacial interstadial and has been attributed to milder and more humid conditions and a decrease in niche partitioning that may have resulted in greater competition between different herbivore species (Drucker, 2022; Drucker et al., 2018; Immel et al., 2015). However, it is important to note that isotopic data do not strictly correspond to niche space but instead to isotopic niche space, and isotopic differences between species are dependent not only on consistently different feeding behaviors but also on the availability of isotopically diverse graze and browse. It may be, that in the absence of either dense forest or abundant lichens, carbon isotopic variability in herbivore food sources was reduced overall.

Despite similarities in $\delta^{13}C$, a comparatively large range of $\delta^{15}N$ values are shown within and between different species, however (from 2.3‰ to 6.0‰). This likely reflect different feeding behaviors within this environment and, through this, implies local environmental variability in $\delta^{15}N$. Multiple factors influence nitrogen isotope values in soils and plants and, along with an animal's physiology, can lead to isotopic diversity in animals otherwise occupying the same broader trophic positions (Sponheimer et al., 2003; Szpak, 2014). Bone collagen $\delta^{15}N$ of large herbivores thus reflects both isotopic variability within local plant communities (which in the past may reflect very different environmental conditions than today) and differences in dietary niche and feeding behavior, the latter of which relates to both the types of plants/plant component consumed (in terms of its isotopic ratio), as well as their nutritional content and digestibility. The range of $\delta^{15}N$ values observed between the different herbivore species at Abri du Maras is evidence for differences in feeding behaviors between taxa. While niche partitioning is commonly seen in other isotope paleoecological studies of herbivores in Western Europe (see reviews in Bocherens, 2003; Drucker, 2022), the data from Abri du Maras highlights that niche feeding behaviors and resource partitioning varied throughout different phases of MIS 3, as well as geographically (e.g., Drucker, 2022; Schwartz-Narbonne et al., 2019). This emphasizes the need to recognize plastic and/or non-analogous behaviors (and the role of isotope analyses in revealing these) when considering the non-analogous animal and plant communities of MIS 3 in northern Europe. In the case of Abri du Maras, given that these differences are far less apparent in $\delta^{13}C$ than $\delta^{15}N$, the value of combining these two isotopic systems in reconstructing Late Pleistocene herbivore feeding behaviors in particular is also highlighted. Finally, another factor that is not often considered alongside dietary isotopic data in studies of faunal paleoecology but could play a part in the large range of nitrogen isotope values observed in this study could be differences in the habitat use/spatial ecology of different individuals, different species and through time, in this region.

4.3. Evidence for interspecific differences in spatial ecology

While more than half of the samples (group 1 = 12/19, across all species and both levels) have $\delta^{34}S$ consistent with anticipated local environmental values (Fig. 6; SOM Fig. S4), six of the remaining seven (group 2) have lower $\delta^{34}S$ values and therefore may have spent a proportion of their lives in a more remote region, and possibly further inland (e.g., along the Rhône Valley where values ~ 3‰ can be found). In addition to highlighting potential differences in faunal geographical range, this may also indicate that the resource catchment for the site (i.e., areas from which hominins using the site took prey) went beyond the immediate locale of the site. A further individual, the single *Rangifer* individual from level 4.2 (M10-121), displayed a far lower value than all other samples analyzed, with a value of 0.0‰. This may hint at a very different biogeographical range for this earlier individual compared to the individuals sampled from level 4.1, perhaps far north of the Ardèche region. Indeed, the strontium isotope data from this same individual (see Section 4.4) support this as the likely explanation.

