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

4  
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33

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41

42

### 43 **Abstract**

44 The exploitation of mid- and large-sized herbivores (ungulates) was central to hominin  
45 subsistence across Late Pleistocene Europe. Reconstructing the paleoecology of prey-taxa is  
46 key to better understanding procurement strategies, decisions and behaviors, and the isotope  
47 analysis of faunal bones and teeth found at archaeological sites represent a powerful means of  
48 accessing information about past faunal behaviors. These isotope zooarchaeological  
49 approaches also have a near-unique ability to reveal environmental conditions contemporary  
50 to the human activities that produced these remains. Here, we present the results of a multi-  
51 isotope, multi-tissue study of ungulate remains from the Middle Paleolithic site of Abri du  
52 Maras, southern France, providing new insights into the living landscapes of the Rhône Valley  
53 during MIS 3 (level 4.2 =  $55 \pm 2$  to  $42 \pm 3$  ka; level 4.1 =  $46 \pm 3$  to  $40 \pm 3$  ka. Isotope data  
54 (carbon, nitrogen) reveal the dietary niches of different ungulate taxa, including the now-  
55 extinct giant deer (*Megaloceros*). Oxygen isotope data are consistent with a mild seasonal  
56 climate during level 4.2, where horse (*Equus*), bison (*Bison*), and red deer (*Cervus elaphus*)

57 were exploited year-round. Strontium and sulphur isotopes, provide new evidence for  
58 behavioral plasticity in Late Pleistocene European reindeer (*Rangifer*) between level 4.2 and  
59 level 4.1, indicating a change from the migratory to the sedentary ecotype. In level 4.1, the  
60 strong seasonal nature of reindeer exploitation, combined with their non-migratory behavior,  
61 are consistent with a seasonally-restricted use of the site by Neanderthals at that time or the  
62 preferential hunting of reindeer when in peak physical condition during the autumn.

63

64 **Keywords:** Middle Paleolithic; Collagen; Enamel; Dietary niche; Biogeography;  
65 Paleotemperatures

66

## 67 **1. Introduction**

### 68 *1.1. Context*

69 The exploitation of mid- and large-sized herbivores was a key adaptive behavior of both  
70 Neanderthal and early *H. sapiens* across north-west Europe throughout the Middle and Late  
71 Pleistocene (Discamps et al., 2011; Kuntz and Costamagno, 2011; Rendu et al., 2012; Marín  
72 et al., 2020). Reconstructing the paleoecology of prey-taxa is vital to better understanding  
73 hominin procurement strategies, decisions and behaviors. While the Last Glaciation (Marine  
74 Isotope Stage [MIS] 4–2; ~74–12 ka) was marked by climate fluctuations, MIS 3 (~57–29 ka)  
75 was a period of profound climatic instability, characterized by short-term and acute climatic  
76 oscillations (Voelker, 2002; Barron et al., 2003; Lisiecki and Raymo, 2005; Clement and  
77 Peterson, 2008; Kindler et al., 2014). While long-term species distribution and turnover is  
78 generally well characterized in the Late Pleistocene (Kahlke, 2014; Puzachenko et al., 2020),  
79 the impact contemporary climatic changes would have had on the behaviors of ungulate species  
80 is less well known, and the relationships between rapid climatic shifts and the dietary and  
81 migratory behaviors of ungulate species are poorly characterized. In turn, the interactions

82 between changes in prey-species behavior and hominin subsistence strategies can be difficult  
83 to elucidate. There is a clear need for site-specific approaches, where the reconstruction of local  
84 environmental and paleoecological conditions can be contrasted to archaeological evidence in  
85 order to gain more nuanced interpretations of the inter-actions between environmental  
86 dynamism, the behaviors of prey-species and the subsistence strategies and landscape use of  
87 early human groups.

88 In recent decades, the stable isotope analysis of zooarchaeological assemblages has emerged  
89 as a leading means of reconstructing past faunal paleoecology, environments and  
90 paleotemperatures. Carbon and nitrogen isotope ratios of bone collagen derive from diet, and  
91 in modern ecosystems and recent-historic case studies have been shown to reflect both broad  
92 environmental conditions and also the niche feeding behaviors of different taxa of large  
93 herbivores over the period of tissue formation (e.g., Ben-David et al., 2001; Drucker et al.,  
94 2001, 2012; Feranec, 2007; Hofman-Kamińska et al., 2018). Sulphur isotope ratios measured  
95 in bone collagen can also prove useful in food web studies but when considering ungulate  
96 species are of most use as a tool for reconstructing geographical range use, with values  
97 corresponding to local soils and lithological unit, rainfall and coastal proximity (see review in  
98 Nehlich, 2015). As strontium isotope ratios of skeletal tissues relate directly to that of local  
99 lithology, soils and plants, these techniques can provide more direct evidence of movement  
100 histories (see Britton, 2020, for an overview). When combined with the serial-sampling of  
101 incrementally-developing tissues that do not undergo subsequent remodeling (Hillson 2005),  
102 such as tooth enamel, these can provide evidence of time-series (i.e., seasonal) movement  
103 information, as demonstrated in modern migratory North American caribou (Britton et al.,  
104 2009). Given the relationship between temperature and the  $\delta^{18}\text{O}$  of local precipitation, and the  
105 near-linear relationship between the  $\delta^{18}\text{O}$  of body water and that of mineralized tissues, the  
106 oxygen isotope analysis of mammalian skeletal tissues can provide valuable insights into past

107 thermal conditions (see Pederzani and Britton, 2019, for an overview). When obligate drinking  
108 species, such as horses or bison, are targeted and sequential sampling approaches are employed  
109 (i.e., of molariform teeth), these approaches can provide evidence of local seasonal climatic  
110 conditions (Fricke et al., 1998; Kohn et al., 1998; Sharp and Cerling, 1998). These techniques  
111 have successfully been applied to European Middle and Late Pleistocene sites, reconstructing  
112 paleoclimate and paleoenvironmental change, faunal niche feeding behaviors and migratory  
113 habits, and through this better understanding hominin subsistence strategies (e.g., Bocherens,  
114 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Pellegrini et al., 2008; Stevens  
115 et al., 2008; Bernard et al., 2009; Britton et al., 2011; Fabre et al., 2011; Britton et al., 2012;  
116 Price et al., 2017; Drucker et al., 2018; Jones et al., 2018; Britton et al., 2019; Jones et al., 2019;  
117 Schwartz-Narbonne et al., 2019; Drucker, 2022).

118

### 119 *1.2. Reconstructing faunal paleoecology and paleoenvironmental conditions using isotope* 120 *zooarchaeology*

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

131

132 Carbon isotopes Carbon isotope techniques are based around the principle that animal body  
133 tissues (e.g., bone collagen) reflect the isotopic composition of the food ingested throughout  
134 life. The relative abundance of the stable isotopes of carbon,  $^{13}\text{C}$  and  $^{12}\text{C}$  ( $\delta^{13}\text{C}$ ), varies  
135 characteristically between different biomes—e.g., between plants of different photosynthetic  
136 pathways (Smith and Epstein, 1971; DeNiro and Epstein, 1978) or between terrestrial and  
137 marine ecosystems (Schoeninger and DeNiro, 1984). Studies of resource partitioning and niche  
138 feeding ecology have generally focused on environments where both  $\text{C}_3$  and  $\text{C}_4$  plants can be  
139 found, such as sub-tropical Africa (e.g., Koch, et al., 1995; Cerling, et al., 1999) and North  
140 America (e.g., Gadbury, et al., 2000; MacFadden, 2008). These plants have different  
141 photosynthetic pathways, selecting against  $^{13}\text{C}$  to different degrees, and therefore display large  
142 differences in their  $\delta^{13}\text{C}$ . However, studies have demonstrated the effectiveness of carbon  
143 isotope analysis to reveal resource partitioning among modern (e.g., Feranec et al., 2007;  
144 Hofman-Kamińska et al., 2018) and Late Pleistocene (e.g., Britton et al., 2012; Schwartz-  
145 Narbonne et al., 2019) ungulates in purely  $\text{C}_3$  environments. Such variations stem from intra-  
146 ecosystems variations in carbon isotope values of different plant communities and reflect  
147 dietary choices of herbivores living within  $\text{C}_3$  environments (see Bocherens, 2003; Drucker,  
148 2022, for an overview). Lichens, for example, exhibit less negative  $\delta^{13}\text{C}$  values than other  
149 terrestrial plants incorporated into the diet of Northern ungulates (Ben-David et al., 2001,  
150 Maguas and Brugnoli, 1996, Park and Epstein, 1960). This has been demonstrated to raise  $^{13}\text{C}$   
151 amounts in the blood and dentine of modern *Rangifer* (Ben-David, et al., 2001, Drucker, et al.,  
152 2001), and is often reflected in bone collagen  $\delta^{13}\text{C}$  values of Late Pleistocene European  
153 *Rangifer* (e.g., Fizet et al., 1995). Closed forest systems, including temperate woodlands  
154 (Bonafini et al., 2013), can feature anomalously  $^{13}\text{C}$ -depleted vegetation, a so-called ‘canopy  
155 effect’. Anticipated differences between the bone collagen  $\delta^{13}\text{C}$  of a species regularly feeding  
156 on lichens or in dense forest have therefore formed the basis of investigations in cervid feeding

157 ecology in Late Pleistocene Europe, inferring both niche partitioning but also broader  
158 environmental conditions (e.g., Drucker et al., 2008; Immel et al., 2015). It should also be noted  
159 that the  $\delta^{13}\text{C}$  of bodily proteins can also reflect physiological differences, such as ruminant  
160 digestion and methane production, which leads to tissue  $^{13}\text{C}$  enrichment (e.g., Cerling and  
161 Harris, 1999).

162

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

171

172 Nitrogen isotopes The  $\delta^{15}\text{N}$  value of ungulate bone collagen depends on a number of factors,  
173 most notably the  $\delta^{15}\text{N}$  values of the plants at the base of the food chain. A range of variables  
174 can lead to depletion or enrichment in plant  $^{15}\text{N}$ , which, in turn could affect the tissue  $\delta^{15}\text{N}$   
175 values of animal feeders. Plant  $\delta^{15}\text{N}$  values depend on nitrogen availability, the source of  
176 nitrogen that is incorporated into the plant, the characteristics of nitrogen cycling in the soils at  
177 any given location, as well the plant's physiology in terms of how they uptake nitrogen  
178 (Högberg 1997; Amundson et al., 2003; Hobbie and Högberg, 2012). Plants which obtain their  
179 nitrogen with the assistance of mycorrhizae, for example, tend to have lower  $\delta^{15}\text{N}$  values than  
180 plants that lack these symbionts (Högberg 1997). This means that in contemporary arctic and  
181 boreal ecosystems, grasses—which do not obtain their nitrogen with the assistance of these



182 fungal associations—are normally  $^{15}\text{N}$  enriched relative to shrubs and trees that do (see data  
183 collated in Bocherens, 2003: 61, Figure 3). In environments that are extremely nutrient-poor,  
184 such as tundra environments, competitive partitioning of the overall nitrogen pool by plants  
185 through a variety of mechanisms can lead to variations in  $\delta^{15}\text{N}$  values of plant species  
186 (Nadelhoffer et al., 1996). In light of these variations, selective feeding on particular plant  
187 species, can lead to variation in bone collagen  $\delta^{15}\text{N}$  amongst large herbivores, interpreted as  
188 evidence of niche partitioning in Late Pleistocene studies (e.g., Bocherens, 2003; Britton et al.,  
189 2012; Schwartz-Narbonne et al., 2019)

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

204 However, in modern ecosystems, while there are general trends with climate, correlations  
205 between soil/plant  $\delta^{15}\text{N}$  and climate on a global level are poor (Hobbie and Högberg, 2012). It  
206 is likely that confounding factors, such as mycorrhizal association and type, along with

207 precipitation are perhaps the most important influences (Hobbie and Högberg, 2012). Other  
208 extraneous influences are also known to influence soil  $\delta^{15}\text{N}$ , such as grazing pressure, which  
209 can serve to raise  $\delta^{15}\text{N}$  values in soils and therefore plants, in a complex cycle of nitrogen  
210 transfer between herbivores and their forage (e.g., Sjögersten et al., 2010). Bone collagen  $\delta^{15}\text{N}$   
211 of large herbivores from the Late Pleistocene is therefore a product of multiple influences, from  
212 soil maturity and broad-scale climatic influences, to precipitation patterns, through to the  
213 individual plant communities and density of animals grazing regularly at a specific location.  
214 Furthermore, when considering the  $\delta^{15}\text{N}$  of large herbivores, potential influences of their  
215 adaptive biology and physiology on tissue  $\delta^{15}\text{N}$  must also be considered. For example, modern  
216 studies have demonstrated that  $^{15}\text{N}$ -enrichment from diet to tissue is dependent on the protein  
217 content of graze and forage consumed, with low protein diets leading to lower diet-tissue  
218 offsets and thus (potentially) lower tissue  $\delta^{15}\text{N}$  values (Sponheimer et al., 2003). Furthermore,  
219 physiological variations, such as pregnancy, lactation, and malnutrition have also been  
220 demonstrated to influence  $^{15}\text{N}$ -enrichment in contemporary forming tissues (e.g., Fuller, et al.,  
221 2004; Fuller et al., 2005; Mekota, et al., 2006).

