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# Temperature and precipitation regime in LGM human refugia of southwestern Europe inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of large mammal remains

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1 Temperature and precipitation regime in LGM human refugia of southwestern  
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18 Abstract – The climate shift of the Last Glacial Maximum (LGM) strongly impacted the  
19 vegetation cover and related trophic chains of western Europe. Harsh, cold and dry conditions  
20 then prevailed in most regions, strongly impacting migrations and survival of human beings.  
21 Nonetheless, environments suitable for mammalian fauna to survive persisted in SW Europe  
22 thus providing refugia for hunters. Tooth enamel from large herbivorous mammal remains  
23 from archeological sites located in southwest France and Spain were analyzed for their stable  
24 carbon and oxygen isotope compositions for documenting paleotemperatures and  
25 paleoprecipitations. These sites were occupied by humans between 25 ky and 16 ky. Skeletal  
26 remains of Cervidae, Equidae and Caprinae suggest colder and drier conditions relative to  
27 present-day. Paleoprecipitations were reconstructed from a modern-based transfer function  
28 using  $\delta^{13}\text{C}$ -values of apatite carbonate, then corrected for the low atmospheric  $\text{pCO}_2$  value of  
29 the LGM. They ranged from  $\approx 250 \text{ mm yr}^{-1}$  on the Mediterranean façade, to  $\approx 550 \text{ mm yr}^{-1}$  on  
30 the Atlantic side. Setting the  $\delta^{18}\text{O}$ -value of the northeastern North Atlantic LGM-surface  
31 water to  $+0.8\text{‰}$ , based on Biscay Golf marine core studies, mean air temperatures inferred  
32 from  $^{18}\text{O}$ -data in apatite calcite were close to  $14\text{--}15^\circ\text{C}$  (Mediterranean) and  $6^\circ\text{C}$  to  $10^\circ\text{C}$   
33 (Atlantic), i.e., about  $4\text{--}5^\circ\text{C}$  and  $5\text{--}8^\circ\text{C}$  higher than pre-industrial temperatures, respectively.  
34 The two areas thus define distinct clusters of air temperatures and precipitation regimes with  
35 strong negative offsets vs the Present. These isotopically-reconstructed climate conditions  
36 indicate a strong control from proximal surface ocean/marine waters, in particular of mean  
37 annual air temperatures.

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41 Keywords: Last Glacial; temperature; precipitation; stable isotopes; apatite; mammals;

42 Western Europe

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45 1. Introduction

46 The Last Glacial, also named Weichselian in Northwest Europe, covers a time period  
47 from 115 ka to 11.7 ka. It was characterized by rapid, large amplitude climatic fluctuations  
48 recorded in the Greenland ice cores (Dansgaard et al., 1993; Grootes et al., 1993; NGRIP  
49 members, 2004; Rasmussen et al., 2014) and North Atlantic marine sediments (Heinrich,  
50 1988; Bond et al., 1992; Sanchez Goñi et al., 2008). During this period, global climate  
51 conditions oscillated between stadial and interstadial conditions, sometimes punctuated by  
52 abrupt climate events known as Heinrich events. These highly contrasted climate regimes  
53 influenced faunal communities, including humans, through the development of new migration  
54 pathways, allopatric speciation in refugia, and enhanced rates of extinction during the coldest  
55 and driest stages of the Last Glacial.

56 The Last Glacial Maximum (LGM), conventionally dated between 23 and 19 ka ago  
57 (MARGO, 2009; Mix et al., 2001), is defined as the most recent period of maximum global  
58 ice volume (Mix et al., 2001). It featured lowered greenhouse gas (CH<sub>4</sub>, CO<sub>2</sub>) concentrations,  
59 a mean sea level ~120 m lower than today and generally cold and dry climatic conditions  
60 resulting in significant modifications of both floral and faunal assemblages (Lister, 2004;  
61 Sommer and Nadachowski, 2006; Clark et al., 2009; Binney et al., 2017; Cao et al., 2019).  
62 During this interval, and in response to global tropospheric cooling, the Northern Hemisphere  
63 experienced a southward expansion of continental ice sheets, which reached as far as 52°N in  
64 western Europe. Various models suggest a decrease in global mean surface air temperatures  
65 during the LGM ranging from 4°C to 10°C vs pre-industrial (PI) climatic conditions (Masson-  
66 Delmotte et al., 2006; Schneider von Deimling et al., 2006; Annan and Hargreaves, 2013).  
67 The main causes of this decrease are thought to be the combined effect of lower atmospheric

68 CO<sub>2</sub> values (with a partial pressure as low as 190 ppm; Bouttes et al., 2011) and ice-sheet  
69 forcing, which would jointly account for about 75% of the total LGM cooling (Schneider von  
70 Deimling et al., 2006). Additional cooling effects are related to changes in atmospheric dust  
71 content and vegetation cover. In response to this maximal extent of continental ice (glaciers  
72 and ice caps), mean global sea level dropped by 120±10 m (Lambeck et al., 2014).

73 Faunal associations described in the archaeological sites of southwestern Europe are  
74 generally compatible with cold and dry, open environments, such as tundra and dry steppe,  
75 but there are important regional differences as suggested by Yravedra and Brugal (2005) who  
76 defined several biogeographic zones in southwest Europe. During the LGM, the vegetation in  
77 Europe was characterized by an expansion of tundra and steppe. In Southwestern France and  
78 in the northern part of the Iberian Peninsula, cold temperate fauna (horse, reindeer, ibex)  
79 dominated vertebrate assemblages during the LGM, but co-existed with cold-adapted fauna  
80 such as mammoth, woolly rhinoceros and reindeer (Yravedra and Brugal, 2005; Sommer and  
81 Nadachowski, 2006; Álvarez-Lao and García, 2011; Álvarez-Lao and García, 2011). Recent  
82 models suggest that the most suitable habitats for humans during the LGM were concentrated  
83 in southwest France and the Iberian Peninsula, excluding the interiors, as also demonstrated  
84 by the distribution of archaeological sites (e.g., Ludwig et al., 2018; Burke et al., 2017; Wren  
85 and Burke, 2019). Modern humans who had arrived in Europe ≈ 45,000 years ago survived  
86 the LGM in the SW Europe refugia (Fu et al., 2016). A post-ice age expansion followed, with  
87 their descendants spreading out in Iberia, after ≈ 19,000 years ago, then defining the  
88 Magdalenian culture (Fu et al., 2016).

89 The LGM in Southwest Europe illustrates a major faunal and vegetation partitioning in  
90 biogeographic provinces, which constrained the human strategy of land occupation. Whether  
91 Mean Annual Precipitation (MAP) or Mean Annual Air Temperature (MAAT) were limiting  
92 factors in this strategy remains to be fully elucidated. In this study, special attention is paid to

93 sites from coastal areas under the influence of the Atlantic Ocean or the Mediterranean Sea.  
94 They represent three distinct biogeographic zones, following the classification of Yravedra  
95 and Brugal (2005) for southwestern Europe: southwest France (zone VI), Cantabria/Asturias  
96 (zone IV) and the Mediterranean coast (zone IIIa).

97 MAAT and MAP may be reconstructed using oxygen and carbon isotope compositions of  
98 the apatite carbonate from vertebrate skeletons. As highlighted by Pederzani and Britton  
99 (2019), in particular the oxygen isotope analyses of skeletal remains ( $\delta^{18}\text{O}$ ) are a powerful  
100 tool for exploring past human-environment interactions as well as to reconstruct paleoclimatic  
101 parameters. An approach not yet used for documenting the LGM refugia of SW Europe will  
102 fill this gap using large mammal remains (teeth) from the above defined human occupation  
103 areas. We also intend to demonstrate that carbon isotope ( $\delta^{13}\text{C}$ ) from such remains may  
104 inform specifically on paleoprecipitation.

105 The basic principles to interpret  $\delta^{13}\text{C}$  as MAP and  $\delta^{18}\text{O}$  as MAAT are summarized as  
106 follows:

107 The most common strategy consists in estimating air temperature from the oxygen isotope  
108 composition of the carbonate or the phosphate groups of the tooth enamel of the vertebrate  
109 apatite. During tooth growth, the oxygen isotope composition of apatite carbonate ( $\delta^{18}\text{O}_c$ )  
110 records body temperature (a near constant close to  $37^\circ\text{C}$ ) and body water composition  
111 ( $\delta^{18}\text{O}_{\text{bw}}$ ) (Koch et al., 1989; Bryant et al., 1996; Chenery et al., 2012). The oxygen isotope  
112 composition of body water reflects that of meteoric water (Bryant and Froelich, 1995; Kohn,  
113 1996; Langlois et al., 2003) and depends principally on the composition of oceanic moisture  
114 source(s), the length and precipitation history of humid air mass trajectories,  
115 evapotranspirative processes along these trajectories, air temperature (MAAT) during  
116 precipitation, the relative amount of precipitation and altitude relative to sea level (Dansgaard,  
117 1964; Rozanski et al., 1992; Fricke and O'Neil, 1999). At mid- and high-latitudes (tropical

118 bands excluded), MAAT of areas close to oceanic moisture sources are linearly related to the  
119 weighted mean annual  $\delta^{18}\text{O}_{\text{mw}}$  (Dansgaard, 1964; Yurtsever, 1975; von Grafenstein et al.,  
120 1996; Fricke and O'Neil, 1999; Skrzypek et al., 2011; Lécuyer, 2013). This property of the  
121 water cycle has already been used for the reconstruction of past air temperatures from the  
122 oxygen isotope composition of vertebrate tooth enamel from large mammals (e.g., Ayliffe et  
123 al., 1992; Bryant et al., 1994; Tütken et al., 2007; Bernard et al., 2009; Fabre et al., 2011).

124 The reconstruction of MAP from the carbon isotope composition of apatite carbonate was  
125 made in several steps. In the first step, the  $\delta^{13}\text{C}$  values of plants ( $\delta^{13}\text{C}_{\text{pl}}$ ) can be estimated from  
126 tooth enamel carbonate ( $\delta^{13}\text{C}_{\text{carb}}$ ) taking into account the isotopic fractionation that takes  
127 place between diet-derived carbon ingested by the herbivores and the carbon mineralized as  
128 carbonate present in the apatite crystal lattice of their teeth (Tejada-Lara et al., 2018). In a  
129 second step, MAP values are calculated using  $\delta^{13}\text{C}_{\text{pl}}$  and a transfer function based on plant  
130 leaf discrimination factors (Kohn, 2010) that may be estimated in the case of animal diets  
131 strictly based on Calvin Cycle (C3) plants. Atmospheric  $\text{pCO}_2$ -changes and reduced biomass  
132 production by plants during glacials (Gerhart and Ward, 2010) may have led to some global  
133 relative increase in the abundance of C4 plants, thus to some possible dietary changes, but  
134 C3/C4 plant ratios within given biomes remained broadly stable if biome distributions  
135 differed (Ehleringer, 2005). Moreover, C4 plants amount to only about 1% in the European  
136 vegetation (Collins and Jones 1985). They are slightly more abundant in herb-dominated  
137 biomes (see their taxonomic distribution in Pyankov et al. (2010). Now, if such biomes  
138 experienced a ~ 10% relative increase over other biomes during the LGM (Binney et al.,  
139 2017), their content in C4 plants is unlikely to have increased as these plants are strongly  
140 sensitive to temperatures (Pyankov et al., 2010), adding to the equivocal response of the  
141 C4/C3 plant ratio of Poaceae, one of their major components, to  $\text{pCO}_2$  changes (Wand et al.,

142 1999). One may thus assume a nearly exclusive C3-plant vegetation during the LGM interval  
143 whatever the changes in biome distribution.