Although two groups are evident in the sulphur isotope data, and the majority do align with predicted local values, it must be borne in mind that sulphur isotope variability in this region in the Late Pleistocene may have been very different compared to more recent periods and could have incorporated lower (or higher) overall environmental $\delta^{34}S$. For example, southern France is a region heavily exposed to dust aerosol deposition from the Sahara, one of the main drivers of the $\delta^{34}S$ isoscape, leading to ^{34}S enrichment in the environment (Bataille et al., 2021). The lower values observed for group 2 could be due to differences in dust deposal rates between the Late Pleistocene and more recent periods as the most recently published sulphur isoscape was established using more recent samples from the Mesolithic to the 20th century (Bataille et al., 2021). A strong correspondence between sulphur isotope values of bone collagen and environmental conditions (in particular, temperature or the extent of permafrost) has also been highlighted by other studies (Drucker et al., 2011; Reade et al., 2020), suggesting that environmental $\delta^{34}S$ not only varies spatially but can vary temporally at the same location. No clear trend in $\delta^{34}S$ was observed through time between level 4.1 and level 4.2 at Abri du Maras and differences observed between animals therefore likely do reflect relative differences in individual biogeography. However, differences in the presence and extent of permafrost across this mountainous region in the past, or other environmental variables, may have produced a more varied sulphur isoscape compared to the present day that could encompass all the values in this study. While there may be relative trends, including two statistically-distinguishable groups (including a larger group of ungulates of all taxa matching the local predicted values) and an individual reindeer with a distinct $\delta^{34}S$ value compared to all other individuals, given uncertainties surrounding the Late Pleistocene sulphur isoscape these patterns are difficult to relate to specific geographical areas and in order to explore the biogeography of species more closely (particularly *Rangifer*), strontium isotope data are required.

4.4. Rangifer *migratory behavior at Abri du Maras*

Evidence for plasticity in behavior of *Rangifer* between levels 4.1 and 4.2 The agreement in strontium isotope values in the earliest forming parts of the second molar for the three *Rangifer* from level 4.1 points to a period spent on a similar lithology to one another during the middle of the first summer of life (~0.709), consistent with bioavailable strontium isotope values found within ~50 km of the site (including areas on eastern side of the Rhône Valley, and slightly further north; SOM Fig. S7). This may be consistent with the calving grounds and summer range for the *Rangifer* in level 4.1 being relatively close to the site, in the eastern part of the Rhône Valley or even the Prealps area. Strontium isotope ratios from the later forming parts of the second molar (corresponding with the first winter of life) of the three individuals from level 4.1, and values from the majority of their third molars (largely forming in the second year of life), are again similar to one another—albeit with a greater intra-tooth variation in the third molar between these three individuals compared to the second molar. This is consistent with modern ecological observations and experimental isotope studies on modern herds which show increased dispersals across the herd range during in the second half of the first year of life, and into the second year of an animal's life (Britton et al., 2009; Britton, 2010). However, despite slight intra-tooth variation, values do not deviate considerably or outside of the range of bioavailable strontium within ~50 km of the site and, significantly, do not demonstrate any clear seasonally-cyclical trend in the second and/or third molar.

With the exception of a fidelity to calving ground (and thus summer range during the first months of life), the data from level 4.1 *Rangifer* do not suggest regular, targeted seasonal migrations during this period. Potential winter and summer ranges identified from the samples closest to the enamel-root junction in both the M_2 and the M_3 can be found in the vicinity of Abri du Maras and show a substantial overlap and continuity. This range may also have incorporated areas to the east, towards the Prealps, or to the south towards the Mediterranean, although it should be noted that (given the sea-spray effect) the absence of δ^{34}S values greater than 6‰ may indicate the latter is unlikely. In modern caribou populations, sedentary behavior is observed in the forest and mountain ecotypes (Festa-Bianchet et al., 2011). However, while modern sedentary caribou do not undertake migrations, they may utilize fairly large home ranges exceeding 1400 km^2, especially where human environmental disturbance is low (Wilson et al., 2019). At Abri du Maras, a non-migratory ecotype, equivalent to the modern forest ecotype would be consistent with the charcoal analysis in level 4.1, the only level yielding an association of *Betula* and *Pinus*, showing that the environment at the time, was probably humid with open forest or forest groves (Daujeard et al., 2019; Moncel et al., 2021). The δ^{13}C values from the reindeer and other cervids in this study (see section 4.2), however, make it unlikely that this contemporary woodland would have been extensive (i.e. there is no ‘canopy effect’). The strontium isotope values from the single *Equus* sampled from this level and the associated assignment maps are also consistent with living in the region close to the site, at least during the period of formation of this tooth, and may indicate both these species may have been regionally available during much of the year during this later phase of site occupation.