222

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

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

255 Applications to Late Pleistocene faunal samples have indicated the potential of these  
256 techniques to infer (at least relative) differences in range use by different species in the same  
257 region (e.g., Wißing et al., 2019: 4, Figure 2) and possible changes in human hunting range  
258 utilized and/or the spatial paleoecology of prey-species through time (e.g., Jones et al., 2019).  
259 However, other studies of Late Pleistocene fauna have also indicated that faunal  $\delta^{34}\text{S}$  values,  
260 via the  $\delta^{34}\text{S}$  of soils and plants, may (like  $\delta^{15}\text{N}$ ) be strongly influenced by prevailing climatic  
261 conditions. This includes temperature and the presence of permafrost, both of which may serve  
262 to influence the rate of mineralization and volatilization of sulphur in soils, altering soil  $\delta^{34}\text{S}$   
263 (e.g., Drucker et al., 2011; Reade et al., 2020). While work is required to characterize this  
264 relationship, variability in soil  $\delta^{34}\text{S}$  induced by climatic change poses a challenge to the further  
265 development of this method as a tracer of past faunal spatial behaviors, especially in diachronic  
266 studies. The potential for baseline variability through time with climatic change, coupled with  
267 modern environmental sulphur contamination, also renders the production of the isoscapes  
268 necessary for the spatial assignment of sulphur isotope data in archaeological case studies  
269 difficult. Despite this, isoscapes built around archaeological datasets can provide useful  
270 approximations of anticipated geographical variability in environmental  $\delta^{34}\text{S}$  (e.g., Bataille et  
271 al., 2021). Furthermore, at any given site, it is still possible to interpret  $\delta^{34}\text{S}$  values of faunal  
272 bone collagen from broadly contemporary samples within a relative framework, allowing the  
273 identification of individuals or particular taxa/groups that may deviate from the range of  $\delta^{34}\text{S}$   
274 values typically measured in fauna at that site and therefore identifying them as having  
275 inhabited a distinct area or range during life. In studies seeking to directly reconstruct seasonal  
276 movement habits or identify the use of particular areas of the landscape, however, alternative  
277 methods such as strontium isotope analysis are required.  
278

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

294 There are, however, a number of caveats and considerations related to the use of strontium  
295 isotope analysis in inferring animal movements. The careful selection of samples is imperative,  
296 requiring teeth that form over a period sufficient to capture at least a year of isotopic inputs.  
297 This may, in some cases, mean multiple teeth are required from the same animals, for example  
298 in *Rangifer* (Britton et al., 2009). Data is typically then obtained via the sequential sampling of  
299 enamel as horizontal bands down the crown followed by ion-exchange column chemistry to  
300 isolate the strontium in the sample, prior to mass spectrometry (e.g., Britton et al., 2011; Funck  
301 et al., 2020), or via the direct laser ablation of the enamel (e.g., Wooller et al., 2021). The  
302 selection of which technique has implications for data precision, sample destruction, and the  
303 resolution achievable (see discussion in Boethius et al., 2022 for a recent summary), but studies

304 of modern animals of known movements have established both techniques as an effective  
305 means of reconstructing movements during the period of tooth formation (e.g., wild migratory  
306 *Rangifer*, Britton et al., 2009; domestic sheep, Lazzerini et al., 2021). The analysis of different  
307 individuals from the same herd in both these modern cases has also allowed an assessment of  
308 the expected level of intra-herd variability.

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

323

324 Oxygen isotope analysis There a number of different applications for oxygen isotope analysis  
325 in archaeology and paleoecology, all based on the relationship between the oxygen isotope  
326 composition ( $\delta^{18}\text{O}$ ) of an animal's body tissues and that of water consumed (Iacumin et al.,  
327 1996; Kohn, 1996; Longinelli, 1984; Luz et al., 1984). The oxygen isotope composition of  
328 environmental water is closely related to the  $\delta^{18}\text{O}$  values of precipitation, reflecting local

329 temperatures and other factors (Clark and Fritz, 1997; Dansgaard, 1964; Gat, 1980; Yurtsever,  
330 1975). Although hydrological processes such as water movement, water mixing, groundwater  
331 recharge and the formation (and evaporation) of surface water bodies can all influence the  
332 oxygen isotope composition of local environmental water (and, by inference, drinking water),  
333 broad correlations between groundwater, mean annual precipitation, and climate at specific  
334 locales are universally apparent (see review in Pederzani and Britton, 2019). In obligate  
335 drinking mammals, where local environmental waters are the primary source of fluids imbibed,  
336 the relationship between the  $\delta^{18}\text{O}$  of local environmental water and the  $\delta^{18}\text{O}$  of an animal's  
337 body tissues is mediated by the  $\delta^{18}\text{O}$  of body water. Homeothermic mammals have a  
338 metabolically-controlled, relatively constant body temperature ( $\sim 37^\circ\text{C}$ ), and therefore the  
339 bioapatite (a carbonated hydroxyapatite) in their mineralized tissues precipitates in oxygen  
340 isotope equilibrium with body water at this temperature (Levinson et al., 1987; Longinelli,  
341 1984; Luz et al., 1984). There is, therefore, a roughly linear relationship between the  $\delta^{18}\text{O}$  of  
342 ingested water, body water, and bioapatite and this relationship has led to the application of  
343  $\delta^{18}\text{O}$  to archaeological and paleontological remains as a means of reconstructing past climatic  
344 conditions. While some variation in this relationship has been noted between species,  
345 fractionation factors have been established for a number of different taxa based on modern  
346 experimental studies (e.g., Delgado Huertas et al., 1995 [horses]), allowing the development of  
347 these techniques on faunal remains from archaeological sites as a means of reconstructing past  
348 paleotemperatures.

349 Paleothermic reconstructions using the oxygen isotope analysis of faunal remains from  
350 European Late Pleistocene sites have focused on a range of different mammalian species, and  
351 have employed analyses of both the carbonate ( $\text{CO}_3$ ) and phosphate ( $\text{PO}_4$ ) components of tooth  
352 enamel, using a range of different Pleistocene mammals (e.g., Delgado Huertas et al., 1997;  
353 Fabre et al., 2011; Skrzypek et al., 2011; Kovács et al., 2012). As obligate drinkers with

354 significant daily water requirements, and taxa found in both glacial and interglacial faunal  
355 assemblages, equids and large bovids are particularly useful for mapping past  $\delta^{18}\text{O}$   
356 precipitation patterns and paleoclimate conditions. The analyses of these taxa from  
357 anthropogenically-derived (archaeofaunal) assemblages have the potential to generate  
358 terrestrial paleoclimate proxy data near-synchronous to human site-use, enabling estimates of  
359 mean annual temperatures when dental tissues are bulk sampled (e.g., Britton et al., 2019) and  
360 of seasonal paleotemperatures when hypsodont teeth are incrementally sampled (e.g.,  
361 Pederzani et al., 2021).

362 In addition to the in-built assumptions inherent in the reconstruction of paleotemperatures  
363 detailed above, a number of other factors can influence data produced and thus  
364 paleotemperature estimates. For example, the choice of tooth sampled is important. Early  
365 forming teeth, in general, should be avoided due to a known enrichment in  $^{18}\text{O}$  in the body  
366 water (and thus tissues) of juvenile animals during nursing compared to adult individuals (see  
367 review in Pederzani and Britton 2019). Sampling strategy therefore must incorporate  
368 knowledge of likely age-at-weaning for species targeted. As well as tooth selected, method of  
369 sampling can influence data generated (Reade et al., 2015). In the determination of bioapatite  
370  $\delta^{18}\text{O}$  different moieties can be targeted, influencing data obtained. In paleotemperature  
371 reconstructions using older Paleolithic materials, the phosphate is often the favored analyte as  
372 it is generally considered to be more resistant to post-depositional alteration compared to the  
373 carbonate component (Iacumin et al., 1996; Zazzo et al., 2004). Furthermore, the vast majority  
374 of modern calibration data for converting bioapatite  $\delta^{18}\text{O}$  to predicted  $\delta^{18}\text{O}$  drinking water has  
375 so far been generated from phosphate data and the use of carbonate  $\delta^{18}\text{O}$  ( $\delta^{18}\text{O}_{\text{CO}_3}$ ) for  
376 paleotemperature estimation would therefore require an additional conversion step to predicted  
377  $\delta^{18}\text{O}$  of bioapatite phosphate ( $\delta^{18}\text{O}_{\text{PO}_4}$ ) prior to paleotemperature calculations, which can  
378 increase uncertainty. Conversion equations themselves, which are required to convert  $\delta^{18}\text{O}_{\text{PO}_4}$



379 to estimates of the  $\delta^{18}\text{O}$  of drinking water ( $\delta^{18}\text{O}_{\text{dw}}$ ) and then to estimates of temperature, also  
380 include inherent assumptions and introduce (often large) compound uncertainties (Pryor et al.,  
381 2014). These conversions, and the uncertainties introduced, are discussed at length in a number  
382 of papers (e.g., Pryor et al., 2014) and are detailed here in the Supplementary Online Material  
383 (SOM) S3.

384

### 385 *1.3. The site of Abri du Maras*

386 The site of Abri du Maras is located on the west bank of the Rhône River, in a small valley at  
387 the confluence of the Ardèche River (Fig. 1). The site is all that remains of a vast southeast  
388 facing rock shelter, situated today 70 m above the river itself at the outer edge of the gorge.  
389 The Rhône Valley lies between mountainous regions—the Massif Central to the west and the  
390 foothills of the Alps to the east—with the valley itself connecting more northerly parts of  
391 France to the Mediterranean. Many tributaries, including the Ardèche River, connect the Rhône  
392 River to the Massif Central. Archaeological and zooarchaeological evidence from the region's  
393 caves and rock shelters suggest a farsighted circulating subsistence model closely associated  
394 with the regional micro-topography, interactions with non-human carnivores and the estimated  
395 availability of (seasonal) resources including prey-species, biotopes and raw material outcrops  
396 (Daujeard and Moncel 2010; Daujeard et al., 2016). Monospecific prey assemblages,  
397 characterized by the high dominance of remains of a single species represented by a large  
398 (minimum) number of individuals (Gaudzinski, 2006), are found at some Middle Paleolithic  
399 sites in the region, including at Abri du Maras with *Rangifer* (Daujeard and Moncel, 2010;  
400 Daujeard et al., 2012; Moncel and Daujeard, 2012; Daujeard et al., 2019; Marin et al., 2020;  
401 Moncel et al., 2021). Monospecific faunal assemblages increase significantly all over Europe  
402 from MIS 5 onwards, and when involving animals that live in large herds, such as reindeer, are  
403 often linked to cooperative and planned mass hunting strategies, and flexible resource

404 utilization against a background of increasing climatic instability (Gaudzinski, 2006). In such  
405 contexts, understanding the spatial paleoecology of the prey taxa can be key to interpreting  
406 these human hunting practices (e.g., interception hunting; Britton et al., 2011).