144 The goal of the present study is thus to build paleoclimate reconstructions for several  
145 archaeological sites of the LGM (Figure 1) using the above isotopic approaches. The specific  
146 sampled sites are Laugerie-Haute (Dordogne, France), El Cierro (Asturias Province), Hornos  
147 de la Peña, El Pendo and El Ruso (Cantabria Province), Nerja (Málaga Province) and  
148 Malladetes (Valencia Province). The present study provides the first quantitative information  
149 about LGM-MAAT and -MAP ranges of these sites. They will be discussed in the light of  
150 proxies based on pollen assemblages (continental climate) and foraminiferal- $\delta^{18}\text{O}$  data  
151 (marine moisture sources), climatic model outputs, past topography, as well as in that of  
152 reconstructed vegetation cover and faunal communities.

153

## 154 2. Archaeological sites and sample collection

### 155 2.1. Description of the sampled archaeological sites

156 *Laugerie Haute Est* (LHE) forms part of a much larger rock-shelter on the right bank of  
157 the Vézère river in the Dordogne region of France (Fig. 1). The shelter, which is about 30 m  
158 deep and 180 m long, is separated into two excavated sections (East and West) due to the  
159 presence of a house occupying the centre of the shelter. First discovered at the end of the 19th  
160 Century the site's stratigraphic integrity has come under close scrutiny (Texier, 2009;  
161 Delpech, 2012; Verpoorte et al., 2019). The occupation sequence of the site spans the  
162 Aurignacian and the Solutrean. For this study, level 4-8, attributed to Magdalenian II, level  
163 10-16 (F. Bordes collection) attributed to Magdalenian I and level 18-20, attributed to  
164 Magdalenian 0, were sampled. Biostratigraphically, levels attributed to Magdalenian I-III  
165 form a unit, with faunal assemblages dominated by reindeer, while the Magdalenian 0 level,  
166 which is dominated by horse, is distinct (Delpech, 2012). The Magdalenian levels are



167 bracketed by ages of ~ 23 and ~21 <sup>14</sup>C cal. kyr (Delpech, 2012) and can thus be assigned to  
168 the LGM. Four sites were sampled in northern Spain, including: El Ruso, Hornos de la Peña  
169 and El Pendo in Cantabria, and El Cierro in Asturias (Fig. 1). El Ruso is a small cave located  
170 about 6 km from the modern coastline, near El Pendo and El Juyo (unsampled). The cave  
171 contains a sequence of occupation that spans from the Mousterian to the Solutrean Level 3,  
172 the Upper Solutrean level sampled here overlies a Solutrean level (IV) dated 20–19 <sup>14</sup>C cal.  
173 kyr (Yravedra, 2010a).

174 At El Pendo level 4, the samples are labelled “level 4” and attributed to the Upper  
175 Solutrean. If this corresponds to level IV (Eschegaray excavations) this level is attributed to  
176 the Late Aurignacian, although it is intercalated between Gravettian and Magdalenian levels  
177 (Hoyos Gómez and Laville, 1982). Unfortunately, the stratigraphic integrity of this site is in  
178 some doubt (de los Terreros and Castanedo, 2010; Barquin, 2014). Consequently, results from  
179 this site must be interpreted with caution.

180 At Hornos de la Peña, we sampled level B. This level is dated 23–21 <sup>14</sup>C cal. kyr and is  
181 attributed to the Aurignacian in its lower part, and the Solutrean in its upper part (Breuil and  
182 Obermeier, 1912 cited in Tejero et al., 2008; Yravedra, 2010b). The faunal assemblage at  
183 Hornos de la Peña is dominated by horse (Tejero et al., 2008). At El Cierro (Asturias),  
184 another deeply stratified cave site excavated by several different teams over the years, a  
185 revised chronostratigraphy and several AMS dates are available (Alvarez-Fernandez et al.,  
186 2016). We sampled levels G (Magdalenian), G1 and H (Solutrean) which form part of the  
187 earliest occupation sequence of the cave. AMS dates obtained for these levels indicate that the  
188 site was occupied during the LGM (<sup>14</sup>C cal. ages of 20–19 kyr) (Alvarez-Fernandez et al.,  
189 2016).

190 Two sites on the Mediterranean seaboard of Spain were sampled: Nerja and  
191 Malladetes (aka Mallaetes) (Fig. 1). Nerja, the southernmost sample site, is a deeply stratified

192 cave located on the coastal plain of eastern Andalusia. The site contains one of the longest  
193 occupation sequences in Mediterranean Spain, spanning the Gravettian to the Copper Age  
194 (Aura Tortosa et al., 2006; Jordá Pardo and Aura Tortosa, 2008). Paleoclimate proxies and a  
195 large number of recently reviewed radiocarbon dates provide a robust chronostratigraphic  
196 frame for the sequence (Jordá Pardo and Aura Tortosa, 2008). Unit 8 (vestibule) was sampled  
197 for this study. This unit contains Solutrean material and is generally considered to date to the  
198 LGM, based on paleoclimate proxies and conventional and AMS radiocarbon dates yielding  
199  $^{14}\text{C}$  cal. ages comprised between 23 and 21 kyr (Vallejo et al., 2005; Aura Tortosa et al.,  
200 2006), although a much younger and possibly unrepresentative AMS date ( $\approx 14.4$   $^{14}\text{C}$  cal.  
201 kyr) has also been reported (Jordá Pardo and Aura Tortosa, 2008).

202 Malladetes (or Mallaetes) is located in the central Mediterranean region of Spain, in  
203 Valencia. The levels sampled for this study include levels 7 (entrada D), 8 and 9 (entrada D)  
204 which should be associated with the Gravettian (de la Peña Alonso, 2013). An AMS  $^{14}\text{C}$  cal.  
205 age of 30–26 kyr was obtained from modern human remains associated with unspecified  
206 Gravettian levels in sector E, likely corresponding to levels VII to XI (Forteza Perez and Jorda  
207 Cerda, 1976; Arsuaga et al., 2002), indicate that our samples probably predate the LGM and  
208 level 8 at Nerja (Fumanal and Dupré, 1983; Aura Tortosa et al., 2006).

209

## 210 2.2. Sample collection

211 The samples recovered from the seven archaeological sites described above (Table 1)  
212 include mammal remains assigned to Cervidae (*Cervus elaphus*, *Rangifer tarandus*), Equidae  
213 (*Equus* sp.) and Caprinae (*Capra pyreneica*, *Rupicapra rupicapra*, *Saiga tatarica*). The  
214 cervids (*Cervus elaphus*) and caprids (*Capra pyreneica*) were sampled as a priority, but  
215 wherever these taxa were poorly represented, we sampled alternate species including smaller

216 cervids and small bovids. At Laugerie Haute Est and Hornos de la Peña we sampled horse  
217 remains because of their abundance at both sites.

218

### 219 2.3. Habitat and diet of Cervidae, Equidae and Caprinae

220 *Cervus elaphus* (red deer) is a large mammal observed in semi-open habitats, often  
221 found in forest margins and clearings, while it also occupied open environments such as  
222 steppes during the Last Glacial (Straus, 1981; Bugalho and Milne, 2003). It tolerates a wide  
223 range of temperature, as long as the habitat is not too dry. Its diet is highly eclectic and  
224 seasonally variable, although it shows a 60-70% herbaceous source. *Cervus elaphus* mainly  
225 browses leaves, conifer needles, twigs, nuts, shoots and bark of trees in winter, and grazes  
226 more on grasses, herbs, ferns, mosses, mushrooms, sedges or even rushes, during the summer  
227 and intermediate seasons.

228 *Rangifer tarandus* (reindeer) lives in subarctic and arctic regions (taiga and tundra),  
229 however some sub-species such as *R. tarandus tarandus* (woodland caribou) occupy the  
230 boreal forests (Ihl and Klein, 2001; Thompson et al., 2015) In winter, reindeers mainly feed  
231 on lichens which they access by digging holes in the snow cover. In the mild seasons, their  
232 diet is mainly based on grasses, green leaves of shrubs, tree bark and sedges as well as tree  
233 shoots such as larch, willow and birch. Mushrooms are also consumed during the late summer  
234 and early autumn.

235 *Equus caballus* (horse) was widely distributed in Eurasia and the Americas during the  
236 late Pleistocene. Equids are adapted to open habitats and are found in steppe, tundra and taiga  
237 habitats, as well as in more temperate grasslands. They are non-selective grazers and tolerate  
238 a wide range of temperatures (Berger, 1986).

239 *Capra pyreneica* (ibex) is a montane species living exclusively in open environments  
240 with high relief (cliffs and stone ravines; pastures in spring) at altitudes ranging from about

241 500 m to about 3500 m as observed in the Alps (Villaret et al., 1997). Its diet is essentially  
242 composed of herbaceous plants.

243 *Rupicapra rupicapra* (chamois) feeds on herbs and lives in mountains meadows and  
244 on the edge of forests. Chamois are well-adapted to rough terrain and tolerate a large range of  
245 temperatures as low as -20°C in winter and up to 25°C in summer (Christie, 1967; La Morgia  
246 and Bassano, 2009) although they are actually distributed in a wide range of temperate  
247 conditions.

248 *Saiga tatarica* (Eurasian antelope) feeds on salt-coated herbs, some grasses (Poaceae),  
249 Euphorbiaceae and Artemisia. This antelope lives in hilly areas and is considered an indicator  
250 of a dry climate (steppe environment) with highly-seasonally contrasted temperatures  
251 (Bekenov et al., 1998).

252 Among these large mammals, obligate to semi-obligate drinkers are horse (strict  
253 obligate drinker), red deer (drinks large amounts of water during the warm season), reindeer  
254 (free water in summer, snow during the cold season) whilst semi-obligate to non-obligate  
255 drinkers are ibex, chamois and antelope that drink free water occasionally (Macdonald, 2006).

256

### 257 3. Sample preparation and isotopic analysis

258 The tooth samples were prepared and analyzed at the Stable Isotopes Laboratory of the  
259 Geotop research center (Université du Québec à Montréal). Prior to any treatment, tooth  
260 crowns were mechanically cleaned to remove any trace of remaining glue or altered hard  
261 tissues. They were then immersed in an ultrasonic bath in order to eliminate potential remains  
262 of sedimentary particles. From 10 mg to 20 mg of enamel powder samples were collected  
263 using a micro-drill equipped with a diamond-studded drill bit. Grooves were drilled  
264 perpendicularly to the tooth growth axis from the cervix to the apex of the tooth crown.