In comparison to the individuals from level 4.1, the intra-tooth strontium isotope profile of the individual from level 4.2 demonstrates a strong seasonal variability (from lower values to higher values, before a return to lower values). While values in the latest forming parts of the third molar (SOM Fig. S9; *Rangifer* M10-121) do overlap with local biosphere values (and with the values measured in the three *Rangifer* from level 4.1), the values from earlier phases in this individual’s life are much higher, particularly in the latest forming parts of the second molar. The complete separation between potential summer and winter ranges inferred from the spatial assignment strongly suggests a migratory behavior. While the potential summer range is very similar to the range used by the individuals from level 4.1, incorporating the area immediately surrounding Abri du Maras, the *Rangifer* from level 4.2 occupied winter areas distinct from the region surrounding the site and completely different from the *Rangifer* from level 4.1. Intra-tooth values closest to the enamel-root junction in the M_2 of this individual are instead consistent with long distance movements between the northern and the southern part of the Rhône valley, or east-west movements, as bioavailable values matching those within the teeth can be found only in excess of 150-200 km from the site. Even areas detected further away, in the southwest France, could be considered as potential winter range habitats, as these are still within the range of distances traveled by modern migratory caribou populations. The distinct sulphur isotope values in the bone collagen of this individual, compared to other herbivores analyzed from the site supports the idea of a distinct total range size, incorporating, perhaps a larger and more (isotopically) diverse area than any of the other animals.

Implications for understanding site and resource use at Abri du Maras These findings provide tentative evidence of differences in ranging behavior in *Rangifer* in the Rhône Valley during MIS 3, and have implications for our understanding of faunal paleoecology and exploitation at Abri du Maras. The data from level 4.2 and 4.1 infer that both migratory reindeer and less mobile/sedentary ecotypes of reindeer could have been found in Late Pleistocene Europe at this time and/or that this behavior was plastic over time. This was also determined to be the case at Jonzac, where *Rangifer* in Quina Mousterian levels (73 ± 7 ka) were revealed to be migratory using strontium isotope analysis, but that *Rangifer* from Denticulate Mousterian levels (56 ± 3 ka) were likely non-migratory (Britton et al., 2011; Britton, 2010; Britton, 2018). If the *Rangifer* were indeed non-migratory in level 4.1 or undertook only very restricted seasonal movements over a small home range, this may suggest that *Rangifer*—like the *Equus*—may have been a year-round local resource at that time in the Rhône Valley. However, the zooarchaeological evidence from this level suggests they were not exploited all year round and instead were hunted exclusively in autumn-winter (Daujeard et al., 2019). This may be consistent with seasonally restricted use of the site by Neanderthals during the accumulation of deposits in level 4.1. Indeed, a subsistence base centred on strongly seasonal movements has been hypothesized for this region more broadly (Daujeard et al., 2012). Targeted autumn-winter hunting may also be consistent with the deliberate selection of this prey taxa only during peak condition. Autumn is a period where female and young reindeer/caribou in particular are in good physical condition (Miller, 1974), with typically higher average body masses (and body fat percentages) in autumn than in spring and summer (Gerhart et al., 1996; Couturier et al., 2009). Autumn may also have been the optimal period to hunt reindeer for their winter coats (i.e., for clothing; e.g., Binford, 1978; Stenton, 1991; Issenman, 2011). Thus, in the presence of other available local resources—such as horse—reindeer may not have been an appealing option at other points of the year. In contrast, zooarchaeological data from level 4.2 point to a more mixed profile, comprising multiple ungulate species without a strong seasonality. Here, intra-tooth samples from a single *Rangifer* indicate a seasonally-repeating mobility pattern, indicating they may have only been found in the immediate region at certain points of the year (i.e., summer). The investigation of *Rangifer* exploitation, and particularly the seasonality of that exploitation at other sites surrounding Abri du Maras and those sites on the eastern side of the Rhône Valley, may allow the further exploration of the relationship between Neanderthal landscape use and the seasonal biogeography of reindeer.