407 Since 2009, excavations of the site have focused on Middle Paleolithic deposits, including  
408 stratigraphic unit 5 (bottom of the currently documented sequence at the site, dating to the end  
409 of MIS 5) and overlying unit 4, which contains two archaeological levels in its upper part  
410 (levels 4.1 and 4.2) which both date to MIS 3. The site has been dated by electron spin  
411 resonance (ESR) and Uranium-Thorium (U-Th) methods, with level 4.1 dating to between 46  
412  $\pm 3$  ka and 40  $\pm 3$  ka and level 4.2 yielding dates ranging between 55  $\pm 2$  to 42  $\pm 3$  ka (Richard  
413 et al., 2015). Further analyses of two enamel hydroxyapatite samples from level 4.2 using these  
414 same methods have yielded ages of 42  $\pm 3$  and 42  $\pm 6$ , which together with an infrared  
415 stimulated luminescence (IRSL) age of 46  $\pm 4$  ka confirm the attribution of this site to MIS 3  
416 (Richard et al., 2021). Both of these levels contain the well-preserved evidence of hominin  
417 occupation, including abundant lithic artefacts, rare cordage remains, traces of combustion and  
418 diffuse ash lenses, and anthropogenically-modified faunal remains. The lithic assemblage  
419 comprises Levallois products and other core technologies, and includes retouched flakes,  
420 blades projectile tips and points largely made of local and semi-local flint (Hardy et al., 2013;  
421 Moncel et al., 2014; Daujeard et al., 2019; Hardy et al., 2020; Ruebens et al., 2022). Despite  
422 being close in date (or even sub-contemporaneous), levels 4.1 and 4.2 have yielded very  
423 different faunal and seasonality-indicator data, along with slightly different patterns of  
424 butchery which may suggest site use by two distinct groups with contrasting traditions (Vetesse  
425 et al., 2022). The faunal spectrum in 4.2 is varied and comprises, in order of abundance,  
426 *Rangifer tarandus*, *Equus ferus* cf. *germanicus*, *Bison priscus*, *Cervus elaphus* and  
427 *Megaloceros giganteus*, with spring-summer and autumn human occupations. Level 4.1 is  
428 largely dominated by *Rangifer* which, combined with indicators of selective butchery and

429 autumn season of death mortality profile, is suggestive of seasonally-restricted, cooperative  
430 and planned mass *Rangifer* hunting strategy and short-term occupations (Daujeard et al., 2019;  
431 Moncel et al., 2021; Vignes, 2021; SOM Table S1). Understanding potential differences in the  
432 paleoecology of species exploited, particularly the spatial ecology of *Rangifer*, would be an  
433 important step in better understanding Neanderthal subsistence strategies in these different  
434 levels.

435 Aside from the (macro-) faunal remains, paleoenvironmental studies have been limited for  
436 levels 4.1 and 4.2 of the site. Micromammals are scarce, largely due to poor preservation,  
437 although the presence of a single sample of *Microtus* ex gr. *arvalis-agrestis* found in level 4.1  
438 is consistent with a rather open environment (Daujeard et al., 2019). Dental microwear analysis  
439 of reindeer from level 4.1 has indicated grass-dominated mixed feeding, which is also  
440 consistent with an open environment, complementing the results of a small isotopic pilot study  
441 on faunal material from the same level indicating a lack of dense forest cover (Daujeard et al.,  
442 2019). Charcoal identified in both levels 4.1 and 4.2, however, suggest the presence of at least  
443 some woodland and taxonomic analyses has identified *Pinus sylvestris* type in both levels 4.1  
444 and 4.2, along with *Betula* in level 4.1 only (Daujeard et al., 2019). While *Pinus sylvestris* grow  
445 in dry and cold conditions, *Betula* require higher soil humidity rates, which may indicate that,  
446 in level 4.1 at least, conditions may have been relatively humid/milder (which is in agreement  
447 with the results of sedimentological analysis for the site, see Daujeard et al., 2019; Moncel et  
448 al., 2021). These data may seem somewhat contradictory to the presence of *Rangifer*, which  
449 are often considered a cold-adapted species and therefore inferring a harsh or steppic  
450 environment. However, it should be noted that there are multiple ecotypes of *Rangifer* today  
451 (Festa-Bianchet et al., 2011) and the behaviors and habitat preferences of Late Pleistocene  
452 European *Rangifer* (and variation therein) should not be assumed. Furthermore, it has long  
453 been recognized that the environments of northern Europe during MIS 3 (and at other phases

454 of the Late Pleistocene) were non-analogous to any modern environment, that is, characterized  
455 by combinations of animals (and plants) living together that are not found in sympatry today  
456 (see Stewart 2005 for discussion of Europe as a whole, and Foury et al., 2016 for discussion of  
457 the Rhône valley specifically). Therefore, given the limited paleoenvironmental data available  
458 from Abri du Maras, the diversity of species present (i.e., *Rangifer* with two other cervids,  
459 including the extinct *Megaloceros*) at the site, and the differences in prey-selection and  
460 seasonality of site use indicated from past zooarchaeological studies between levels 4.1 and 4.2,  
461 elucidating further information about the paleoecology of the species exploited, or the broader  
462 paleoenvironmental suite, using isotope zooarchaeological approaches is of key interest.  
463 Here, we present the results of a multi-isotope, multi-tissue study of herbivore remains from  
464 level 4.1 ( $46 \pm 3$  to  $40 \pm 3$  ka) and level 4.2 ( $55 \pm 2$  to  $42 \pm 3$  ka) at the Middle Paleolithic site  
465 of Abri du Maras (Ardèche, France), with the goal of providing new insights into the  
466 paleoenvironmental and paleoecological context of Neanderthal activity in the Rhône Valley  
467 during MIS 3. The specific aims of this study are: 1) to provide evidence of local paleothermic  
468 conditions; 2) to assess niche feeding behaviors and landscape use by key subsistence species;  
469 3) to examine potential relationships between herbivore ecology and/or seasonal biogeography  
470 at the site, the paleoenvironment, and the subsistence behaviors of contemporary hominin  
471 groups.

472

## 473 **2. Materials and methods**

### 474 *2.1. Sample selection*

475 Ungulate bone and teeth from the recent excavations at Abri du Maras (levels 4.1 and 4.2) were  
476 selected for destructive sampling and isotope analysis, including teeth of *Equus* and *Rangifer*  
477 for oxygen and strontium isotope analysis respectively, and *Bison*, *Cervus*, *Equus*,  
478 *Megaloceros* and *Rangifer* bone for carbon, nitrogen and sulphur isotope analysis (see Table 1

479 for all samples involved in this study). These samples are part of collections currently housed  
480 at the Institut de Paléontologie Humaine (IPH), Paris, for their ongoing study following  
481 taxonomic identification.

482 Due to sample availability, two complete *Equus* mandibular second premolars were sampled  
483 and analyzed for oxygen ( $\delta^{18}\text{O}$ ) isotope analyses for climate reconstruction from level 4.2 only.

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

497 In order to explore the seasonal mobility of *Rangifer*, two mandibular teeth (second and third  
498 molars) were selected from four *Rangifer* for strontium ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) isotope analyses. Due to the  
499 availability of material, samples included three individuals from level 4.1, but only a single  
500 individual from level 4.2. While intra-tooth  $\delta^{18}\text{O}$  can be helpful in ‘anchoring’  $^{87}\text{Sr}/^{86}\text{Sr}$  within  
501 a seasonal context, given that *Rangifer* are non-obligate drinkers and long-distance and/or  
502 altitudinal migrations can cause intra-tooth  $\delta^{18}\text{O}$  profiles to deviate substantially from a classic  
503 seasonal sinusoid (Britton et al., 2009), coupled with the need for minimally-destructive intra-

504 tooth sampling, the decision was made not to sample the *Rangifer* teeth for oxygen isotope  
505 analysis. However, in the absence of oxygen isotope data, the periodicity of *Rangifer* tooth  
506 crown formation and mineralization, and thus the seasonality of intra-tooth  $^{87}\text{Sr}/^{86}\text{Sr}$  can still  
507 be approximated based on previous studies, including a single radiograph study (Wu et al.,  
508 2012) and from comparable datasets from other cervid species. For example, Brown and  
509 Chapman (1991: 373) determined that formation of the second and third molar crowns of *Dama*  
510 *dama* commence at <3.5 and 9 months of age and complete at 9 and <18 months respectively.  
511 While intra-tooth oxygen isotope studies on *Rangifer* are not straight forward for the reasons  
512 stated above, the scant intra-tooth oxygen isotope data from modern migratory and non-  
513 migratory individuals (Britton et al., 2009; Britton 2010) suggest these estimates of enamel  
514 mineralization time are appropriate. Therefore, sampling of the se second and third molars can  
515 (depending on extent of wear) provide evidence of calving grounds, summer and winter range  
516 during the first year of life, and summer/autumn range during the second year of life (Britton  
517 et al., 2009). It must be noted, however, that any intra-tooth isotope study using archaeological  
518 materials has unavoidable assumptions inbuilt with regards to both the growth  
519 rate/mineralization time and birth seasonality of ancestral species being similar to extant  
520 individuals today. Anticipated to be a likely non-migratory species, an *Equus* third molar was  
521 selected from level 4.1 for strontium isotope analyses as a comparator to the *Rangifer*.  
522 Following on from a previous pilot study of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic  
523 niche variability in *Equus* ( $n = 3$ ), *Megaloceros* ( $n = 2$ ) and *Rangifer* ( $n = 3$ ) from level 4.1  
524 (Daujeard et al., 2019), further bone samples from five ungulate taxa were selected for collagen  
525 extraction and analyses from level 4.2, including *Equus* ( $n = 5$ ), *Megaloceros* ( $n = 2$ ), *Rangifer*  
526 ( $n = 1$ ), *Bison* ( $n = 2$ ) and *Cervus elaphus* ( $n = 5$ ). It should be noted that, with the exception  
527 of the *Rangifer* sample from level 4.2 (M10-121) from which both mandibular teeth and bone  
528 were sampled, bone samples and the teeth sampled for strontium and oxygen described did not

529 (to our knowledge) originate from the same individuals. While, ideally, these different isotope  
530 analyses would be undertaken from the same individuals, the horse teeth were all loose and it  
531 was not possible to sample the mandibles from the reindeer from which teeth were selected in  
532 level 4.1 due to their poor preservation/friability. Conversely, while bone was successfully  
533 sampled from other *Rangifer* mandibles in level 4.1, their teeth were insufficient for strontium  
534 isotope analyses (e.g., lacking in a complete and relatively unworn second and/or third molar,  
535 both of which are required to reconstruct a full year of movement history).