265 Following the protocol used by Vigeant et al. (2017), organic matter was removed from  
266 tooth enamel apatite by soaking an aliquot of the untreated sample in a 2% sodium  
267 hypochlorite (NaOCl) solution for 24 h. Then, the samples were rinsed with large amounts of  
268 water, then dried before being treated with 1 M acetic acid-Ca acetate buffer (pH = 4.75) for  
269 24h at 20°C to remove secondary carbonate phases (Bocherens et al., 1996), and finally  
270 washed with distilled water and dried at ambient temperature. For each sample, about 1 mg of  
271 enamel powder was analyzed for  $\delta^{13}\text{C}$ -values (‰ VPDB) and  $\delta^{18}\text{O}$ -values (‰VPDB) of the  
272 carbonate using a Micromass Isoprime™ isotopic ratio mass spectrometer operated in dual  
273 inlet mode and coupled to a Multicarb™ system. Overall analytical uncertainties ( $\pm 1\sigma$ ) for  
274  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  were close to 0.05‰ and 0.1‰, respectively, based on statistics from replicate  
275 measurement of samples, compared to  $\pm 0.02$  and  $\pm 0.03$ ‰, respectively, on reference  
276 carbonate materials (e.g., NBS 19, IAEA-603 and the home reference carbonate), thus  
277 suggesting some isotopic heterogeneity in the ground carbonate samples.

#### 278 4. Results 279

280 The dataset is characterized by  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values ranging respectively from -12.89‰  
281 to -8.93‰ (mean =  $-10.42 \pm 0.76$ ‰) and -8.65 to -0.14‰ (mean =  $-5.19 \pm 1.99$ ‰). An  
282 examination of data compiled in Table 1 reveals that they form two distinct clusters  
283 corresponding to sites located on the Atlantic side and along the Mediterranean coast (Figure  
284 1). As a first approach, pooling the taxa in each geographic cluster reveals that the  $\delta^{18}\text{O}$   
285 values of mammal remains from Nerja and Malladetes have much higher  $\delta^{18}\text{O}$  values (-  
286  $1.45 \pm 0.74$ ) than those ( $-6.03 \pm 0.94$ ) from the sites located on the Atlantic side (Table 1). The  
287 difference is not so striking for  $\delta^{13}\text{C}$  values which average  $-10.60 \pm 0.70$ ‰ in the Atlantic sites,  
288 i.e., slightly but significantly lower than that the mean value of Mediterranean sites, which is -  
289  $9.65 \pm 0.44$ ‰ (Welch t-test:  $p = 4.4 \times 10^{-7}$ ;  $H_0 = \text{means are equal}$ ).

290 Discrimination between the datasets increases further when distinguishing Cervidae from  
291 Caprinae in the cluster of Atlantic sites, which removes a sampling bias as only Caprinae  
292 were sampled in the Mediterranean sites. In the case of Cervidae, the distribution of data  
293 satisfies the statistical criteria required by a normal distribution when using Shapiro-Wilk test  
294 ( $p = 0.30$  and  $W = 0.963$  in the 95% critical range [0.937; 1.000] for  $\delta^{13}\text{C}$  values;  $p = 0.15$  and  
295  $W = 0.953$  in the 95% critical range [0.937; 1.000] for  $\delta^{18}\text{O}$  values). Similar conclusions are  
296 obtained for the Caprinae when using Shapiro-Wilk test ( $p = 0.50$  and  $W = 0.964$  in the 95%  
297 critical range [0.920; 1.000]) for  $\delta^{13}\text{C}$ -values;  $p = 0.37$  and  $W = 0.957$  in the 95% critical  
298 range [0.920; 1.000] for  $\delta^{18}\text{O}$ -values).

299 Cervidae have  $\delta^{13}\text{C}$  values ranging from  $-12.89\text{‰}$  to  $-9.47\text{‰}$  (mean =  $-10.96 \pm 0.66\text{‰}$ )  
300 and  $\delta^{18}\text{O}$  values ranging from  $-8.65\text{‰}$  to  $-3.67\text{‰}$  (mean =  $-5.96 \pm 1.03\text{‰}$ ) in the Atlantic sites.  
301 These data statistically differ for  $\delta^{13}\text{C}$  values (Welch t-test:  $p = 1.03 \times 10^{-6}$ ;  $H_0 =$  mean are  
302 equal), but not for  $\delta^{18}\text{O}$  values (Welch t-test:  $p = 0.71$ ;  $H_0 =$  mean are equal) of Caprinae  
303 coming from the same sites (mean  $\delta^{13}\text{C} = -10.12 \pm 0.49\text{‰}$  and mean  $\delta^{18}\text{O} = -6.06 \pm 0.88\text{‰}$ ).

304 Caprinae from the Atlantic sites have slightly lower  $\delta^{13}\text{C}$ -values ( $-10.12 \pm 0.49\text{‰}$  against -  
305  $9.65 \pm 0.44\text{‰}$ ) and much lower  $\delta^{18}\text{O}$ -values ( $-6.06 \pm 0.88\text{‰}$  against  $-1.45 \pm 0.74\text{‰}$ ), than those  
306 originating from Mediterranean sites with  $\delta^{13}\text{C}$ -values of  $-9.65 \pm 0.44\text{‰}$  and  $\delta^{18}\text{O}$  -values of -  
307  $1.45 \pm 0.74\text{‰}$  (Welch t-test for  $\delta^{13}\text{C}$ :  $p = 3.6 \times 10^{-3}$ ;  $H_0 =$  mean are equal; Welch t-test for  $\delta^{18}\text{O}$ :  
308  $p = 1.7 \times 10^{-16}$ ;  $H_0 =$  mean are equal).

309 Few samples are available for Equidae: 2 samples from Hornos de la Peña and 2 from  
310 Laugerie-Haute, have  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values in the range of values from other herbivorous  
311 mammals at sites located on the Atlantic side. It is worth pointing out that no temporal trend  
312 is observed for either  $\delta^{13}\text{C}$ - or  $\delta^{18}\text{O}$ -values of both Cervidae and Caprinae in the Atlantic sites  
313 (Table 1). Nevertheless, whatever their age, Caprinae from this study are characterized by

314 lower  $\delta^{18}\text{O}$  values and higher  $\delta^{13}\text{C}$  values than Cervidae. In addition, statistics that show a  
315 normal distribution with relatively small standard deviations are consistent with inter-annual  
316 variations of considered climatic parameters.

317

## 318 5. Discussion

### 319 5.1. Preservation and meaning of the isotopic compositions

320 Assessing the potential blurring effect of diagenetic processes represents the greatest  
321 challenge for geochemists hoping to reconstruct environmental parameters based on isotopic  
322 proxies. Biogenic apatites have undergone diagenesis, at least during the first step of the  
323 mineral transformation commonly referred to as “early diagenesis”, which follows the decay  
324 of the organic matter. Changes in the content of major and trace elements of biogenic apatites  
325 do not necessarily mean that their initial stable C- and O-isotope compositions have been  
326 fully reset or even partly modified (Goedert et al., 2018). The acquisition of secondary  
327 isotopic signatures mainly takes place during the first stages of burial, when processes of  
328 mineral dissolution and recrystallization under microbially-mediated conditions may alter the  
329 skeletal tissues (Kolodny et al., 1996; Trueman et al., 2003; Zazzo et al., 2004). Enamel is  
330 considered a more suitable material for paleoenvironmental or paleoclimatic reconstructions  
331 because its apatite carbonate fraction has been shown to be generally resistant to isotopic  
332 alteration during early diagenesis due to its highly dense and packed crystallites (Zazzo et al.,  
333 2004).

334 Nonetheless, the preservation of pristine isotopic records needs to be assessed before  
335 attempting paleoenvironmental interpretations of the oxygen and carbon isotope compositions  
336 of fossil apatites. Whereas there is no method for determining whether the original isotopic  
337 compositions are preserved, several tests may help assess the preservation state of the initial  
338 isotopic signatures. In the present study, three complementary approaches are used:

339 i) Although  $\delta^{13}\text{C}$ - and  $\delta^{18}\text{O}$ -values may covariate in the case of specific climate variations,  
340 usually detected through geographic or temporal trends (e.g., a combination of higher  
341 precipitation and lower temperatures), a linear correlation generally indicates a mixing  
342 relationship between two endmembers: the original isotopic signature and a contaminant,  
343 such as soil carbonate. Our data do not reveal any such mixing (Atlantic sites {2 outliers}:  $n =$   
344  $61$ ;  $R^2 = 10^{-3}$ ;  $p = 0.76$  for  $H_0$ : no correlation; Mediterranean sites:  $n = 13$ ;  $R^2 = 3 \times 10^{-2}$ ;  $p =$   
345  $0.57$  for  $H_0$ : no correlation).

346 ii) Loose clusters and scrambling of isotopic compositions should affect all tooth material  
347 independently of the taxa. Here, the systematic differences in  $\delta^{13}\text{C}$ - and  $\delta^{18}\text{O}$ -values of  
348 Cervidae vs Caprinae supports the hypothesis of a preserved isotopic imprint of their  
349 respective diets and habitats.

350

## 351 5.2. Reconstitutions of MAP

### 352 5.2.1. Method: principles and limits

353 The  $\delta^{13}\text{C}$  of consumed food by vertebrates mainly controls the  $\delta^{13}\text{C}$  of their skeleton  
354 (Ambrose, 1993; Ballasse et al., 1999; Szostek, 2009). Carbon isotope ratios of apatite  
355 carbonate may be considered as a “dirty window” that opens on a combination of factors: the  
356 diet, the degree of openness of the environment (exposure to light) and the amount of  
357 precipitation. The reconstruction of MAP is thus done in two steps.

358 The first step consists in converting the  $\delta^{13}\text{C}$  of carbonate ( $\delta^{13}\text{C}_{\text{carb}}$ ) into the  $\delta^{13}\text{C}$  of diet  
359 ( $\delta^{13}\text{C}_{\text{diet}}$ ), and the second one in converting the  $\delta^{13}\text{C}_{\text{diet}}$  into MAP values ( $\text{mm.yr}^{-1}$ ). As a MAP  
360 proxy,  $\delta^{13}\text{C}_{\text{carb}}$  is basically tarnished with several important sources of uncertainty. Therefore,  
361 we consider that only broad estimates may be obtained. The commonly used isotopic  $\delta^{13}\text{C}_{\text{carb}}$   
362  $-\delta^{13}\text{C}_{\text{diet}}$  offset value ( $\Delta^{13}\text{C}_{\text{pi}}$ ) of  $14.1\text{‰}$  (Cerling and Harris, 1999) cannot be used in this study  
363 as it varies from one species to another. More recently, Tejada-Lara et al. (2018) proposed a



364 series of equations that consider the specificities in the digestive system as well as the body  
 365 mass of different herbivorous mammals. Calculations of  $\delta^{13}\text{C}_{\text{diet}}$  of the study taxa in Table 1  
 366 follow this model. It must be kept in mind that animal diets do not necessarily reflect the  
 367 composition of the vegetation cover; the stricter an animal's food preferences, the larger the  
 368 bias between the isotopic composition of the diet and that of the vegetation cover.