In addition to the strontium isotope data from the *Rangifer* samples, the results of other analyses undertaken here also have implications for our understanding of Neanderthal activities at the site. The presence of two statistically significant groups revealed by hierarchical cluster analysis of sulphur isotope data may suggest that Neanderthals at the site were extracting their prey from at least two isotopically-distinct areas (in terms of $\delta^{34}S$), including locally as well as perhaps further inland along the Rhône valley. This hints at the potential for isotope zooarchaeological approaches to reveal such aspects of landscape use in subsistence behaviors. However, such a pattern could also be produced through the hunting of animals close to site that had more extensive ranges than others, and thus incorporated a more diverse range of $\delta^{34}S$ values. Further work, incorporating strontium isotope analysis of multiple species would be required to characterize this, ideally in comparison with similar data from other archaeological sites in the region. Comparison with data derived from fauna from non-anthropogenic contexts (e.g., natural accumulations) could be helpful in characterizing variability due to differences in faunal spatial behaviors from variability due to differences in human hunting ranges.

Finally, the oxygen isotope data generated from level 4.2 suggest that, in this phase at least, the climate was comparatively mild for the period, albeit with a pronounced seasonality, with higher and lower seasonal extremes in temperature than experienced in the region today. On the basis of zooarchaelogical data, occupations in level 4.2 at Abri du Maras were restricted to spring-summer, and to autumn (Vignes, 2021). While sample size, and the lack of comparative data from level 4.1 necessitates caution in data interpretation, this may indicate a preference for other sites and/or areas during cooler winter months. The collection of similar data from other sites in the region, combined with site-seasonality data, would help us to better understand the relationship between the seasonal climate and the seasonal use of sites and resources by Neanderthals in the Rhône valley during MIS 3.

5. Conclusions

The data presented in this paper provide evidence for both environmental conditions during MIS 3 in southeastern France, but also for the ecology of key species that Neanderthal groups depended upon. Oxygen isotope analysis of horse teeth from level 4.2 evidence mild climatic conditions, albeit with a seasonality more pronounced than today. Carbon and nitrogen isotope analysis of bone collagen suggest different niche feeding behaviors amongst herbivore species at the site, mostly expressed through variability in $\delta^{15}N$. Carbon isotope data from *Rangifer* are similar to other taxa studied, which is unusually for Late Pleistocene case studies, particular from later (colder) phases of MIS 3, which indicate that lichens were not making up a significant component of *Rangifer* diet in this area at this time. This may also therefore provide indirect evidence for a lack of contemporary lichen cover, which could be consistent with milder and also moister climatic conditions, notably during level 4.1. Conversely, the $\delta^{13}C$ values from the reindeer and other cervids in this study, however, do not indicate woodland was extensive (i.e. there is no ‘canopy effect’) and may have been restricted to groves as part of a moasic environment, which is in agreement with the limited contemporary paleoenvironmental data (Daujeard et al., 2019). The strontium and sulphur isotope data from *Rangifer* provide direct evidence for both migratory and non-migratory ecotypes at the site, correlating with differences in seasonal exploitation between the two levels. While environmental strontium values surrounding Abri du Maras are most consistent with those observed in the winter-forming parts of *Rangifer* teeth in level 4.1, environmental values matching other periods of the level 4.1 individuals' lives can be found within ~50 km of the site. Thus, in this part of the Rhône Valley, reindeer may have represented a year-round resource. In light of this, we can infer perhaps that the targeted hunting of reindeer in autumn during this phase of site use may be consistent with seasonally-restricted use of the site by Neanderthals and/or the selection of *Rangifer* in prime condition rather than their seasonally-restricted availability. In contrast, a single *Rangifer* sampled from level 4.2 demonstrates a very different trend in intra-tooth strontium and bulk bone collagen sulphur isotope data, suggesting a distinct biogeographical range incorporating other regions and also different seasonal mobility. Data from this individual suggests reindeer may only have been found in the area seasonally (in spring/summer). Thus, the integration of isotope data with the zooarchaeological analyses and other paleoenvironmental proxy data at Abri du Maras evidence not only diversity in animal behavior and ecology during MIS 3, but also demonstrate the inter-relationships between the dynamic ecosystem and Neanderthal land use and hunting strategies. The determination of seasonality of site use and hunting at different archaeological sites in the eastern and western areas of the southern Rhône Valley, combined with further analysis of faunal biogeography and seasonal paleoenvironmental conditions, may help to further illuminate these relationships.