536

## 537 2.2. Tooth and bone sampling protocols

538 For all teeth, the buccal face of the anterior loph was selected for sampling as it tends to have  
539 thicker enamel than the lingual side. The whole face was abraded (using air abrasion) to remove  
540 superficial enamel. Each complete tooth was then ultrasonicated in Milli-Q ultrapure water for  
541 5 mins. Incremental enamel samples were taken as horizontal bands, perpendicular to the tooth  
542 growth axis, using a diamond-coated tungsten carbide cutter point (NTI-Kahla) from the  
543 enamel-root junction (ERJ) to the occlusal surface. Sampling increments were 1–2 mm,  
544 measured as distances from the ERJ in each specimen using digital calipers. For the *Equus*  
545 from level 4.2, between 25 and 28 samples of fine enamel powder, ranging in weight from ~5  
546 to ~15 mg, were collected from each tooth. For the *Rangifer*, between 5 and 10 serial samples  
547 of fine enamel powder, ranging in weight between ~3 and ~8 mg (albeit with a single sample,  
548 SEVA32976IX, weighing ~1mg) were collected from each tooth depending on crown height  
549 available to sample/extend of wear. A single sample of dentine, presumed to be diagenetically  
550 altered and therefore reflecting of local soil values, was taken from the molar roots of each of  
551 the *Rangifer* teeth samples in order to provide a secondary indicator of local environmental  
552 strontium  $^{87}\text{Sr}/^{86}\text{Sr}$  at the site. For the single *Equus* tooth from level 4.1, three samples, spaced  
553 evenly down the crown (~12–14 mm apart), were taken in a similar way. Bone (~1–2 g) was

554 sampled for collagen extraction using rotary stainless-steel cutting implements and cleaned  
555 using air abrasion.

556

### 557 *2.3. Oxygen isotope analysis*

558 Silver phosphate precipitations and mass spectrometry Serial samples of *Equus* tooth enamel  
559 (~10 mg) were prepared for phosphate oxygen isotope analysis in the Archaeological  
560 Chemistry Laboratories, Department of Archaeology, University of Aberdeen following  
561 methods described in Britton et al. (2019) using a rapid precipitation method, after Tütken et  
562 al. (2006) and based on O'Neil et al. (1994) and Dettmann et al. (2001: Appendix, GSA Data  
563 Repository item 20018), with minor modifications.

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

575

576 Modelling of intra-tooth oxygen isotope data, conversion equations and air temperature  
577 estimations The extended process of tooth enamel growth and mineralization of ungulate teeth  
578 causes a predictable damping of the seasonal amplitude of oxygen isotopic change expressed



579 tooth enamel compared to the seasonal amplitude in consumed environmental water (Kohn et  
580 al., 1996; Passey and Cerling, 2002; Kohn, 2004; Blumenthal et al., 2014; Green et al., 2017;  
581 Trayler and Kohn, 2017). Therefore, a correction procedure is necessary in order to obtain  
582 faithful paleotemperature reconstructions on a seasonal time scale, which can be achieved using  
583 an inverse model (Passey et al., 2005; Green et al., 2018). Such models take into account the  
584 sampling geometry and species-specific characteristics of tooth enamel formation to estimate  
585 the original  $\delta^{18}\text{O}$  input. In this study, horse tooth enamel  $\delta^{18}\text{O}$  seasonal curves were inverse  
586 modelled following methods in Passey et al. (2005) using R v.4.1.2 (R Core Team, 2021) and  
587 an R code translation of the originally published MATLAB code. Details of the modelling  
588 procedure are described in SOM S2 and we provide all code and data necessary to reproduce  
589 this step in the SOM File S1.

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

600

#### 601 *2.4. Bone collagen extraction and analysis*

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

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

611 An additional aliquot of collagen was analyzed for stable sulphur ( $\delta^{34}\text{S}$ ) isotopes at the Scottish  
612 Universities Research Centre (SUERC) for all collagen extracts, including those from which  
613  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data have been previously presented (Table 1; Daujeard et al., 2019). This was  
614 conducted on a Delta V Advantage continuous-flow isotope ratio mass spectrometer coupled  
615 via a ConfloIV to an IsoLink elemental analyzer (Thermo Scientific, Bremen), a system which  
616 enables the co-measurement of carbon, nitrogen and sulphur stable isotope ratios (Sayle et al.,  
617 2019), generating additional  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements as well as  $\delta^{34}\text{S}$  with an analytical  
618 precision of  $\pm 0.3\text{‰}$  (1 SD) or better for each isotope (see SOM S2 for method statement and  
619 details of normalization of data and standards). As multiple sets of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements  
620 were obtained from each sample (see SOM Table S3 and Table S4 for MPI-EVA and SUERC  
621 data, respectively), for the purposes of this study the calculated mean of all measurements is  
622 used for each sample (SOM Table S5), which slightly modifies the values reported for some of  
623 the same samples from level 4.1 previously reported in Daujeard et al. (2019). However, across  
624 the two laboratories, the average standard deviation (1 SD) about the mean for the measurement  
625 of all individual aliquots was lower than the largest long-term reproducibility/analytical error  
626 reported by either laboratory. Thus, the data are considered comparable. No subsequent  
627 statistical treatments were applied to the carbon and nitrogen isotope data, beyond the  
628 descriptive statistics in the text below (mean, standard deviation, etc.). However, we explored

629 the partition of the samples according to their  $\delta^{34}\text{S}$  values using hierarchical clustering ('hclust'  
630 base function, R v.4.1.2). We used the 'average' agglomeration method to define the clusters  
631 as it provided the highest cophenetic correlation coefficient for our dataset ( $c = 0.896$ ) among  
632 the different agglomeration methods (Legendre and Legendre 1998).

633

## 634 2.5. Strontium isotope analysis

635 Sample preparation and mass spectrometry All samples of *Rangifer* tooth enamel (plus the  
636 dentine, and three sub-samples of *Equus* tooth enamel from level 4.1) were analyzed for  
637 strontium isotope ratios using the ion-exchange solution method described in Copeland et al.  
638 (2008) and Britton et al. 2009, a modification of the method from Deniel and Pin (2001).  
639  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios were determined using a Thermo Fisher (Thermo Fisher Scientific, Bremen,  
640 Germany) Neptune multi-collector inductively coupled plasma mass spectrometer (MC-ICP-  
641 MS) in the Department of Human Evolution at the Max Planck Institute for Evolutionary  
642 Anthropology. Strontium concentrations of the enamel samples were determined using the  
643 method described in Copeland et al. (2008), which is accurate to within  $\pm 31$  ppm. Analytical  
644 precision was  $\pm 0.00003$  (2 SD) or better, based on the repeat analysis of external and in-house  
645 standards. For detailed descriptions of sample preparation, correction of mass spectrometry  
646 data and details of standards and blanks see SOM S5.

647

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

654 based on variability of environmental  $^{87}\text{Sr}/^{86}\text{Sr}$  across the landscape (the strontium isoscape;  
655 Fig. 2). We used the global bioavailable  $^{87}\text{Sr}/^{86}\text{Sr}$  isoscape, and the associated spatial error  
656 raster produced by Bataille et al. (2020). The three sample locations in each *Rangifer* sampled  
657 selected for spatial assignment include: 1) the sample closest to the occlusal surface of the  
658 second molar (the earliest forming section of the intra-tooth profiles obtained, expected to  
659 broadly correspond with location during the first summer of life); 2) the sample closest to the  
660 ERJ of the second molar (broadly corresponding to location during the first winter of life); and  
661 3) the sample closest to the ERJ of the third molar (broadly corresponding to location during  
662 the second summer/autumn of life). For *Equus*, the three samples were taken from the M3,  
663 close to the occlusal surface, at the midpoint, and close to the ERJ. For each sample, treated as  
664 sample of unknown origin, we generated the posterior probability surface of origin rescaled to  
665 1, then we extracted the area corresponding to 80% of the posterior probability density. R code  
666 is provided in SOM File 2.

667

### 668 **3. Results**

#### 669 *3.1 Intra-tooth enamel oxygen isotope data from level 4.2 Equus*

670 Oxygen isotope data generated from two *Equus* teeth (lower second premolars) from level 4.2  
671 demonstrate sinusoidal intra-tooth patterns, with values ranging from 16.3 to 19.3‰ with a  
672 midpoint (mean of summer and winter extremes) of 17.8‰ (N6-767) and 15.2 to 18.9‰ with  
673 a midpoint of 17.1‰ (N6-687; Fig. 3, and full data in SOM Table S2 and summary of seasonal  
674 extrema in SOM Table S6). This results in a seasonal  $\delta^{18}\text{O}$  amplitude of ~ 3‰. Given the well  
675 documented linear relationship between *Equus* sp. enamel  $\delta^{18}\text{O}$  and drinking water  $\delta^{18}\text{O}$   
676 (Bryant et al., 1994; Sánchez Chillón et al., 1994; Delgado Huertas et al., 1995), we take the  
677 characteristic sinusoidal  $\delta^{18}\text{O}$  curves seen here in sequentially sampled tooth enamel to be  
678 reflective of seasonal changes in  $\delta^{18}\text{O}$  of environmental water consumed by these individuals,

679 that most likely in turn reflect seasonal temperature changes. Based on the linear relationship  
680 between  $\delta^{18}\text{O}$  of enamel ( $\delta^{18}\text{O}_{\text{enamel}}$ ) and  $\delta^{18}\text{O}$  of drinking water ( $\delta^{18}\text{O}_{\text{dw}}$ ) and in turn with  $\delta^{18}\text{O}$   
681 of precipitation, as described in SOM S3, we estimated  $\delta^{18}\text{O}_{\text{dw}}$  and paleotemperatures in order  
682 to facilitate comparisons with other paleoclimate information and with modern climates. This  
683 approach relies on some inherent assumptions including a certain degree of physiological  
684 similarity between modern and Pleistocene animals, a broadly comparable system of  
685 atmospheric circulation, and that drinking water sources of the studied animals isotopically  
686 reflect precipitation inputs. These are mostly thought to be justified for European Late  
687 Pleistocene settings, although local hydrotopography and drinking water sources need to be  
688 studied on a case-by-case basis. Additionally, it should be noted that they introduce a certain  
689 unavoidable (and mathematically not fully captured) degree of uncertainty to paleotemperature  
690 estimations (see Pryor et al., 2014 and SOM S2 for details on error sources that are accounted  
691 for).

692 An overview of unmodelled summer, mean and winter  $\delta^{18}\text{O}_{\text{enamel}}$ , inverse modelled summer  
693 and winter  $\delta^{18}\text{O}$ , and corresponding  $\delta^{18}\text{O}_{\text{dw}}$  and paleotemperature estimates is provided in SOM  
694 Table S6. Drinking water  $\delta^{18}\text{O}$  estimates fall at  $-0.6 \pm 2.1\text{‰}$  for summer,  $-7.6 \pm 2.1\text{‰}$  for annual  
695 means, and at  $-16.2 \pm 2.2\text{‰}$  for winter (Fig. 4). In comparison, interpolated estimates of modern  
696 precipitation  $\delta^{18}\text{O}$  indicate that current precipitation at the site exhibits  $\delta^{18}\text{O}$  values of  $-1.5\text{‰}$   
697 in July and  $-9.9\text{‰}$  in January and mean annual  $\delta^{18}\text{O}$  of  $-6.3 \pm 0.1\text{‰}$  (95% CI; Bowen and  
698 Revenaugh, 2003; Bowen et al., 2005; Bowen, 2022), Paleotemperature conversions for the  
699 two individuals from level 4.2 indicate summer temperatures of  $31 \pm 4.8^\circ\text{C}$ , winter  
700 temperatures of  $-10 \pm 4.3^\circ\text{C}$  and mean annual temperatures of  $12 \pm 4.0^\circ\text{C}$  (Fig. 4), where error  
701 ranges indicate the compound error of the paleotemperature estimation as described in Pryor et  
702 al. (2014). This compares to modern day (1981-2009) temperatures of  $4.3 \pm 1.6^\circ\text{C}$  in January,

703  $23.3 \pm 1.1^{\circ}\text{C}$  in July and an annual average of  $13.4 \pm 0.5^{\circ}\text{C}$  estimated for the site using the  
704 ClimateEU model (Marchi et al., 2020).