369 The second step consists in estimating MAP from the  $\delta^{13}\text{C}$  of vegetation, here  
 370 assumed to be close to  $\delta^{13}\text{C}_{\text{diet}}$ . The empirical relationship proposed by Rey et al. (2013),  
 371 which we will use below, is valid if the vegetation cover was composed of C3 plants. This is  
 372 still an open debate, however, and conflicting reconstructions of the LGM paleovegetation of  
 373 western Europe from models vs pollen data exist in the literature (e.g., Elenga et al., 2000;  
 374 Leng, 2006; Woillez et al., 2011; Hatté et al., 2013; Binney et al., 2017; see a discussion and  
 375 an explanatory hypothesis in Kaplan et al., 2016). Thus, our estimates of MAP from  $\delta^{13}\text{C}$ -data  
 376 must be seen as a first approximation that needs to be confronted with estimates from other  
 377 approaches. The method established by Rey et al. (2013), using a least square regression from  
 378 the dataset of Kohn (2010), is based on relationship (1) below, established between plant leaf  
 379 discrimination ( $\Delta^{13}\text{C}_{pl}$ ) as defined above and mean annual precipitations (MAP):

$$380 \quad \text{Log}_{10}(\text{MAP} + 300) = 0.092(\pm 0.004)\Delta^{13}\text{C}_{pl} + 1.148(\pm 0.074) \quad (1)$$

$$381 \quad \text{with } \Delta^{13}\text{C}_{pl} = \frac{\delta^{13}\text{C}_{atm} - \delta^{13}\text{C}_{pl}}{1 + \frac{\delta^{13}\text{C}_{pl}}{1000}} \quad \text{and MAP in mm yr}^{-1}$$

382  $\delta^{13}\text{C}_{atm}$  values of atmospheric  $\text{CO}_2$  have been measured in air bubbles trapped within the  
 383 Vostok ice cores between 20 and 43 ka (Leuenberger et al., 1992; Schmitt et al., 2012). For  
 384 the LGM, this value has been estimated to be close to  $-7\text{‰}$  (VPDB). Calculations of MAP are  
 385 given in Table 1. However, this equation does not consider the  $\text{pCO}_2$  effect on  $\delta^{13}\text{C}$  values of  
 386 the vegetation (Farquhar et al., 1982; Schubert and Jahren, 2012). Hare et al. (2018) related  
 387 the  $\delta^{13}\text{C}$  increase by  $\approx 1\text{‰}$  of plants and faunal collagen to the low  $\text{pCO}_2$  values ( $\approx 180$  ppm)

388 of the LGM relatively to those ( $\approx 300$  ppm) of the post deglacial rise that took place about 15  
389 kyr ago (Peacock et al., 2006). Consequently, it is most likely that our calculated MAP values  
390 according to equation (1) are underestimated by about  $150 \text{ mm y}^{-1}$ . Final estimates from the  
391 model will thus be corrected using this offset.

392 The validity and robustness of this empirical approach were tested successfully in a study  
393 (Prud'homme et al., 2018) devoted to the reconstruction of MAP in Germany (Nussloch)  
394 during the Last Glacial, which was based on the  $\delta^{13}\text{C}$  of earthworm granule calcite crystals. In  
395 this study, the estimated MAP values range from  $\sim 270$  to  $460$  mm with a mean value of  $\sim$   
396  $370$  mm for the Upper Pleniglacial ( $\sim$ LGM) and of  $\sim 300$  mm, for the Middle Pleniglacial,  
397 covering a time interval between  $17$  ka and  $55$  ka. Uncertainties associated with the estimated  
398 MAP values are on the order of  $\pm 100$  to  $200$  mm. Based on  $\delta^{13}\text{C}$  values of organic matter  
399 preserved in the Nussloch loess deposits and using an inverse modelling approach (BIOME  
400 4), Hatté and Guiot (2005) estimated MAP values ranging from  $280^{+120}_{-60}$  to  $460^{+80}_{-160}$  mm.  
401 Considering the large uncertainties associated with the various methods of MAP  
402 reconstructions, Prud'homme et al. (2018) concluded that the empirical method developed by  
403 Kohn (2010) may be used for MAP estimates in the absence of other proxies or modelling  
404 approaches.

405

#### 406 5.2.2. Interpretation

407 The reconstructed  $\delta^{13}\text{C}$ -values of animal diet ( $\delta^{13}\text{C}_{\text{diet}}$ ) suggest that they mainly fed on  
408  $\text{C}_3$  plants as revealed by a mean  $\delta^{13}\text{C}_{\text{diet}}$  of  $-23.5 \pm 1.0\text{‰}$  for the whole data base (Table 1),  
409 thus supporting the scenario of a  $\text{C}_3$ -plant dominated vegetational cover (compare with Hare  
410 et al., 2018). The  $\text{C}_3$  Calvin-Benson pathway ( $\sim 75$  wt% of the present-day vegetal biomass  
411 including trees, temperate grasses, some forbs, shrubs) is the most discriminating regarding  
412 the heavy carbon isotopes, thus leading to low  $\delta^{13}\text{C}$  values ranging from  $-34\text{‰}$  to  $-22\text{‰}$  and

413 averaging  $-26\text{‰}$  (Park and Epstein, 1960; 1961; Smith and Epstein, 1971; O’Leary, 1981).  
414 Variations within this range of  $\delta^{13}\text{C}$  values result from external factors such as air  
415 temperature, water stress, exposure to light,  $\delta^{13}\text{C}$  of atmospheric  $\text{CO}_2$ ,  $\text{pCO}_2$  and rate of  $\text{CO}_2$   
416 recycling (O’Leary, 1981). Worth mentioning is the fact that a  $\delta^{13}\text{C}_{\text{diet}}$  of  $-23.5\pm 1.0\text{‰}$  could  
417 as well be compatible with a diet of up to  $\sim 20\%$  of  $\text{C}_4$  plants, as illustrated for grazers from  
418 modern steppe environments (Auerswald et al., 2009). Interestingly, this study also  
419 demonstrates that despite a large overall variability of the relative abundance of  $\text{C}_4$ - vs  $\text{C}_3$ -  
420 plants, no preferential grazing is observed.

421 Nevertheless, on the Atlantic side of the Iberian Peninsula, Caprinae have higher  $\delta^{13}\text{C}_{\text{diet}}$   
422 (mean =  $-22.8\pm 0.5\text{‰}$ ) than Cervidae and Equidae (mean for both =  $-24.3\pm 0.6\text{‰}$ ), all  
423 populations being characterized by normal distributions (Caprinae:  $p = 0.11$  and  $W = 0.953$  in  
424 the 95% critical range [0.944; 1.000]; Cervidae and Equidae:  $p = 0.19$  and  $W = 0.960$  in the  
425 95% critical range [0.942; 1.000]). Such distinct carbon isotope compositions reflect diet  
426 differences related to distinct habitats or grazing habits (Figure 2). This observation is in  
427 agreement with Jones et al. (2020) who concluded that ibex adapted their niche during the  
428 LGM.

429 Among Cervidae, *C. elaphus* have lower  $\delta^{13}\text{C}_{\text{diet}}$  values (mean =  $-24.4\pm 0.6\text{‰}$ ) than *T.*  
430 *rangifer* (mean =  $-23.2\pm 0.36\text{‰}$ ), even though only three samples were available of *C.*  
431 *elaphus*. A higher  $\delta^{13}\text{C}_{\text{diet}}$  for reindeers, relative to other animals, has been explained by their  
432 specific diet mainly based on lichens, especially consumed during the cold season (Park and  
433 Epstein, 1960; Máguas and Brugnoli, 1996; Ben-David et al., 2001)

434 Based on the estimated  $\delta^{13}\text{C}_{\text{diet}}$  values, MAP values were calculated in the range  $\sim 100$  to  
435  $400 \text{ mm}\cdot\text{yr}^{-1}$  for Atlantic sites ( $100$  to  $200 \text{ mm}\cdot\text{yr}^{-1}$  recorded by Caprinae and  $200$  to  $400$

436 mm.yr<sup>-1</sup> recorded by Cervidae and Equidae), while they are close to 100 mm.yr<sup>-1</sup> for the two  
437 Mediterranean sites (Table 2). The present-day reference values (Table 2) extracted from  
438 meteorological records (IAEA/WMO database) correspond to cities in the vicinity of the  
439 studied archaeological sites, specifically Almeria (202±66 mm.yr<sup>-1</sup>), for the Nerja site,  
440 Valencia (532±173 mm.yr<sup>-1</sup>), for the Malladetes site , Santander (1050±140 mm.yr<sup>-1</sup>), for the  
441 sites located in Asturias and Cantabria (Spain), and Cestas-Pierroton ( 937±192 mm.yr<sup>-1</sup>), for  
442 the Laugerie-Haute site. The Caprinae record of drier environmental conditions than those  
443 inferred from Cervidae and Equidae, suggests differences in diets and/or seasonal/altitudinal  
444 grazing habitats between some of the representative herbivorous species sampled.

445 Diet preferences between C3 and C4 may cause δ<sup>13</sup>C differences by several ‰ between  
446 sheep and goat, for example, as shown by Balasse and Ambrose (2005) for C4 grassland  
447 environments of the Central Rift Valley of Kenya. However, C4 was most likely absent or  
448 very scarce in the studied LGM-environments (Collins and Jones, 1985). δ<sup>13</sup>C differences  
449 among C3-eating large mammals may result from differences in water stress and/or exposure  
450 to light (O’Leary, 1981). It means that δ<sup>13</sup>C values of Caprinae should be higher than those of  
451 Cervidae and Equidae if the Caprinae habitat was open (sparse vegetation cover in a rocky  
452 environment) and characterized by a vegetation submitted to water stress (e.g. dry sides of  
453 mountains).

454 Nevertheless, during the LGM, precipitation followed a pattern similar to the modern one  
455 (Figure 3), with sites under Atlantic vs Mediterranean influence defining two distinct clusters.  
456 The Mediterranean cluster is significantly drier than the Atlantic one, but both depict much  
457 drier conditions than at present. LGM precipitation estimates obtained here broadly agree  
458 with pollen-based reconstructions (e.g., Peyron et al., 1998), but disagree with the wetter  
459 conditions reconstructed from climate model experiments (e.g., Ludwig et al., 2016; Arpe et  
460 al., 2011).

461

### 462 5.3. Reconstitutions of MAAT

#### 463 5.3.1. Method: principles and limits

464 Oxygen isotope ratios of apatite carbonate may be seen as a “frosted glass window” open  
465 on the composition of dietary sources of water and local meteoric water, ultimately used as a  
466 proxy for air temperatures (e.g. Fricke and O’Neil, 1998; Daux et al., 2005). The  $\delta^{18}\text{O}$  of  
467 consumed water by vertebrates mainly controls the  $\delta^{18}\text{O}_c$  of their skeleton (Longinelli, 1984;  
468 Kohn, 1996). The oxygen isotope composition of leaf water can somewhat blur the  
469 relationship between the  $\delta^{18}\text{O}_c$  of apatite carbonate and the  $\delta^{18}\text{O}$  of drinking water (Ayliffe  
470 and Chivas, 1990; Cormie et al., 1994; Luz et al., 1990; Pederzani and Britton, 2019). It  
471 constitutes, however, a good indicator of aridity (Levin et al., 2016; Blumenthal et al., 2017).