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Figure captions

Figure 1. Elevation map of the Rhône Valley (southeast France) showing the location of Abri du Maras and other key Middle Paleolithic sites in the region.

Figure 2. Strontium isoscape of the Rhône Valley (based on Bataille et al., 2020).

Figure 3. Measured oxygen isotope signal ($\delta^{18}O_{enamel}$; blue dots) from Abri du Maras for two *Equus* teeth (both lower second premolars, Maras 687 and Maras 767) from level 4.2, and inverse modelled isotopic input (grey line) with 95% confidence interval (grey shaded area). Abbreviation: VSMOW = Vienna standard mean ocean water.

Figure 4. Estimated mean annual, summer and winter oxygen isotope values of drinking water ($\delta^{18}O_{dw}$) and estimated paleotemperatures for the study site, calculated from archaeological $\delta^{18}O_{enamel}$ data, with associated compound errors shown as error bars. Lines represent modern $\delta^{18}O_{precip}$ data (left) and modern temperatures (right) for the area of the study site, with associated standard deviations shown as shaded ribbons. $\delta^{18}O_{precip}$ data was obtained from the OIPC (Bowen, 2022; Bowen and Revenaugh, 2003; Bowen et al., 2005) and temperature data from the ClimateEU model and averaged for 1981–2009 (Marchi et al., 2020).

Figure 5. Bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ of bone collagen from *Bison*, *Cervus elaphus*, *Equus*, *Rangifer* and *Megaloceros* from Abri du Maras (levels 4.1 and 4.2). Analytical error (± 1 SD) is also shown.

Figure 6. Stable sulphur isotope data of bone collagen from *Bison*, *Cervus elaphus*, *Equus*, *Rangifer* and *Megaloceros* from Abri du Maras (levels 4.1 and 4.2). Analytical error (± 1 SD) is shown.

Figure 7. Sequential strontium isotope data from incrementally-sampled dental enamel of second and third molars from four *Rangifer* from Abri du Maras. The mean strontium isotope value of dentine sampled is shown (± 1 SD) as well as the range of strontium values observed in the third molar of a *Equus* from the site. Analytical error is within the data points. Abbreviation: ERJ = enamel-root junction.

Figure 8. Spatial assignment of strontium isotope data from the enamel sampled closest to the enamel-root junction (ERJ) of the second and third molars of four *Rangifer* (level 4.1 and level 4.2) from Abri du Maras, corresponding broadly to the potential ranges use by the individuals in winter and summer respectively, based on anticipated enamel mineralization times. Potential seasonal areas correspond to the minimal areas where each sample have 80% chance to originate, and were assessed using the assignR package in R (Ma et al., 2020). Assignments of the samples from close to the occlusal surface and close to the ERJ of the M_3 from one *Equus* are also provided as a reference for an expected local individual.

Figure 9. Summer, winter and mean annual $\delta^{18}O$ data points from Abri du Maras (ADM; Marine Isotope Stage [MIS] 3) level 4.2 exhibit similar values to previously published $\delta^{18}O$ horse enamel data from MIS 3 deposits in southern France (Combe Grenal [CG], La Baume Gigny [BG]), with relatively high summer values and more pronounced seasonality. Values are substantially higher than those reported at the much older site of Payre (MIS 6 and MIS 7–8). Individual data points and error bars represent individual measurements and one standard

deviation of replicate measurements (ADM, CG, BG) or Layer means and standard deviations around the mean (Payre, number of teeth per mean are 3, 5 and 6 for levels D, F and G, respectively). Comparative data obtained from Fabre et al. (2011; for BG), Richards et al. (2017; for CG) and Ecker et al. (2013; for Payre). Note that the large spread in CG data may be related to the large number of different layers representing MIS 3 at the site, the sampling of unidentified tooth fragments of differing lengths and the relatively uncertain chronology of the site. Abbreviation: VSMOW = Vienna standard mean ocean water.