705

706 *3.2. Bone collagen carbon, nitrogen and sulphur isotope data of ungulates from level 4.1 and*  
707 *4.2*

708 Full results of the faunal bone collagen extracted and analyzed from Abri du Maras can be  
709 found in the SOM (SOM Table S3 [Leipzig], SOM Table S4 [SUERC], and SOM Table S5  
710 [means]), including all quality (%C, %N, %S, C:N, C:S and N:S) data.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all  
711 specimens are shown in Figure 5, and corresponding  $\delta^{34}\text{S}$  data of all samples with sufficient  
712 remaining collagen for that analysis are shown in Figure 6. Although approximately half of the  
713 samples have %C and %N marginally lower than that of modern collagen (i.e. less than  $\sim 35 \pm$   
714  $8.8$  wt% for C, and 11–16 wt% for N; van Klinken 1999), their atomic C:N ratios are between  
715 3.2 and 3.5, and are therefore within the expected range for well-preserved bone (DeNiro, 1985;  
716 Ambrose, 1990; van Klinken, 1999; Dobberstein et al., 2009). Furthermore,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
717 values are not significantly correlated with %C or %N respectively, or with C:N ratios (see  
718 SOM Figs. S1–S4). The atomic C:S ratios range from 545 to 827 and the N:S ratios range from  
719 157 to 250, and are therefore within the range expected for modern mammalian bone collagen  
720 (C:S =  $600 \pm 300$  and N:S =  $200 \pm 100$ ; Nehlich and Richards, 2009).

721 Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $\pm 1$  SD) for horses ( $n = 8$ ) are  $-20.3 \pm 0.2\text{‰}$  and  $3.3 \pm 0.8\text{‰}$ , and  
722 values are similar within both levels. Mean values from the *Bison* samples ( $n = 2$ ), both level  
723 4.2, are elevated relative to the horses with being  $-19.7 \pm 0.0\text{‰}$  and  $5.6 \pm 0.0\text{‰}$  for carbon and  
724 nitrogen respectively. The three cervid taxa all have similar mean  $\delta^{13}\text{C}$  (*Megaloceros*:  $-19.5 \pm$   
725  $0.1\text{‰}$  [ $n = 4$ ]; *Rangifer*:  $-19.9 \pm 0.2\text{‰}$  [ $n = 4$ ]; *Cervus elaphus*:  $-19.8 \pm 0.2\text{‰}$  [ $n = 5$ ]), but differ  
726 in their  $\delta^{15}\text{N}$ , with *Cervus elaphus* (all from level 4.2) having the lowest values ( $3.9 \pm 0.4\text{‰}$ ),

727 *Megaloceros* have the most elevated values ( $5.5 \pm 0.1\text{‰}$ ) and *Rangifer* displaying the greatest  
728 range of values from 3.9 to 6.0‰ (mean =  $4.8 \pm 0.9\text{‰}$ ).

729 Of the 23 bone collagen extractions, 19 yielded sufficient material for the measurement of  
730 sulphur isotope ratios. While species  $\delta^{34}\text{S}$  means ( $\pm 1$  SD) are similar in some species (e.g.,  
731 *Megaloceros*:  $5.2 \pm 0.6\text{‰}$  [ $n = 3$ ]; *Bison*:  $5.5 \pm 0.2\text{‰}$  [ $n = 2$ ]; as well as between *Rangifer*:  $3.7$   
732  $\pm 2.8\text{‰}$  [ $n = 4$ ] and *Cervus elaphus*:  $3.3 \pm 1.2\text{‰}$  [ $n = 4$ ]), there are notable differences between  
733 species and, in some cases, between levels. *Rangifer* and *Cervus elaphus* display a greater range  
734 of values than other species, including an outlier value of 0‰ in the single *Rangifer* sampled  
735 from level 4.2 (Fig. 6). Of the samples that have sulphur data, both *Cervus elaphus* ( $n = 4$ ; level  
736 4.2 only) and *Equus* ( $n = 6$ ) have a fairly wide range of  $\delta^{34}\text{S}$  values (from 2.0‰ to 4.9‰; and  
737 2.3‰ to 6.8‰ respectively), although not as large as the range of sulphur isotope ratios shown  
738 in the *Rangifer* (which varies from 0.0‰ to 6.0‰). With the exception of the single *Rangifer*  
739 sample from level 4.2, according to the hierarchical cluster analysis, the animals at Abri du  
740 Maras fall into two broad groups with regards to sulphur: group 1) 4.8–6.8‰ and group 2) ~2–  
741 3.2‰ (SOM Fig. S3). All species analyzed are present in group 1, and *Equus*, *Rangifer* and  
742 *Cervus* can be found in group 2, with animals from both levels found in each of the groups. A  
743 recently produced sulphur isoscape for the region (based on bone collagen data from the  
744 Mesolithic to the modern day) suggests that  $\delta^{34}\text{S}$  values around Abri du Maras could be  
745 expected to range from 4 to 7‰ (SOM Fig. S4, based on data from Bataille et al., 2021). Thus,  
746 individuals from sulphur group 1 are consistent with this local range, but those in group 2 are  
747 comparatively low, and not consistent with values found within the immediate region.

748

### 749 3.3. Intra-tooth strontium isotope data from *Rangifer* and *Equus* from level 4.1 and 4.2

750 Tooth enamel strontium (Sr) concentrations of archaeological *Rangifer* samples ranged from  
751 86–200 ppm (SOM Table S7), which are similar to those measured in modern caribou (Britton

752 et al., 2009) and in domestic cattle (Evans et al., 2007). Strontium concentrations of *Equus*  
753 enamel were higher (~250 ppm), but also in line with values expected from archaeological  
754 herbivore teeth (Evans et al., 2007; Groot et al., 2020). Data from the M<sub>2</sub> and M<sub>3</sub> of intra-tooth  
755 samples of all three individual *Rangifer* sampled from level 4.1 bear similar isotope values  
756 (Fig. 7; SOM Table S7), ranging from 0.7085 to 0.7101 with a mean of  $0.7089 \pm 0.0003$ . This  
757 average is a little higher than the mean of three samples of horse tooth enamel sampled from a  
758 single horse from the same level, close to the occlusal surface, mid-crown and at the enamel  
759 root junction ( $0.7086 \pm 0.0001$ ). The strontium isotope values measured in all dentine samples  
760 from *Rangifer* from both level 4.1 and level 4.2 range from 0.7086 and 0.7092 (mean =  $0.7088$   
761  $\pm 0.0003$ ), are a secondary confirmation of the expected range of local values (see Fig. 2 for a  
762 predicted strontium isoscape of the region). In contrast, the intra-tooth values of the single  
763 reindeer individual sampled from level 4.2 shows a different trend to the reindeer from level  
764 4.1, with a higher degree of intra-tooth variability, the values ranging from 0.7090 to 0.7125  
765 (mean =  $0.7112 \pm 0.0012$ ).

766 The raw posterior probability distribution maps assessed from the  $^{87}\text{Sr}/^{86}\text{Sr}$  spatial assignment  
767 from the three different locations on the crowns of four *Rangifer* and one *Equus* are provided  
768 in SOM Figures S7, S8, and S9. Based on the spatial assignment of the samples closest to the  
769 occlusal surface of both the M<sub>2</sub> and the M<sub>3</sub>, we determined the areas where the samples have  
770 an 80% chance of originating, and considered these areas respectively as the winter and  
771 summer areas potentially used by each *Rangifer* (Fig. 8). For the *Equus* we determined the  
772 potential areas corresponding to the highest and the lowest  $^{87}\text{Sr}/^{86}\text{Sr}$  values of its profile,  
773 respectively the sample closest to the M<sub>3</sub> ERJ (0.7086) and the sample closest to the occlusal  
774 surface (0.7085), which are almost entirely overlapping (91.8% of overlap; Fig. 8). The three  
775 *Rangifer* from level 4.1, as well as the *Equus*, show potential use of areas within of ~50 km of  
776 Abri du Maras in both winter and summer but also areas on the eastern side of the Rhône Valley



777 or southwest of Abri du Maras (Fig. 8). Summer and winter ranges of *Rangifer* J6-306 almost  
778 overlap entirely (88.4% of overlap) and show a strong agreement with the *Equus*' range. A  
779 similar pattern is observed for *Rangifer* 80/133 while the overlap between potential summer  
780 and winter ranges is less pronounced (48.6%). *Rangifer* N6-178 seems to show a higher  
781 segregation in its seasonal range use (21.4% of overlap) but both potential summer and winter  
782 ranges can still be found close to Abri du Maras. Spatial assignment also highlighted for this  
783 individual potential areas in summer slightly further north of Abri du Maras (Fig. 8). *Rangifer*  
784 M10-121 from level 4.2, shows a complete separation between the potential summer and winter  
785 areas (0% of overlap, Fig. 8). Summer assignment highlights areas similar to the ones used by  
786 the *Equus* and the *Rangifer* from level 4.1, in the vicinity of Abri du Maras. However, winter  
787 assignment suggests the use of areas away from Abri du Maras with potential areas located  
788 150-200 km from the site, in the northern most parts of the Rhône valley or further to the east,  
789 or even more distant, in the southwest direction (Fig. 8).

790

## 791 **4. Discussion**

### 792 *4.1. Paleoclimatic context*

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

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

805 The number of individuals analyzed here is relatively small, which increases the uncertainty  
806 around paleotemperature estimates. However, both individuals are remarkably similar in their  
807  $\delta^{18}\text{O}$  seasonal curves, indicating a consistent reflection of environmental parameters across  
808 individuals. At the same time, sinusoidal  $\delta^{18}\text{O}$  curves with a pronounced seasonal amplitude in  
809 both individuals indicates that they were unlikely to have obtained much drinking water from  
810 a seasonally buffered water source such as large rivers or springs fed from groundwater. This  
811 further indicates that *Equus* at Abri du Maras most likely reflect climatic impacts on  $\delta^{18}\text{O}$  of  
812 local environmental water sourced from precipitation. Impacts of slight differences in habitat  
813 and water source use on enamel  $\delta^{18}\text{O}$  between animals drinking water from the Rhône River  
814 compared to those drinking precipitation-fed water sources on the local limestone plateaus have  
815 been suggested for the data set from Payre (Ecker et al., 2013; Bocherens et al., 2016), a site  
816 located on a similar hydrotopographic setting in close proximity to the Rhône ~50 km upstream  
817 of Abri du Maras. A similar scenario could potentially also be envisaged for Abri du Maras,  
818 which is also situated only a few hundred of meters from the Rhône River. However, the  
819 seasonally pronounced  $\delta^{18}\text{O}$  variation in the level 4.2 horses does not support this. As larger  
820 rivers generally exhibit low seasonal  $\delta^{18}\text{O}$  variability due to higher water residence times, and  
821 incorporate snow melt and mixing of water from different locations/altitudes (Rank et al.,  
822 2018), a year-round consumption of Rhône River water would most likely result in a lack of  
823 seasonal variation in  $\delta^{18}\text{O}$ , which is not observed here. Indeed, estimates of  $\delta^{18}\text{O}_{\text{dw}}$  show  
824 stronger seasonal differences than expected from local precipitation, rather than an attenuated  
825 amplitude that could be expected if animals were sourcing from a strongly buffered water  
826 source. A substantial contribution of river water to the drinking water of the Abri du Maras