472 In this approach, the reconstitution of MAAT is done in four steps.

473 First, oxygen isotope compositions of apatite carbonate ( $\delta^{18}\text{O}_c$ ) measured on the VPDB  
474 scale (Coplen et al., 1983) must be converted into those of their phosphate counterparts  
475 ( $\delta^{18}\text{O}_p$ ) before being used to estimate the composition of drinking water on the basis of the  
476 equations available in the literature. This step is achieved by using equation (2) that was  
477 determined by Iacumin et al. (1996) for modern herbivorous mammals. Unfortunately, this  
478 step is a source of large uncertainties ( $\delta^{18}\text{O}_p$ : standard error of estimate = 0.73). We computed  
479 Equation (2) using the original data set published in Iacumin et al. (1996) in order to tighten  
480 uncertainties as follows:

$$481 \delta^{18}\text{O}_p = 0.975(\pm 0.031) \delta^{18}\text{O}_c - 8.43(\pm 0.81) \quad (n = 17; R^2 = 0.985) \quad (2)$$

482 The second step consists in calculating the oxygen isotope composition of water  
483 consumed (free water and water derived from the food such as leaves and herbs) by the  
484 animals. Several oxygen isotope fractionation equations between apatite phosphate ( $\delta^{18}\text{O}_p$ )  
485 and water ( $\delta^{18}\text{O}_w$ ) have been published for large herbivorous mammals, covering all taxa

486 investigated in the present study. It is worthy to note that animal physiology is integrated in  
487 the oxygen isotope fractionation equations (Longinelli, 1984; Luz and Kolodny, 1985; Kohn,  
488 1996; Langlois et al., 2003) that have been established on present-day fauna, either the same  
489 species or close relatives. The relevant equations have also been recalculated to set the  $\delta^{18}\text{O}_w$   
490 variable as the estimator (Y-axis) in the regression line along with the associated statistics, as  
491 follows:

492 - Deer (*Cervus elaphus*) (D'Angella and Longinelli, 1990):

$$493 \quad \delta^{18}\text{O}_w = 0.88(\pm 0.03)\delta^{18}\text{O}_p - 22.50(\pm 0.52) \quad (n = 7; R^2 = 0.99) \quad (3)$$

494 - Reindeer (*Rangifer tarandus*) (Iacumin and Longinelli, 2002):

$$495 \quad \delta^{18}\text{O}_w = 1.21(\pm 0.01)\delta^{18}\text{O}_p - 26.41(\pm 1.31) \quad (n = 34; R^2 = 0.74) \quad (4)$$

496 Note that 2 outliers were removed from the original database for the setting of equation 4, as  
497 recommended by Iacumin and Longinelli (2002).

498 - Horse (*Equus burchelli*, *E. zebra*, *E. caballus*) (Bryant et al., 1994; Sanchez Chillon et al.,  
499 1994; Delgado-Huertas et al., 1995):

$$500 \quad \delta^{18}\text{O}_w = 1.09(\pm 0.128)\delta^{18}\text{O}_p - 25.83(\pm 1.08) \quad (n = 25; R^2 = 0.77) \quad (5)$$

501 Note again that 2 outliers were removed from the original database deduced from linear  
502 regression analysis

503 - Wild Goat (*Capra hircus* and *C. ibex*) (Delgado-Huertas et al., 1995)

$$504 \quad \delta^{18}\text{O}_w = 1.09(\pm 0.06)\delta^{18}\text{O}_p - 26.45(\pm 0.98) \quad (n = 21; R^2 = 0.95) \quad (6)$$

505 A major caveat here is the possibility of distinct  $\delta^{18}\text{O}_w$  vs  $\delta^{18}\text{O}_p$  relationships during  
506 the cold LGM, due to reduced evapotranspiration (e.g., Kohn, 1996). Isotope enrichment from  
507 precipitation to plant-water and finally to the animal body-water could have prevailed. Thus,  
508 under LGM conditions, the  $\delta^{18}\text{O}_w$ -value calculated with the above equations must be seen as a  
509 maximum value.

510 The third step consists in correcting the  $\delta^{18}\text{O}$  of seawater from the volume of  
511 continental ice. Indeed, any change in the isotopic composition of oceanic sources will  
512 propagate throughout the entire surface water cycle. Knowing that the mean depth of the  
513 oceans is 3,700 m (Charette and Smith, 2010), a decrease in sea level by  $120\pm 10$  m (Lambeck  
514 et al., 2014) results in a mean increase of the global ocean reservoir  $\delta^{18}\text{O}$ -value by  $+1.2\pm 0.1\text{‰}$   
515 provided the mean  $\delta^{18}\text{O}$  of the LGM ice-sheets is close to  $-40\text{‰}$  (Blunier and Brook, 2001).  
516 This isotopic offset is very close to that proposed by Schrag et al. (2002) and Steele et al.  
517 (2009), but perhaps a little overestimated, based on isotopic composition for the Laurentide  
518 Ice Sheet proposed by Hillaire-Marcel and Causse (1989) or Sima et al. (2006). Duplessy et  
519 al. (2002) proposed an offset of  $1.05\pm 0.20\text{‰}$  probably encompassing the effective overall  
520 change in the ocean isotopic composition. However, moisture sources relate to ocean surface  
521 water masses: their isotopic composition differs from that of the whole ocean, and may show  
522 large regional offsets, especially in the present case, between the Bay of Biscay and the  
523 western Mediterranean. The Bay of Biscay was likely the major moisture supplier for the  
524 Atlantic sites, whereas a mixture of Atlantic and western Mediterranean moisture supplies  
525 may be hypothesized for the Mediterranean sites. The two marine areas were of course  
526 characterized by distinct MAAT, mean salinity and isotopic composition.

527 Based on Schrag et al. (2002), one may assume an isotopic composition of surface  
528 waters from the northeast North Atlantic in the  $+0.7\pm 0.1$  to  $+0.8\pm 0.1\text{‰}$  range vs VSMOW, a  
529 range compatible with model estimates from Paul et al. (2001). According to Loncaric et al.  
530 (1998), MAAT depicted large amplitude oscillations between  $<5^\circ\text{C}$  and up to  $15^\circ\text{C}$ , with a  
531 mean value of about  $7$  to  $9^\circ\text{C}$  (e.g., Kuhlemann et al., 2008). Comparatively, surface waters  
532 from the western Mediterranean were not only warmer but enriched in  $^{18}\text{O}$ . Planktic  
533 foraminifera (Hayes et al., 2005) and biomarkers (Rodrigo-Gámiz et al., 2014), both  
534 suggesting a mean LGM sea-surface temperature (SST) of  $\sim 13.5^\circ\text{C}$ , whereas  $\delta^{18}\text{O}_{\text{carb}}$  values

535 reported from this sector of the Mediterranean during the same interval range from  
536  $+3.5\pm 0.5\text{‰}$  vs VPDB in planktic foraminifera (Thunell and Williams, 1989) to  $+3.9\pm 0.2\text{‰}$  in  
537 shallow mollusk shells (Fergusson et al., 2011). Combining these values, one may set the  
538 LGM  $\delta^{18}\text{O}_{\text{sw}}$ -value at about  $+3\text{‰}$  vs VSMOW in the western Mediterranean, to be compared  
539 with a modern value of  $\sim +1.3\text{‰}$  (Goddard Institute data base; Schmidt et al., 1999; see also  
540 Benetti et al., 2017). Potential moisture generated during the evaporation of the western  
541 Mediterranean Sea, which had a  $\delta^{18}\text{O}$  higher than the Atlantic Ocean by  $\sim +2\text{‰}$ , may thus  
542 have played some role during the LGM. However, climate models suggest a southward shift  
543 of the North Atlantic jet stream during the LGM, governing the relatively abundant winter  
544 precipitation in comparison with summer rains which were somewhat controlled by local  
545 processes (e.g., Beghin et al., 2016). Thus, the most likely LGM moisture source, for both the  
546 Mediterranean and the Atlantic sites, would have been the northeastern North Atlantic Ocean,  
547 leading to adopt the  $\delta^{18}\text{O}_{\text{sw}} \sim +0.8\text{‰}$  value for the primary source water, and allowing for  
548 some  $^{18}\text{O}$ -enriched precipitation in summer, influenced by the high  $\delta^{18}\text{O}_{\text{sw}}$ -values of the  
549 western Mediterranean waters ( $\sim +3\text{‰}$ ). Perhaps worth of mention here is the fact that under  
550 the modern conditions, i.e., with a  $\Delta\delta^{18}\text{O}$  offset of  $\sim +0.8\text{‰}$  between surface waters of the  
551 western Mediterranean ( $\delta^{18}\text{O}_{\text{sw}} \sim 1.3\text{‰}$ ) and those of the northeastern North Atlantic ( $\delta^{18}\text{O}_{\text{sw}}$   
552  $\sim 0.5\text{‰}$ ; Benetti et al., 2017), the long-term isotopic composition of precipitation in both areas  
553 is almost similar ( $\sim -6\text{‰}$ ; Araguas-Araguas et al., 2005), thus pointing even today to a major  
554 contribution of Atlantic moisture sources to precipitation on the Iberian Peninsula.

555 We used the  $+0.8\text{‰}$  offset between modern vs LGM moisture sources as a base line  
556 for both regions and subtracted it from the  $\delta^{18}\text{O}_{\text{w}}$ -values derived from equations (3) to (6) (see  
557 Table 1). Nevertheless, we also increased this offset to  $+1.2\text{‰}$  for the Mediterranean sites, a  
558 value that would account for about 20% of Mediterranean moisture source supplies on a  
559 yearly basis, based on the  $\sim 2\text{‰}$  offset in  $\delta^{18}\text{O}_{\text{sw}}$ -values between the Bay of Biscay and the



560 Western Mediterranean. Again, this seems a reasonable estimate considering the regional  
561 atmospheric circulation in SW Europe during the LGM (cf. Ludwig et al., 2016; see also  
562 Kuhlemann et al., 2008; Beghin et al., 2016).

563         The fourth step aims at converting  $\delta^{18}\text{O}_w$  to MAAT. Here again, one may question  
564 whether or not present-day relationships fully apply to the LGM. Firstly, all of the sites of the  
565 present study are close to coastlines, thus, they are not affected by continental Rayleigh-  
566 evolution of humid air-masses or by major altitudinal effects (e.g., Gat et al., 2001), a process  
567 well illustrated by Rozanski et al. (1982) for inland precipitation patterns in Europe. Isotopic  
568 compositions of precipitation at the study sites should then follow a relatively linear  
569 relationship with mean annual temperatures, as observed at global scale, despite some  
570 latitudinal/regional variations in the slope and intercept of the local regression lines (e.g., Lee  
571 et al., 2008). The slope of a MAT– $\delta^{18}\text{O}_{mw}$  linear relationship is mainly temperature–  
572 dependent at mid- and high-latitudes. This point is firstly well illustrated by the existence of a  
573 strongly positive linear correlation ( $R^2 = 0.83$ ) between the dew point ( $T_d$ ) and the oxygen  
574 isotope composition of meteoric water (Figure 4).  $T_d$ , expressed in °C, represents the  
575 temperature at which the actual water vapour pressure equals the saturated water vapour  
576 pressure (RH = 100%). This climatic parameter plays a key role in the distribution of  $\delta^{18}\text{O}_{mw}$   
577 over the continental masses located in the mid-latitudes (Lécuyer et al., 2020). Secondly,  
578 there is a unique MAT– $\delta^{18}\text{O}_{mw}$  linear relationship for present-day (Figure 5A) for latitudes >  
579 32°, even if it samples various continental areas from both hemispheres, which are submitted  
580 to various moisture-bearing prevailing winds.

