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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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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 ± 2 to 42 ± 3 ka; level 4.1 = 46 ± 3 to 40 ± 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}C and ^{12}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 C_3 and 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}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 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 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}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}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}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}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}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}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}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}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}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 ~ 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}Sr to ^{86}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 (CO_3) and phosphate (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}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 ± 3 ka and 40 ± 3 ka and level 4.2 yielding dates ranging between 55 ± 2 to 42 ± 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 ± 3 and 42 ± 6 , which together with an infrared
415 stimulated luminescence (IRSL) age of 46 ± 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 (Vettese
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 ± 3 to 40 ± 3 ka) and level 4.2 (55 ± 2 to 42 ± 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 ± 31 ppm. Analytical
644 precision was ± 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‰
697 in July and -9.9‰ 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 ± 300 and N:S = 200 ± 100 ; Nehlich and Richards, 2009).

721 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (± 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‰ [$n = 4$]; *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 (± 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 M₂ and M₃ 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 ± 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 ± 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 ± 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 ± 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 M₂ and the M₃, 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 M₃ 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}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}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}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}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}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‰ . 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}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 20th 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 (~ 0.709), consistent with bioavailable strontium isotope values found
1073 within ~ 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 M₂ and the M₃ 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 km², 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 M₂ 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 ± 7 ka) were revealed to be
1136 migratory using strontium isotope analysis, but that *Rangifer* from Denticulate Mousterian
1137 levels (56 ± 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

1224 **References**

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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 (± 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 (± 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 (± 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 M₃ 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.