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

832 Finally, one aspect of the local paleoenvironment that remains unknown and may have had the  
833 potential to influence faunal  $\delta^{18}\text{O}$  values is aridity. High aridity induces  $^{18}\text{O}$ -enrichment  
834 compared to local precipitation in plants and stagnant open water bodies and therefore in some  
835 herbivores, with leaf water or open water signatures superimposing (and therefore obscuring)  
836 relationships with precipitation  $\delta^{18}\text{O}$  (e.g., Ayliffe and Chivas, 1990; Cormie et al., 1994; Levin  
837 et al., 2006). However, in contrast to evaporation sensitive species (including cervids and  
838 caprines), obligate drinkers, such as equids and large bovids, are considered evaporation  
839 insensitive and the  $\delta^{18}\text{O}$  of their body tissues are unlikely to be strongly influenced by leaf  
840 water changes given their dependency on drinking for meeting their water requirements (Levin  
841 et al., 2006). At the same time, drinking from evaporatively enriched water bodies such as large  
842 lakes, similarly to larger rivers, would result in a lack of seasonal  $\delta^{18}\text{O}$  variation in animal teeth,  
843 which is not observed. It is therefore unlikely the phosphate  $\delta^{18}\text{O}$  of the horses included in this  
844 study, and the seasonal enrichment observed, is reflecting high aridity. There are few other site-  
845 specific indicators of paleoenvironment beyond the faunal suite and isotopic data generated in  
846 this study, with the exception of charcoal analysis which has identified wood species include  
847 *Pinus sylvestris* type and *Betula*, the latter of which has been found in level 4.1 (Daujeard et  
848 al., 2019; Moncel et al., 2021). While *Pinus sylvestris* grow in dry and cold conditions, *Betula*  
849 require higher soil humidity rates. This may indicate that, in level 4.1 at least, conditions were  
850 not overly arid. Future studies at the site could incorporate the oxygen isotope analysis of non-  
851 obligate drinking species, such as *Cervus elaphus*, as a comparison to the obligate drinking

852 species in order to establish water deficiency and, through this, establish an aridity index for  
853 the site (e.g., Levin et al., 2006). Future paleoclimatic studies using oxygen isotopes would  
854 ideally incorporate strontium isotope analyses, at the very least for serial-samples  
855 corresponding to seasonal  $\delta^{18}\text{O}$  peaks and troughs. Although studies of Late Pleistocene  
856 European horses have not indicated migratory behavior (e.g., Pellegrini et al., 2008), and the  
857  $^{87}\text{Sr}/^{86}\text{Sr}$  data from the level 4.1 horse analyzed here is also consistent with sedentary behavior,  
858 conservation of this behavior in all phases of the Late Pleistocene cannot be assumed.  
859 Furthermore, other species, such as red deer, which could be useful comparators in calculating  
860 aridity index, may undertake seasonal movements.

861

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

877 similar winter  $\delta^{18}\text{O}$  values, but comparatively lower summer and mean annual  $\delta^{18}\text{O}$  values than  
878 at Abri du Maras.  $\delta^{18}\text{O}$  values from Combe Grenal were bulk sampled from tooth fragments of  
879 varying lengths from a variety of tooth types, which may contribute to a relatively large scatter  
880 of  $\delta^{18}\text{O}$  values (Richards et al., 2017). Individuals that most closely resemble Abri du Maras  
881 level 4.2 stem from Layer 10 (18.1‰), Layer 12 (17.3‰) and Layer 14 (18.1‰), which have  
882 been tentatively assigned to early MIS 3. Based on these comparisons, the  $\delta^{18}\text{O}$  results from  
883 Abri du Maras level 4.2 fall comparatively high in the range of published  $\delta^{18}\text{O}$  values for MIS  
884 3 southern France, with relatively high summer peak values and a comparatively pronounced  
885 seasonal summer/winter difference. This may indicate relatively warm mean annual climatic  
886 conditions with warm summers, compared to other sites from MIS 3. Oxygen isotope data from  
887 *Equus* teeth from the geographically closest site of Payre (Ecker et al., 2013; Bocherens et al.,  
888 2016) unfortunately predate the data from Abri du Maras that are discussed here making direct  
889 comparison difficult. Predicted phosphate  $\delta^{18}\text{O}$  values (converted from carbonate  $\delta^{18}\text{O}$ ) from  
890 samples from Levels D, F and G at Payre fall noticeably below the results from Abri du Maras  
891 (Fig. 9). Given the close spatial proximity to Abri du Maras, it is likely that the *Equus* from  
892 Payre either experienced far colder climatic conditions in this region during MIS 6 and earlier  
893 (Richard et al., 2021) than those at Abri du Maras during MIS 3, or sourced a larger amount of  
894 drinking water from rivers of alpine origin, as was proposed by Ecker et al. (2013) and  
895 Bocherens et al. (2016).

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

902 Maras are ~5 °C higher and winter temperatures ~ 10 to 15°C lower than temperature estimates  
903 from La Ferrassie. As a consequence, the *Equus*  $\delta^{18}\text{O}$  data from Abri du Maras seems to  
904 indicate stronger summer-winter differences in climate. La Ferrassie Layer 5 is similar in age  
905 to Abri du Maras level 4.2, but is located ~ 350 km west of Abri du Maras and closer to the  
906 Atlantic rather than the Mediterranean coast. Climatic differences between the two sites may  
907 also stem from slight differences in age, as chronometric dates for both deposits show a  
908 considerable uncertainty that is typical for this time period. On the other hand, geographic  
909 differences in climate and circulation may also play a role. Given that the modern-day climate  
910 at both locations is very comparable, this means that either age related climatic differences are  
911 a more likely explanation or that geographic climate gradient between the Dordogne and the  
912 Ardèche were more pronounced during MIS 3. While these options are difficult to distinguish  
913 based on available data, comparisons with both other Pleistocene data and modern-day climatic  
914 data indicates that the *Equus* from Abri du Maras level 4.2 lived in a relatively mild climate in  
915 terms of mean annual temperature but with a pronounced seasonal temperature difference. The  
916 latter is perhaps of most significance when considering past animal (and human) experience of  
917 climate in the region. Seasonal temperature extremes may have impacted the seasonality of  
918 Neanderthal landscape use, particularly of higher altitude areas in this region. Indeed, a  
919 framework of strong seasonal mobility that has been hypothesized on the basis of  
920 archaeological, zooarchaeological and material culture evidence for this region of southeastern  
921 France between the plains of the Rhone Valley and the mid-mountains of the Massif Central  
922 from MIS 7 to MIS 3 (Daujeard et al., 2012). However, it must be noted that the seasonal  
923 temperature estimations in the current study bear unavoidably large errors of between 4 and  
924 5°C. Although the lower end of these estimations would still result in cooler winters and  
925 warmer summers than are found in the region today, these estimations (and conclusions drawn  
926 from them) must be considered with appropriate caution.

927

#### 928 4.2. Faunal dietary ecology and broader paleoenvironment

929 Despite the modest size of the dataset, as shown in Figure 5, interspecies differences,  
930 particularly in  $\delta^{15}\text{N}$  are clear. *Equus* exhibit both the lowest mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. While  
931 these values are typical of grazers living in temperate (C3) ecosystems (e.g., Fizet et al., 1995;  
932 Bocherens, 2003), given that grasses are normally  $^{15}\text{N}$  enriched relative to shrubs in  
933 contemporary arctic and boreal ecosystems (see Bocherens, 2003: 61) it is interesting that the  
934 *Bison* are elevated in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  relative to *Equus*. These differences are similar to  
935 those measured in equids and bovids at the older Eemian site of Neumark-Nord 2, Germany  
936 (~126 ka; Britton et al., 2012) and the (broadly) contemporary French site of Marillac (45–40  
937 ka; Fizet et al., 1995). Differences in  $\delta^{13}\text{C}$  are likely attributable to differences in the production  
938 levels of methane between these different species. Ruminant methane has negative  $\delta^{13}\text{C}$  values  
939 (Metges et al., 1990), potentially leading to tissue enrichment in  $^{13}\text{C}$  (e.g., Cerling and Harris,  
940 1999), and similar patterns have been determined in a range of isotopic studies of European  
941 Late Pleistocene fauna (see discussion and Britton et al., 2012: Figure 3). However, there is  
942 less compelling evidence for a consistent ‘offset’ in  $\delta^{15}\text{N}$  between equids and bovids and the  
943 factors influencing  $\delta^{15}\text{N}$  values in herbivores are complex. Given that modern European bison  
944 are mixed/intermediate feeders (Merceron et al., 2014) and shrubs are often depleted in  $^{15}\text{N}$   
945 relative to grasses, one may expect collagen  $\delta^{15}\text{N}$  values of potential mixed feeders should also  
946 be lower. However, another factor known to influence collagen  $\delta^{15}\text{N}$  values of herbivores is  
947 the protein content of the diet, with the consumption of higher protein plants leading to  
948 increased diet-tissue offsets and  $^{15}\text{N}$ -enrichment (Sponheimer et al., 2003). Horses are  
949 generally considered to be adapted to live on high fiber, low quality forage (Duncan et al.,  
950 1990), which could influence diet-tissue offsets and lead to lower  $\delta^{15}\text{N}$  tissue values. In  
951 contrast, the elevated  $\delta^{15}\text{N}$  values of *Bison* seen here may indicate the incorporation of higher

952 nutrient food such as short grasses, sedges, forbs and leaves. It should be noted, however, that  
953 lower  $\delta^{15}\text{N}$  values are not always observed in European Pleistocene horses relative to other  
954 herbivore species, suggesting that the selection of low quality forage by horses is not  
955 necessarily habitual and may be plastic, shaped by local habitat structure (see discussion in  
956 Britton et al., 2012). At Abri du Maras, however, grazing on low quality forage may indeed  
957 account for the  $\delta^{15}\text{N}$  determined in the equids, whereas *Bison* were likely able to feed more  
958 flexibly and here are occupying a similar isotopic niche to *Megaloceros*.

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



977 The isotope values exhibited in the different deer species at Abri du Maras perhaps reflect the  
978 contemporary environmental and ecological suite of this part of France at the time (i.e., that  
979 woodland environments may have been mosaic and not extensive/dense). This is consistent  
980 with other paleoenvironmental proxy evidence from the site, including charcoal evidence,  
981 which is consistent with open forests or forest groves and also with the characterization of  
982 mosaic environments in the Rhône valley and along its tributaries, and other parts of central  
983 and southern France, and northern Iberia, during MIS 3 (see discussion in Daujeard et al.,  
984 2019). The higher  $\delta^{15}\text{N}$  values seen in *Megaloceros* at Abri du Maras could also be consistent  
985 with this, and the similarity between  $\delta^{13}\text{C}$  in *Rangifer*, *Cervus* and *Megaloceros* may indicate  
986 that lichen did not comprise any significant part of *Rangifer* diet in this period and—by  
987 inference—that lichen coverage may have been lower during these mild phases (as indicated  
988 by the oxygen isotope data from level 4.2 at least). Lichen declines are common described in  
989 the context of modern global warming and long-term vegetation-specific studies in the Arctic  
990 have demonstrated that warmer, and especially more humid conditions, favor mosses and  
991 vascular plants and lead to the physiological impairment of lichens and their subsequent decline  
992 (Olthof et al., 2008).

993 When comparing the cervid data from Abri du Maras to that from cooler periods of the Late  
994 Pleistocene (e.g., Drucker, 2022), it may be that niche spacing between these species was  
995 reduced in this earlier phase of MIS 3. A similar pattern has been seen in deer species during  
996 the Lateglacial interstadial and has been attributed to milder and more humid conditions and a  
997 decrease in niche partitioning that may have resulted in greater competition between different  
998 herbivore species (Drucker, 2022; Drucker et al., 2018; Immel et al., 2015). However, it is  
999 important to note that isotopic data do not strictly correspond to niche space but instead to  
1000 isotopic niche space, and isotopic differences between species are dependent not only on  
1001 consistently different feeding behaviors but also on the availability of isotopically diverse graze

1002 and browse. It may be, that in the absence of either dense forest or abundant lichens, carbon  
1003 isotopic variability in herbivore food sources was reduced overall.