581         The MAAT (in °C) vs  $\delta^{18}\text{O}_w$  linear relationship from equation (7), established for  
582 Europe (Skrzypek et al., 2011), is indistinguishable in terms of slope and intercept from  
583 equation (8) obtained at a global scale (Figure 5A). For a reliable comparison, equation (8)

584 was computed by excluding data from the tropics as well as those corresponding to air  
585 temperatures lower than 0°C (Figure 5B).

$$586 \quad \text{MAAT } (^{\circ}\text{C}) = 1.41 \delta^{18}\text{O}_{\text{w-MAP}} + 21.63 \quad (7)$$

587 where MAT represents the mean annual temperature and  $\delta^{18}\text{O}_{\text{w-MAP}}$ , the weighted mean  
588 isotopic composition of annual precipitation.

$$589 \quad \text{MAAT } (^{\circ}\text{C}) = 1.40(\pm 0.08) \delta^{18}\text{O}_{\text{w-MAP}} + 21.86(\pm 0.64) \quad (8)$$

$$590 \quad (n = 90; R^2 = 0.81)$$

591 Equation (7) was thus used to calculate MAAT (reported in Table 1) during the LGM in  
592 southwestern Europe. There are three caveats when using this method:

593 1) Altitude effect: in Spain, the rate of air-temperature decrease with altitude is close to 5°C  
594 per 1000 m in mountain areas (Navarro-Serrano et al., 2018). In the Pyrenees, altitudinal  
595 oxygen isotope gradients average -3‰ per 1000 m (Hughes et al., 2018), a value within  
596 the range observed in southern Europe (e.g., Tazioli et al., 2019). Consequently,  
597 differences between present-day reference stations (cities are close to sea-level) and  
598 mammal ranges (between 0 and 1000 m) during the LGM may lead to overestimates of  
599 temperature differences by about 2°C in northern Spain and up to 4°C in south and  
600 southeast Spain.

601 2) Source effect: the source of drinking water may differ isotopically from local meteoric  
602 waters, for example in rivers since their sources are located at altitudes. A comparison  
603 between present-day river and precipitation  $\delta^{18}\text{O}$  maps (Nan et al., 2019) reveals that  
604 differences between those two parameters are close to 2‰ over Europe on a yearly  
605 average. Once again, true air temperatures may be higher than those calculated following  
606 the above method. Similarly, animals that seasonally migrate may have a  $\delta^{18}\text{O}_{\text{w}}$  record  
607 that is biased relative to their place of death.

608 3) Reservoir effect: water stored in ponds, lakes or in snow cover may suffer evaporation or  
609 sublimation that tends to enrich the residual liquid–solid water in heavy isotopes. Such  
610 processes may induce oxygen isotope biases in the order of a few per mil.

611 However, a sporadic influence of the above boundary conditions on the isotopic approach  
612 should be detectable by altering the normal distribution of the studied population; which does  
613 not seem to be the case here.

614

### 615 5.3.2. Interpretation

616  $\delta^{18}\text{O}_{\text{w-MAP}}$  have been calculated according either to ocean surface water having a  $\delta^{18}\text{O}$  of  
617 +1.2 or +0.8‰. Inferred temperatures using equation (7) are shifted by  $\approx +0.6^\circ\text{C}$ . In the case  
618 of a prevailing oceanic surface source of moisture having a  $\delta^{18}\text{O}$  of +1.2‰, calculated mean  
619  $\delta^{18}\text{O}_{\text{w-MAP}}$  are  $-10.1\pm 0.9\text{‰}$  ( $n = 46$ ) and  $-10.3\pm 1.0\text{‰}$  ( $n = 17$ ) for northern Spain and  
620 Laugerie-Haute, respectively (Table 1). Pooled data follow a normal distribution (Figure 6)  
621 according to the Shapiro-Wilk test ( $p = 0.26$  and  $W = 0.976$  in the 95% critical range [0.9620;  
622 1.000]). The range of  $\delta^{18}\text{O}_{\text{w-MAP}}$  values comprised between  $\sim -12\text{‰}$  and  $\sim -8\text{‰}$  correspond to  
623 present-day compositions of precipitation in south Scandinavia and Central Europe  
624 (IAEA/WMO database and maps). Calculated mean  $\delta^{18}\text{O}_{\text{w-MAP}}$  are  $-5.4\pm 0.8\text{‰}$  ( $n = 8$ ) and -  
625  $5.8\pm 0.8\text{‰}$  ( $n = 6$ ) for Malladetes and Nerja, respectively. Pooled data follow a normal  
626 distribution (Figure 6) according to the Shapiro-Wilk test ( $p = 0.93$  and  $W = 0.975$  in the 95%  
627 critical range [0.875; 1.000]). The range of  $\delta^{18}\text{O}_{\text{mw}}$  values between  $\sim -7\text{‰}$  and  $\sim -4\text{‰}$   
628 correspond to present-day compositions of precipitation along the Mediterranean rim  
629 (IAEA/WMO database and maps).

630 The calculated  $\delta^{18}\text{O}_{\text{w-MAP}}$  values based on a  $\delta^{18}\text{O}_{\text{sw}}$  of +0.8‰ range from  $\sim 6^\circ\text{C}$  to  $\sim$   
631  $10^\circ\text{C}$  for Atlantic sites. This range may be explained by altitudinal gradients recorded by the  
632 faunal remains and/or by the large amplitude oscillations of LGM-SST and LGM- $\delta^{18}\text{O}_{\text{carb}}$

633 values in the Bay of Biscay reported by Loncaric et al. (1998). It is interesting that the range  
634 of temperature inferred for the Atlantic sites in the present study is within the range proposed  
635 by these authors for surface waters of the Bay of Biscay during the LGM. On the  
636 Mediterranean side, the estimated LGM-MAAT values are close to 14–15°C for both sites  
637 ( $\delta^{18}\text{O}_{\text{sw}}$  of +0.8‰) or close to 13.5–14.5°C ( $\delta^{18}\text{O}_{\text{sw}}$  of +1.2‰) when accounting for some  
638 contribution of Mediterranean moisture to summer precipitations (Table 2). Here also, this  
639 value is practically identical to LGM-SST values in the Western Mediterranean estimated by  
640 Hayes et al. (2005) or by Rodrigo-Gámiz et al., (2014).

641 The air temperatures reconstructed during the LGM are lower than the present-day ranges  
642 recorded in meteorological stations located either in the vicinity of the Atlantic sites  
643 (Santander:  $14.8 \pm 0.4^\circ\text{C}$  and Cestas-Pierroton:  $13.1 \pm 0.6^\circ\text{C}$ ), or close to the Mediterranean  
644 sites (Almeria:  $19.2 \pm 0.4^\circ\text{C}$ ; Valencia:  $18.5 \pm 0.6^\circ\text{C}$ ). As shown in Figure 7, MAAT decreased  
645 during the LGM from South to North according to a trend roughly similar to the modern one.  
646 As a whole, MAAT values in southern Spain were about 4–5°C below modern pre-industrial  
647 temperatures, and by 5–8°C in northern Spain and southwest France (Figure 7).

648

#### 649 5.4. LGM climate inferred from large mammal isotopes and biogeographic patterns.

650 Faunal associations described in the archaeological sites of southwestern Europe are  
651 generally compatible with cold and dry, open environments, such as tundra and dry steppe,  
652 but there are important regional differences. The sites sampled in this study are from three  
653 distinct biogeographic zones, following the classification suggested by Yravedra and Brugal  
654 (2005) for southwestern Europe. The zones sampled for this study are: southwest France  
655 (zone VI), Cantabria/Asturias (zone IV) and the Mediterranean coast (zone IIIa). A general  
656 reduction in faunal diversity is observable in Southwestern Europe during the LGM, signaling  
657 the severity of the climate downturn, but the relative diversity of herbivores and carnivores

658 differs between zones. Diversity decreases in zone VI reaching minimum levels during the  
659 LGM, in zone IV (Cantabria/Asturias) diversity also decreases but reaches a minimum after  
660 the LGM, while carnivore diversity actually increases with time, whereas the opposite pattern  
661 occurs in zone IIIa (e.g., Valencia) where a gradual increase in herbivore diversity is  
662 observable over the course of the last Glacial (Yravedra and Brugal, 2005).

663 In SW France (zone VI), horse dominates sites such as Laugerie Haute Est at the  
664 beginning of the LGM (e.g., in the Magdalenian 0 level; Table 1) but reindeer, a taxon  
665 associated with tundra environments, increases dramatically in importance throughout the  
666 sequence, eventually dominating during Magdalenian I and II (see: Delpech, 2012). In  
667 northwest Spain (zone IV), on the other hand red deer, a taxon generally considered more  
668 indicative of temperate, wooded contexts often dominates late Glacial faunal assemblages,  
669 while the proximity of sites to the coastal ranges is signaled by the presence of ibex and  
670 chamois (Straus, 2018). Our results are consistent with the biogeographic patterns described  
671 above, indicating strong contrasts between Mediterranean sites (in Zone IIIa) and sites in  
672 zones IV and VI in terms of MAAT and MAP.

673 During the LGM, tundra extended across northern Europe while steppes dominated  
674 the Mediterranean areas, resulting in a geographic reduction and fragmentation of boreal  
675 evergreen forests (taiga) and temperate deciduous forests (Tarasov et al., 2000). The mean  
676 value of  $350 \pm 100 \text{ mm.yr}^{-1}$  reconstructed for MAP from the  $\delta^{13}\text{C}_{\text{carb}}$  of the dental apatite of  
677 herbivorous mammals (above) is consistent with this observation. However, a few samples of  
678 *Cervus elaphus* from zone IV, El Cierro and El Ruso, the closest to the Atlantic ocean depict  
679 a  $\delta^{13}\text{C}_{\text{carb}}$ -value low enough to suggest that some years or periods in the year were  
680 characterized by  $\text{MAP} \geq 500 \text{ mm.yr}^{-1}$ . This could mean that the climate in northern Spain was  
681 rather unstable at inter-decadal or inter-centennial scales towards the end of the LGM, or

682 simply that *C. elaphus* used a large seasonal altitudinal range, as observed in modern  
683 specimens in the Alps (Luccarini et al., 2006) or from the Rockies (Morgantini et al., 1989).

684         Geochemical proxies similar to those used in this study were applied to faunal remains  
685 (horse, deer and ibex) recovered from the archaeological site of Peña Capón (Yravedra et al.,  
686 2016), a rock shelter located in central Iberia which contains sedimentary deposits assigned to  
687 Marine Isotope Stage 2 (MIS 2). Yravedra et al. (2016) estimated MAAT for archaeological  
688 levels with a  $^{14}\text{C}$  cal. age of ~23.8 kyr, ranging from 9°C to 12°C, i.e. only slightly below the  
689 present-day MAAT of 12°C–13°C recorded in the locality of Muriel. These estimates for the  
690 central part of the Iberian Peninsula may reflect milder conditions prior to the onset of the  
691 LGM. Nevertheless, it is interesting to note that they are bracketed by our results. It is also  
692 worthy to note that ibex recorded higher  $\delta^{13}\text{C}$  values and lower  $\delta^{18}\text{O}$  values than the other co-  
693 habitating mammals such as Cervidae and Equidae. These data point to a specific habitat for  
694 Caprinae as recently suggested by Jones et al. (2020) who analyzed both carbon and nitrogen  
695 isotope compositions of bone collagen. These authors concluded that the existence of refugia  
696 in south Europe allowed most herbivores to adapt despite harsh and fluctuating climatic  
697 conditions.

698         The LGM climate conditions have been reconstructed from palynological data (e.g.,  
699 Peyron et al., 1998). In the north of Spain (Lago Ajo) and in the south (Padul), MAAT values  
700 were estimated in the 10°C to 5°C range. Palynological estimates of MAP, range from 900-  
701 600 mm in the north of Spain, to close to 200 mm in the south. The temperatures from  
702 palynological records are congruent with the estimates of the present study. However,  
703 whereas paleoprecipitation estimates from palynology or from the present isotopic approach  
704 fit well in zone IIIa, on the Mediterranean side, the MAP estimates for Northern Spain from  
705 pollen proxies are somewhat higher than those based on  $\delta^{13}\text{C}_{\text{carb}}$  values. This leads us to  
706 consider the possibility that isotopic reconstructions, such as used here, vs reconstructions

707 from transfer function using palynological assemblages, do not necessarily encompass the  
708 same space-time dimensions. For example, differences in the seasonality of pollen production  
709 and patterns of altitudinal grazing may result in distinct signals.

710 As mentioned above, the study sites are close to either the Bay of Biscay (in zones IV  
711 and VI) or the western Mediterranean (zone IIIa). Hayes et al. (2005) and Rodrigo-Gámiz et  
712 al. (2014) estimated LGM-SSTs of  $\sim 13.5^{\circ}\text{C}$  off the Mediterranean coastline of Spain,  
713 whereas Kucera et al. (2005) estimated LGM-SST of  $\sim 8^{\circ}\text{C}$  for the Bay of Biscay on the basis  
714 of foraminifera  $\delta^{18}\text{O}$  values. Both values fit with the corresponding inland, but coastal  
715 temperatures reconstructed here, highlighting the strong influence of adjacent marine basin  
716 SSTs on proximal inland MAAT. Moreover, these temperature estimates based on marine as  
717 well as on continental proxies, enforce the hypothesis of cold regional conditions as well as of  
718 a marked difference between the Atlantic and Mediterranean zones; the latter being less  
719 affected by global LGM cooling.

720 At odds with these results are the model outputs of paleo-glaciers (Allen et al., 2008),  
721 which provided both large amounts of precipitation (1000 to 1400  $\text{mm}\cdot\text{yr}^{-1}$ ) and temperature  
722 anomalies from  $-16^{\circ}\text{C}$  to  $-11^{\circ}\text{C}$  in northern and southern Spain, respectively. Such climatic  
723 patterns cannot be easily reconciled with the present knowledge of the LGM vegetation cover  
724 and faunal associations (Sommer and Nadachowski, 2006; Benito Garzón et al., 2007;  
725 Morales-Molino and García-Antón, 2014; Binney et al., 2017; Quinzin et al., 2017).

726 Atmosphere-ocean global climate models (GCMs) computed global mean LGM-air  
727 temperatures  $4^{\circ}\text{C}$  to  $7^{\circ}\text{C}$  lower than Present, when adding feedback effects due to changes in  
728 the vegetation cover and the amount of atmospheric dust (Crucifix and Hewitt, 2005; Jansen  
729 et al., 2007; Roche et al., 2007; Cao et al., 2019). In southwest Europe, the air temperature  
730 anomaly was estimated between  $-8^{\circ}\text{C}$  and  $-4^{\circ}\text{C}$  based on a multi-model regression of proxy  
731 data and PMIP2 model output (Annan and Hargreaves, 2013). Mean annual air temperatures

732 anomalies were also estimated in the range  $-10^{\circ}\text{C}$  to  $-5^{\circ}\text{C}$  for ice-free areas of Europe, based  
733 on a regional climate model (Strandberg et al., 2011). Jost et al. (2005) emphasized the need  
734 of high-resolution spatial climate models to solve discrepancies with reconstructions based on  
735 proxies such as pollen assemblages. Models tend to underestimate the magnitude of cooling  
736 (especially in winter) with the consequence of overestimating the amount of precipitation.  
737 When applied to Europe, most simulated climates, such as the those of the *Paleoclimate*  
738 *Modelling Intercomparison Project* (PMIP) or from refined General Climate Model (GCM),  
739 generate warmer and wetter LGM-conditions than those inferred from palynological or  
740 geochemical proxies (Kageyama et al., 2001; Latombe et al. 2018; present study). Latombe et  
741 al. (2018) study indicates temperatures and precipitation were close to  $5\text{-}6^{\circ}\text{C}$  and  $200\text{-}250$   
742  $\text{mm y}^{-1}$  in northern Spain, close to  $7^{\circ}\text{C}$  and  $160 \text{ mm y}^{-1}$  at Laugerie-Haute, and close to  $11^{\circ}\text{C}$   
743 and  $225 \text{ mm y}^{-1}$  at Nerja, in southern Spain. Within uncertainties, such air temperatures are  
744 coherent with those estimated from our isotopic proxy approach even though Latombe et al.  
745 (2018) obtained slightly lower temperatures for Nerja. Our MAP estimates are generally  
746 slightly higher than those modeled by Latombe et al. (2018), especially in the case of northern  
747 Spain.

748         Spatial resolution is critical in areas either close to the ocean (e.g., Atlantic Ocean) or  
749 along a mountain range (e.g., Pyrenees). Kageyama et al. (2006) performed a comparison of  
750 PMIP models, SSTs from MARGO (*Multiproxy Approach for the Reconstruction of the*  
751 *Glacial Ocean surface*) and pollen-based reconstructions over Europe. These authors  
752 highlighted the main data-model discrepancy observed for western Europe, with winter  
753 temperatures underestimated by all models that could be at least partly explained by a high  
754 interannual variability in the temperatures of the coldest months. However, more recent high-  
755 resolution climatic simulations tend to reduce the discrepancy vs geochemical proxy-derived  
756 temperature estimates. This is for example the case of the central part of Iberia ( $\sim 21 \text{ ka}$ ) with



757 a computed MAAT close to  $7\pm 3^{\circ}\text{C}$  (Burke et al., 2014) that are comparable or only slightly  
758 higher than those inferred from the oxygen isotope composition of large mammals (Yravedra  
759 et al., 2016).

760 The geochemical data presented in our study do not provide a temporal resolution at  
761 the seasonal scale, but large inter-annual variations in winter air temperatures should be  
762 imprinted on the half-year or full year time record provided by mammal tooth enamel. For the  
763 studied archaeological sites located on the Atlantic side, the range of  $\delta^{18}\text{O}_{\text{w-MAP}}$  is 4‰ (Figure  
764 6), which corresponds to a temperature variation of  $\pm 5.5^{\circ}\text{C}$  around the mean, according to  
765 equation (7). If interpreted as inter-decadal or inter-centennial variations in MAAT, such a  
766 magnitude is higher than that observed ( $2\pm 1^{\circ}\text{C}$ ) during periods of relative climate steadiness  
767 (e.g., Corona et al., 2010; Ljungqvist et al., 2019). Whether this temperature variation of  
768  $\pm 5.5^{\circ}\text{C}$  indicates high-frequency climate instabilities in western Europe during the LGM, in  
769 agreement with Jones et al. (2020)'s or Loncaric et al. (1998), remains to be further  
770 investigated.

771 Climate conditions on the Iberian Peninsula are driven by large-scale processes that  
772 create strong regional contrasts in rainfall and temperature values. Our results demonstrate  
773 that these contrasts are reliably recorded in hard tissues and that isotope analyses of vertebrate  
774 remains can be used as proxies of mean annual temperature and precipitations on a regional  
775 scale. We confirm that, during the LGM, populations living in Franco-Cantabria and on the  
776 Mediterranean coast faced different environmental challenges. As the paleontological and  
777 archaeozoological records demonstrate it (Brugal and Yravedra, 2005) this difference  
778 impacted the relative availability of different prey species, which would have required  
779 adjustments of human hunting strategies, potentially driving technological change. Indeed, the  
780 LGM coincides with the appearance of the Solutrean technocomplex, which is geographically  
781 limited to the Iberian Peninsula and France. Three Solutrean “culture areas” (Andalucia,

782 Portugal and Vasco-Cantabria) are described for the Iberian Peninsula (Straus, 2000) and  
783 these differences in the material culture used by human groups could reflect regional  
784 adaptations to contrasting environmental conditions such as those described here. These  
785 results are also consistent with archaeological research using an agent-based model that  
786 suggests that the population of Western Europe was spatially fragmented during the LGM as  
787 a result of climate-driven differences in habitat suitability (Wren and Burke, 2018). In this  
788 latter study, the SE region of the Iberian Peninsula was described as a “sink” during the LGM,  
789 with human population numbers declining periodically and being replenished from a larger  
790 “source” population, located in SE France and NE Spain.

791         Considering the uncertainties associated with our stable isotope proxy approach,  
792 including the altitudinal effect that is not easy to constrain, the present MAAT estimates are  
793 coherent with those inferred from other proxies (pollens, foraminifera) and some recent model  
794 outputs. In the case of MAP reconstructions, the isotopic approach suggests dry environments  
795 in agreement with our knowledge of LGM-flora and faunal associations. However, most  
796 modeling approaches still generate divergent patterns with some of them suggesting  
797 paleoenvironments as wet as those of today, or even more, along with similar MAAT.

798         Future research priorities may focus on the initial conditions required by the GCM  
799 models to reproduce the dry and cold conditions of the LGM in southwestern Europe. In  
800 addition, reconstructing the amplitude of precipitation and air temperature seasonality by  
801 high-resolution incremental sampling of tooth enamel may be of great interest. Indeed,  
802 mammals could have fed on resources (water, vegetation) mainly renewed during the winter  
803 and intermediate seasons, not in summer, hence biasing the isotopic record at least toward too  
804 negative mean air temperatures.

805

806 6. Conclusions

807 Our study documents the carbon and oxygen isotope composition of tooth enamel  
808 carbonate of Cervidae, Equidae and Caprinae remains dated to the LGM in southwest Europe.  
809 The  $\delta^{13}\text{C}$  of tooth enamel carbonate was ultimately used to obtain semi-quantitative estimates  
810 of MAP. Precipitation in the range of  $\sim 250$  to  $550 \text{ mm.yr}^{-1}$  were obtained for Atlantic sites  
811 and values close to  $250 \text{ mm.yr}^{-1}$  for the Mediterranean sites; both estimates are lower than  
812 local precipitation today ( $200\text{--}1000 \text{ mm.yr}^{-1}$ ). Despite the large uncertainties associated with  
813 each step of the method, the reconstruction of a dry and cold LGM environment is consistent  
814 with the faunal and floral associations documented for this period. The limitation of the  $\delta^{13}\text{C}$   
815 method for estimating paleo-precipitation is mainly related to the behavior of the studied  
816 vertebrate species. The observed  $\delta^{13}\text{C}$  differences between Caprinae and Cervidae or Equidae,  
817 for example, most likely reflects habitat use, with Caprinae occupying possibly drier habitats.

818 The  $\delta^{18}\text{O}$  of tooth enamel carbonate was used for estimating MAAT. In southern Spain,  
819 temperatures during the LGM were lower by about  $4\text{--}5^\circ\text{C}$  relative to modern times and lower  
820 by  $5\text{--}8^\circ\text{C}$  in northern Spain and southwest France. Several steps are necessary to calculate  
821 MAAT, and each one potentially propagates sizable uncertainties due to the combined use of  
822 empirical linear equations relating the isotopic compositions of the biomineral, the meteoric  
823 water and the air temperature. Moreover, we identified additional sources of uncertainties.  
824 The first two are related to an “altitude effect” and a “source effect” that lead to an  
825 overestimate of the air temperature differences between the LGM and the present day on the  
826 order of a few  $^\circ\text{C}$ . The third one, which we refer to as the “reservoir effect”, relates to the  $^{18}\text{O}$ -  
827 enrichment of meteoric waters stored in a natural reservoir (pond, lake, snow cover) open to  
828 the atmosphere and subsequently exposed to evaporation. In this case, the lower the residence  
829 time of water in the reservoir, the higher the increase in the  $\delta^{18}\text{O}$  of stored water, hence  
830 leading to a potential overestimation of air temperatures.