1004 Despite similarities in  $\delta^{13}\text{C}$ , a comparatively large range of  $\delta^{15}\text{N}$  values are shown within and  
1005 between different species, however (from 2.3‰ to 6.0‰). This likely reflect different feeding  
1006 behaviors within this environment and, through this, implies local environmental variability in  
1007  $\delta^{15}\text{N}$ . Multiple factors influence nitrogen isotope values in soils and plants and, along with an  
1008 animal's physiology, can lead to isotopic diversity in animals otherwise occupying the same  
1009 broader trophic positions (Sponheimer et al., 2003; Szpak, 2014). Bone collagen  $\delta^{15}\text{N}$  of large  
1010 herbivores thus reflects both isotopic variability within local plant communities (which in the  
1011 past may reflect very different environmental conditions than today) and differences in dietary  
1012 niche and feeding behavior, the latter of which relates to both the types of plants/plant  
1013 component consumed (in terms of its isotopic ratio), as well as their nutritional content and  
1014 digestibility. The range of  $\delta^{15}\text{N}$  values observed between the different herbivore species at Abri  
1015 du Maras is evidence for differences in feeding behaviors between taxa. While niche  
1016 partitioning is commonly seen in other isotope paleoecological studies of herbivores in Western  
1017 Europe (see reviews in Bocherens, 2003; Drucker, 2022), the data from Abri du Maras  
1018 highlights that niche feeding behaviors and resource partitioning varied throughout different  
1019 phases of MIS 3, as well as geographically (e.g., Drucker, 2022; Schwartz-Narbonne et al.,  
1020 2019). This emphasizes the need to recognize plastic and/or non-analogous behaviors (and the  
1021 role of isotope analyses in revealing these) when considering the non-analogous animal and  
1022 plant communities of MIS 3 in northern Europe. In the case of Abri du Maras, given that these  
1023 differences are far less apparent in  $\delta^{13}\text{C}$  than  $\delta^{15}\text{N}$ , the value of combining these two isotopic  
1024 systems in reconstructing Late Pleistocene herbivore feeding behaviors in particular is also  
1025 highlighted. Finally, another factor that is not often considered alongside dietary isotopic data  
1026 in studies of faunal paleoecology but could play a part in the large range of nitrogen isotope

1027 values observed in this study could be differences in the habitat use/spatial ecology of different  
1028 individuals, different species and through time, in this region.

1029

#### 1030 *4.3. Evidence for interspecific differences in spatial ecology*

1031 While more than half of the samples (group 1 = 12/19, across all species and both levels) have  
1032  $\delta^{34}\text{S}$  consistent with anticipated local environmental values (Fig. 6; SOM Fig. S4), six of the  
1033 remaining seven (group 2) have lower  $\delta^{34}\text{S}$  values and therefore may have spent a proportion  
1034 of their lives in a more remote region, and possibly further inland (e.g., along the Rhône Valley  
1035 where values  $\sim 3\text{‰}$  can be found). In addition to highlighting potential differences in faunal  
1036 geographical range, this may also indicate that the resource catchment for the site (i.e., areas  
1037 from which hominins using the site took prey) went beyond the immediate locale of the site. A  
1038 further individual, the single *Rangifer* individual from level 4.2 (M10-121), displayed a far  
1039 lower value than all other samples analyzed, with a value of  $0.0\text{‰}$ . This may hint at a very  
1040 different biogeographical range for this earlier individual compared to the individuals sampled  
1041 from level 4.1, perhaps far north of the Ardèche region. Indeed, the strontium isotope data from  
1042 this same individual (see Section 4.4) support this as the likely explanation.

1043 Although two groups are evident in the sulphur isotope data, and the majority do align with  
1044 predicted local values, it must be borne in mind that sulphur isotope variability in this region  
1045 in the Late Pleistocene may have been very different compared to more recent periods and  
1046 could have incorporated lower (or higher) overall environmental  $\delta^{34}\text{S}$ . For example, southern  
1047 France is a region heavily exposed to dust aerosol deposition from the Sahara, one of the main  
1048 drivers of the  $\delta^{34}\text{S}$  isoscape, leading to  $^{34}\text{S}$  enrichment in the environment (Bataille et al., 2021).  
1049 The lower values observed for group 2 could be due to differences in dust deposal rates between  
1050 the Late Pleistocene and more recent periods as the most recently published sulphur isoscape  
1051 was established using more recent samples from the Mesolithic to the 20<sup>th</sup> century (Bataille et

1052 al., 2021). A strong correspondence between sulphur isotope values of bone collagen and  
1053 environmental conditions (in particular, temperature or the extent of permafrost) has also been  
1054 highlighted by other studies (Drucker et al., 2011; Reade et al., 2020), suggesting that  
1055 environmental  $\delta^{34}\text{S}$  not only varies spatially but can vary temporally at the same location. No  
1056 clear trend in  $\delta^{34}\text{S}$  was observed through time between level 4.1 and level 4.2 at Abri du Maras  
1057 and differences observed between animals therefore likely do reflect relative differences in  
1058 individual biogeography. However, differences in the presence and extent of permafrost across  
1059 this mountainous region in the past, or other environmental variables, may have produced a  
1060 more varied sulphur isoscape compared to the present day that could encompass all the values  
1061 in this study. While there may be relative trends, including two statistically-distinguishable  
1062 groups (including a larger group of ungulates of all taxa matching the local predicted values)  
1063 and an individual reindeer with a distinct  $\delta^{34}\text{S}$  value compared to all other individuals, given  
1064 uncertainties surrounding the Late Pleistocene sulphur isoscape these patterns are difficult to  
1065 relate to specific geographical areas and in order to explore the biogeography of species more  
1066 closely (particularly *Rangifer*), strontium isotope data are required.

1067

#### 1068 *4.4. Rangifer migratory behavior at Abri du Maras*

1069 Evidence for plasticity in behavior of *Rangifer* between levels 4.1 and 4.2 The agreement in  
1070 strontium isotope values in the earliest forming parts of the second molar for the three *Rangifer*  
1071 from level 4.1 points to a period spent on a similar lithology to one another during the middle  
1072 of the first summer of life ( $\sim 0.709$ ), consistent with bioavailable strontium isotope values found  
1073 within  $\sim 50$  km of the site (including areas on eastern side of the Rhône Valley, and slightly  
1074 further north; SOM Fig. S7). This may be consistent with the calving grounds and summer  
1075 range for the *Rangifer* in level 4.1 being relatively close to the site, in the eastern part of the  
1076 Rhône Valley or even the Prealps area. Strontium isotope ratios from the later forming parts of

1077 the second molar (corresponding with the first winter of life) of the three individuals from level  
1078 4.1, and values from the majority of their third molars (largely forming in the second year of  
1079 life), are again similar to one another—albeit with a greater intra-tooth variation in the third  
1080 molar between these three individuals compared to the second molar. This is consistent with  
1081 modern ecological observations and experimental isotope studies on modern herds which show  
1082 increased dispersals across the herd range during in the second half of the first year of life, and  
1083 into the second year of an animal’s life (Britton et al., 2009; Britton, 2010). However, despite  
1084 slight intra-tooth variation, values do not deviate considerably or outside of the range of  
1085 bioavailable strontium within ~50 km of the site and, significantly, do not demonstrate any  
1086 clear seasonally-cyclical trend in the second and/or third molar.

1087 With the exception of a fidelity to calving ground (and thus summer range during the first  
1088 months of life), the data from level 4.1 *Rangifer* do not suggest regular, targeted seasonal  
1089 migrations during this period. Potential winter and summer ranges identified from the samples  
1090 closest to the enamel-root junction in both the M<sub>2</sub> and the M<sub>3</sub> can be found in the vicinity of  
1091 Abri du Maras and show a substantial overlap and continuity. This range may also have  
1092 incorporated areas to the east, towards the Prealps, or to the south towards the Mediterranean,  
1093 although it should be noted that (given the sea-spray effect) the absence of  $\delta^{34}\text{S}$  values greater  
1094 than 6‰ may indicate the latter is unlikely. In modern caribou populations, sedentary behavior  
1095 is observed in the forest and mountain ecotypes (Festa-Bianchet et al., 2011). However, while  
1096 modern sedentary caribou do not undertake migrations, they may utilize fairly large home  
1097 ranges exceeding 1400 km<sup>2</sup>, especially where human environmental disturbance is low (Wilson  
1098 et al., 2019). At Abri du Maras, a non-migratory ecotype, equivalent to the modern forest  
1099 ecotype would be consistent with the charcoal analysis in level 4.1, the only level yielding an  
1100 association of *Betula* and *Pinus*, showing that the environment at the time, was probably humid  
1101 with open forest or forest groves (Daujeard et al., 2019; Moncel et al., 2021). The  $\delta^{13}\text{C}$  values

1102 from the reindeer and other cervids in this study (see section 4.2), however, make it unlikely  
1103 that this contemporary woodland would have been extensive (i.e. there is no ‘canopy effect’).  
1104 The strontium isotope values from the single *Equus* sampled from this level and the associated  
1105 assignment maps are also consistent with living in the region close to the site, at least during  
1106 the period of formation of this tooth, and may indicate both these species may have been  
1107 regionally available during much of the year during this later phase of site occupation.

1108 In comparison to the individuals from level 4.1, the intra-tooth strontium isotope profile of the  
1109 individual from level 4.2 demonstrates a strong seasonal variability (from lower values to  
1110 higher values, before a return to lower values). While values in the latest forming parts of the  
1111 third molar (SOM Fig. S9; *Rangifer* M10-121) do overlap with local biosphere values (and  
1112 with the values measured in the three *Rangifer* from level 4.1), the values from earlier phases  
1113 in this individual’s life are much higher, particularly in the latest forming parts of the second  
1114 molar. The complete separation between potential summer and winter ranges inferred from the  
1115 spatial assignment strongly suggests a migratory behavior. While the potential summer range  
1116 is very similar to the range used by the individuals from level 4.1, incorporating the area  
1117 immediately surrounding Abri du Maras, the *Rangifer* from level 4.2 occupied winter areas  
1118 distinct from the region surrounding the site and completely different from the *Rangifer* from  
1119 level 4.1. Intra-tooth values closest to the enamel-root junction in the M<sub>2</sub> of this individual are  
1120 instead consistent with long distance movements between the northern and the southern part of  
1121 the Rhône valley, or east-west movements, as bioavailable values matching those within the  
1122 teeth can be found only in excess of 150-200 km from the site. Even areas detected further  
1123 away, in the southwest France, could be considered as potential winter range habitats, as these  
1124 are still within the range of distances traveled by modern migratory caribou populations. The  
1125 distinct sulphur isotope values in the bone collagen of this individual, compared to other

1126 herbivores analyzed from the site supports the idea of a distinct total range size, incorporating,  
1127 perhaps a larger and more (isotopically) diverse area than any of the other animals.

1128

1129 Implications for understanding site and resource use at Abri du Maras These findings provide  
1130 tentative evidence of differences in ranging behavior in *Rangifer* in the Rhône Valley during  
1131 MIS 3, and have implications for our understanding of faunal paleoecology and exploitation at  
1132 Abri du Maras. The data from level 4.2 and 4.1 infer that both migratory reindeer and less  
1133 mobile/sedentary ecotypes of reindeer could have been found in Late Pleistocene Europe at  
1134 this time and/or that this behavior was plastic over time. This was also determined to be the  
1135 case at Jonzac, where *Rangifer* in Quina Mousterian levels ( $73 \pm 7$  ka) were revealed to be  
1136 migratory using strontium isotope analysis, but that *Rangifer* from Denticulate Mousterian  
1137 levels ( $56 \pm 3$  ka) were likely non-migratory (Britton et al., 2011; Britton, 2010; Britton, 2018).  
1138 If the *Rangifer* were indeed non-migratory in level 4.1 or undertook only very restricted  
1139 seasonal movements over a small home range, this may suggest that *Rangifer*—like the  
1140 *Equus*—may have been a year-round local resource at that time in the Rhône Valley. However,  
1141 the zooarchaeological evidence from this level suggests they were not exploited all year round  
1142 and instead were hunted exclusively in autumn-winter (Daujeard et al., 2019). This may be  
1143 consistent with seasonally restricted use of the site by Neanderthals during the accumulation  
1144 of deposits in level 4.1. Indeed, a subsistence base centred on strongly seasonal movements has  
1145 been hypothesized for this region more broadly (Daujeard et al., 2012). Targeted autumn-  
1146 winter hunting may also be consistent with the deliberate selection of this prey taxa only during  
1147 peak condition. Autumn is a period where female and young reindeer/caribou in particular are  
1148 in good physical condition (Miller, 1974), with typically higher average body masses (and body  
1149 fat percentages) in autumn than in spring and summer (Gerhart et al., 1996; Couturier et al.,  
1150 2009). Autumn may also have been the optimal period to hunt reindeer for their winter coats

1151 (i.e., for clothing; e.g., Binford, 1978; Stenton, 1991; Issenman, 2011). Thus, in the presence  
1152 of other available local resources—such as horse—reindeer may not have been an appealing  
1153 option at other points of the year. In contrast, zooarchaeological data from level 4.2 point to a  
1154 more mixed profile, comprising multiple ungulate species without a strong seasonality. Here,  
1155 intra-tooth samples from a single *Rangifer* indicate a seasonally-repeating mobility pattern,  
1156 indicating they may have only been found in the immediate region at certain points of the year  
1157 (i.e., summer). The investigation of *Rangifer* exploitation, and particularly the seasonality of  
1158 that exploitation at other sites surrounding Abri du Maras and those sites on the eastern side of  
1159 the Rhône Valley, may allow the further exploration of the relationship between Neanderthal  
1160 landscape use and the seasonal biogeography of reindeer.

1161 In addition to the strontium isotope data from the *Rangifer* samples, the results of other analyses  
1162 undertaken here also have implications for our understanding of Neanderthal activities at the  
1163 site. The presence of two statistically significant groups revealed by hierarchical cluster  
1164 analysis of sulphur isotope data may suggest that Neanderthals at the site were extracting their  
1165 prey from at least two isotopically-distinct areas (in terms of  $\delta^{34}\text{S}$ ), including locally as well as  
1166 perhaps further inland along the Rhône valley. This hints at the potential for isotope  
1167 zooarchaeological approaches to reveal such aspects of landscape use in subsistence behaviors.  
1168 However, such a pattern could also be produced through the hunting of animals close to site  
1169 that had more extensive ranges than others, and thus incorporated a more diverse range of  $\delta^{34}\text{S}$   
1170 values. Further work, incorporating strontium isotope analysis of multiple species would be  
1171 required to characterize this, ideally in comparison with similar data from other archaeological  
1172 sites in the region. Comparison with data derived from fauna from non-anthropogenic contexts  
1173 (e.g., natural accumulations) could be helpful in characterizing variability due to differences in  
1174 faunal spatial behaviors from variability due to differences in human hunting ranges.



1175 Finally, the oxygen isotope data generated from level 4.2 suggest that, in this phase at least, the  
1176 climate was comparatively mild for the period, albeit with a pronounced seasonality, with  
1177 higher and lower seasonal extremes in temperature than experienced in the region today. On  
1178 the basis of zooarchaeological data, occupations in level 4.2 at Abri du Maras were restricted to  
1179 spring-summer, and to autumn (Vignes, 2021). While sample size, and the lack of comparative  
1180 data from level 4.1 necessitates caution in data interpretation, this may indicate a preference  
1181 for other sites and/or areas during cooler winter months. The collection of similar data from  
1182 other sites in the region, combined with site-seasonality data, would help us to better understand  
1183 the relationship between the seasonal climate and the seasonal use of sites and resources by  
1184 Neanderthals in the Rhône valley during MIS 3.

1185

## 1186 **5. Conclusions**

1187 The data presented in this paper provide evidence for both environmental conditions during  
1188 MIS 3 in southeastern France, but also for the ecology of key species that Neanderthal groups  
1189 depended upon. Oxygen isotope analysis of horse teeth from level 4.2 evidence mild climatic  
1190 conditions, albeit with a seasonality more pronounced than today. Carbon and nitrogen isotope  
1191 analysis of bone collagen suggest different niche feeding behaviors amongst herbivore species  
1192 at the site, mostly expressed through variability in  $\delta^{15}\text{N}$ . Carbon isotope data from *Rangifer* are  
1193 similar to other taxa studied, which is unusually for Late Pleistocene case studies, particular  
1194 from later (colder) phases of MIS 3, which indicate that lichens were not making up a  
1195 significant component of *Rangifer* diet in this area at this time. This may also therefore provide  
1196 indirect evidence for a lack of contemporary lichen cover, which could be consistent with  
1197 milder and also moister climatic conditions, notably during level 4.1. Conversely, the  $\delta^{13}\text{C}$   
1198 values from the reindeer and other cervids in this study, however, do not indicate woodland  
1199 was extensive (i.e. there is no ‘canopy effect’) and may have been restricted to groves as part

1200 of a moasic environment, which is in agreement with the limited contemporary  
1201 paleoenvironmental data (Daujeard et al., 2019). The strontium and sulphur isotope data from  
1202 *Rangifer* provide direct evidence for both migratory and non-migratory ecotypes at the site,  
1203 correlating with differences in seasonal exploitation between the two levels. While  
1204 environmental strontium values surrounding Abri du Maras are most consistent with those  
1205 observed in the winter-forming parts of *Rangifer* teeth in level 4.1, environmental values  
1206 matching other periods of the level 4.1 individuals' lives can be found within ~50 km of the  
1207 site. Thus, in this part of the Rhône Valley, reindeer may have represented a year-round  
1208 resource. In light of this, we can infer perhaps that the targeted hunting of reindeer in autumn  
1209 during this phase of site use may be consistent with seasonally-restricted use of the site by  
1210 Neanderthals and/or the selection of *Rangifer* in prime condition rather than their seasonally-  
1211 restricted availability. In contrast, a single *Rangifer* sampled from level 4.2 demonstrates a very  
1212 different trend in intra-tooth strontium and bulk bone collagen sulphur isotope data, suggesting  
1213 a distinct biogeographical range incorporating other regions and also different seasonal  
1214 mobility. Data from this individual suggests reindeer may only have been found in the area  
1215 seasonally (in spring/summer). Thus, the integration of isotope data with the zooarchaeological  
1216 analyses and other paleoenvironmental proxy data at Abri du Maras evidence not only diversity  
1217 in animal behavior and ecology during MIS 3, but also demonstrate the inter-relationships  
1218 between the dynamic ecosystem and Neanderthal land use and hunting strategies. The  
1219 determination of seasonality of site use and hunting at different archaeological sites in the  
1220 eastern and western areas of the southern Rhône Valley, combined with further analysis of  
1221 faunal biogeography and seasonal paleoenvironmental conditions, may help to further  
1222 illuminate these relationships.

1223

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1729 **Figure captions**

1730 **Figure 1.** Elevation map of the Rhône Valley (southeast France) showing the location of Abri  
1731 du Maras and other key Middle Paleolithic sites in the region.

1732

1733 **Figure 2.** Strontium isoscape of the Rhône Valley (based on Bataille et al., 2020).

1734

1735 **Figure 3.** Measured oxygen isotope signal ( $\delta^{18}\text{O}_{\text{enamel}}$ ; blue dots) from Abri du Maras for two  
1736 *Equus* teeth (both lower second premolars, Maras 687 and Maras 767) from level 4.2, and  
1737 inverse modelled isotopic input (grey line) with 95% confidence interval (grey shaded area).  
1738 Abbreviation: VSMOW = Vienna standard mean ocean water.

1739

1740 **Figure 4.** Estimated mean annual, summer and winter oxygen isotope values of drinking water  
1741 ( $\delta^{18}\text{O}_{\text{dw}}$ ) and estimated paleotemperatures for the study site, calculated from archaeological  
1742  $\delta^{18}\text{O}_{\text{enamel}}$  data, with associated compound errors shown as error bars. Lines represent modern  
1743  $\delta^{18}\text{O}_{\text{precip}}$  data (left) and modern temperatures (right) for the area of the study site, with  
1744 associated standard deviations shown as shaded ribbons.  $\delta^{18}\text{O}_{\text{precip}}$  data was obtained from the  
1745 OIPC (Bowen, 2022; Bowen and Revenaugh, 2003; Bowen et al., 2005) and temperature data  
1746 from the ClimateEU model and averaged for 1981–2009 (Marchi et al., 2020).

1747

1748 **Figure 5.** Bivariate plot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of bone collagen from *Bison*, *Cervus elaphus*, *Equus*,  
1749 *Rangifer* and *Megaloceros* from Abri du Maras (levels 4.1 and 4.2). Analytical error ( $\pm 1$  SD)  
1750 is also shown.

1751

1752 **Figure 6.** Stable sulphur isotope data of bone collagen from *Bison*, *Cervus elaphus*, *Equus*,  
1753 *Rangifer* and *Megaloceros* from Abri du Maras (levels 4.1 and 4.2). Analytical error ( $\pm 1$  SD)  
1754 is shown.

1755  
1756 **Figure 7.** Sequential strontium isotope data from incrementally-sampled dental enamel of  
1757 second and third molars from four *Rangifer* from Abri du Maras. The mean strontium isotope  
1758 value of dentine sampled is shown ( $\pm 1$  SD) as well as the range of strontium values observed  
1759 in the third molar of a *Equus* from the site. Analytical error is within the data points.  
1760 Abbreviation: ERJ = enamel-root junction.

1761  
1762 **Figure 8.** Spatial assignment of strontium isotope data from the enamel sampled closest to the  
1763 enamel-root junction (ERJ) of the second and third molars of four *Rangifer* (level 4.1 and level  
1764 4.2) from Abri du Maras, corresponding broadly to the potential ranges use by the individuals  
1765 in winter and summer respectively, based on anticipated enamel mineralization times. Potential  
1766 seasonal areas correspond to the minimal areas where each sample have 80% chance to  
1767 originate, and were assessed using the assignR package in R (Ma et al., 2020). Assignments of  
1768 the samples from close to the occlusal surface and close to the ERJ of the M<sub>3</sub> from one *Equus*  
1769 are also provided as a reference for an expected local individual.

1770  
1771 **Figure 9.** Summer, winter and mean annual  $\delta^{18}\text{O}$  data points from Abri du Maras (ADM;  
1772 Marine Isotope Stage [MIS] 3) level 4.2 exhibit similar values to previously published  $\delta^{18}\text{O}$   
1773 horse enamel data from MIS 3 deposits in southern France (Combe Grenal [CG], La Baume  
1774 Gigny [BG]), with relatively high summer values and more pronounced seasonality. Values  
1775 are substantially higher than those reported at the much older site of Payre (MIS 6 and MIS 7–  
1776 8). Individual data points and error bars represent individual measurements and one standard

1777 deviation of replicate measurements (ADM, CG, BG) or Layer means and standard deviations  
1778 around the mean (Payre, number of teeth per mean are 3, 5 and 6 for levels D, F and G,  
1779 respectively). Comparative data obtained from Fabre et al. (2011; for BG), Richards et al.  
1780 (2017; for CG) and Ecker et al. (2013; for Payre). Note that the large spread in CG data may  
1781 be related to the large number of different layers representing MIS 3 at the site, the sampling  
1782 of unidentified tooth fragments of differing lengths and the relatively uncertain chronology of  
1783 the site. Abbreviation: VSMOW = Vienna standard mean ocean water.