831 At first glance, our estimates of MAP and MAAT are compatible with the faunal  
832 associations described in the archaeological sites of southwestern Europe with generally cold  
833 and dry, open environments such as tundra and dry steppe. Sea surface temperatures inferred  
834 from the oxygen isotope composition of planktonic foraminifera enforce the hypothesis of  
835 cold regional conditions as well as a marked difference between the Atlantic and  
836 Mediterranean sides; the latter being less impacted by the global cooling.

837 Close to montane areas, topography is highly variable with a juxtaposition of micro-  
838 climates that makes a comparison of geochemical proxy results with model outputs risky and  
839 potentially fruitless, considering the unresolved differences in temporal and spatial resolution  
840 inherent in both scientific approaches. Nevertheless, there is room for improvement with, for  
841 example, the reconstitution of the seasonal amplitude of precipitation and air temperature  
842 performed by high-resolution incremental sampling of vertebrate tooth enamel. Precipitation  
843 and air temperature for the coldest and warmest months could be directly compared to model  
844 output with the aim to identify potential biases intrinsic to each method.

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861

862

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**Table captions:**

Table 1: Carbon and oxygen isotope compositions of tooth enamel from large herbivorous mammal remains of the LGM recovered from southwest France (Laugerie-Haute), north Spain (El Cierro, El Ruso, El Pendo, Hornos de la Peña), east Spain (Malladetes) and southeast Spain (Nerja). See the Figure 1 for the geographic locations of these archaeological sites. Studied taxa and  $^{14}\text{C}$  ages are also provided along with the calculated oxygen isotope compositions of drinking and diet water ( $\delta^{18}\text{O}_w$ ) and the carbon isotope composition of their diet ( $\delta^{13}\text{C}_{\text{diet}}$ ). See the text for more explanations. Calendar ages were determined using the most recent calibration curve data for the Northern Hemisphere, IntCal20 (Reimer et al., 2020). Calibrated date ranges correspond to 92.9% probability ( $2\sigma$ ).

Table 2: Synthesis of calculated mean annual air temperatures (MAAT) and mean annual precipitation (MAP) during the LGM, estimated. from the  $\delta^{13}\text{C}$ - and  $\delta^{18}\text{O}$ -values of tooth enamel carbonate from large herbivorous mammal remains.

1449

1450 **Figure captions:**

1451

1452 Figure 1: Location of the archaeological sites investigated: Laugerie-Haute, in southwestern  
1453 France; El Cierro in the Province of Asturias, Hornos de la Peña, El Pendo and El Ruso  
1454 in Cantabria, Nerja in the Province of Málaga and Malladetes, in the Province of  
1455 Valencia.

1456

1457 Figure 2: Frequency histogram of the calculated  $\delta^{13}\text{C}$ -value of mammal diets. Cervidae and  
1458 Equidae are represented in blue; Caprinae, in red. The Gaussian curves were obtained  
1459 by parametric estimation using PAST4.02 software (Hammer et al., 2001). These curves  
1460 may slightly differ from those obtained by least-squares approximations (performed  
1461 using 10,000 iterations) according to the general equation of normal distribution as  
1462 follows:  $y = m1 + m2 * \exp\left(-\frac{(x-m3)^2}{(m4)^2}\right)$ . Constant uncertainties are  $\pm 1\sigma$ . For Cervidae  
1463 and Equidae:  $m1 = 0.35 \pm 0.37$ ;  $m2 = 7.75 \pm 1.24$ ;  $m3 = -24.02 \pm 0.06$  and  $m4 = 0.48 \pm 0.09$   
1464 with  $R^2 = 0.71$ ; for Caprinae:  $m1 = 0.17 \pm 0.20$ ;  $m2 = 8.33 \pm 0.62$ ;  $m3 = -22.46 \pm 0.03$  and  
1465  $m4 = -0.60 \pm 0.05$  with  $R^2 = 0.92$ .

1466

1467 Figure 3: A) Modern and reconstructed MAP ( $\text{mm yr}^{-1}$ ) for the various French and Spanish  
1468 archaeological sites. Modern cities (Cestas-Pierroton for Laugerie-Haute, Santander for  
1469 northern Spain, Valencia for Malladates and Almeria for Nerja) in the vicinity of  
1470 studied sites were ranked according to increasing MAP that roughly follow a S–N  
1471 geographic trend. See Table 2 for the output of calculation. B) estimated MAP taking  
1472 into account the lower atmospheric  $\text{pCO}_2$  during the LGM relatively to the Holocene  
1473 (see section 5.2.1 for a detailed explanation).

1474

1475 Figure 4: Present-day linear relationship between the dew point temperature in °C ( $T_d$ ) and  
1476 the mean weighted  $\delta^{18}\text{O}$ -value ( $\delta^{18}\text{O}_{\text{mw}}$ ) of precipitations, extracted from the  
1477 IAEA/WMO database. The database was filtered to only include meteorological sites  
1478 above  $|32^\circ|$  latitude.  $T_d$  is the dew point (°C). The equation of the linear regression is  $T_d$   
1479  $= 1.30(\pm 0.06)\delta^{18}\text{O}_{\text{mw}} + 15.69(\pm 0.67)$  with  $R^2 = 0.83$ .

1480

1481 Figure 5: Present-day MAAT– $\delta^{18}\text{O}_{\text{mw}}$  linear relationships extracted from the IAEA/WMO  
1482 database. A) Global data above  $32^\circ\text{N}$  with 15 outliers removed after linear regression  
1483 analysis:  $\text{MAAT} = 1.42(\pm 0.04)\delta^{18}\text{O}_{\text{mw}} + 22.02(\pm 0.44)$ ; B) Global data for sites above  
1484  $32^\circ\text{N}$  and with a MAAT  $> 0^\circ\text{C}$ :  $\text{MAAT} = 1.40(\pm 0.08)\delta^{18}\text{O}_{\text{mw}} + 21.86(\pm 0.64)$ .

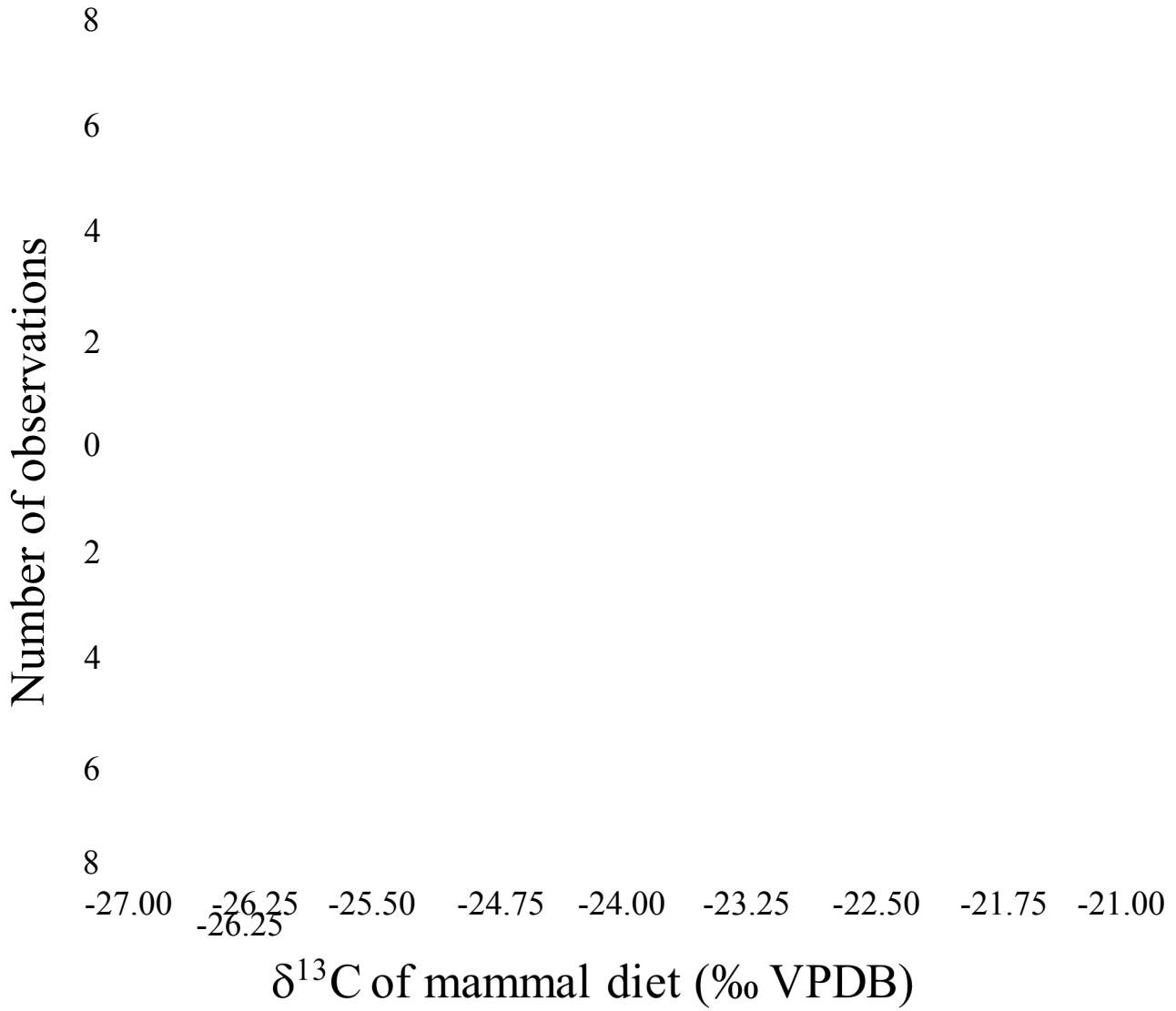
1485

1486 Figure 6: Frequency histogram of  $\delta^{18}\text{O}$  of meteoric waters calculated from the  $\delta^{18}\text{O}$  of apatite  
1487 carbonate from the sampled teeth of Cervidae, Equidae and Caprinae. Archaeological  
1488 sites located from northern Spain and SW France, are represented in blue while the  
1489 Mediterranean sites of Malladates and Nerja are represented in red. The Gaussian  
1490 curves were obtained by parametric estimation using PAST4.02 software (Hammer et  
1491 al., 2001). These fitting curves may slightly differ from those obtained by least-squares  
1492 approximations (performed by using 10,000 iterations) according to the general  
1493 equation of normal distribution as follows:  $y = m1 + m2 * \exp\left(-\frac{(x-m3)^2}{m4}\right)$ . For Atlantic  
1494 sites:  $m1 = 1.35\pm 0.79$ ;  $m2 = 13.17\pm 1.57$ ;  $m3 = -9.98\pm 0.09$  and  $m4 = 0.97\pm 0.15$  with  $R^2$   
1495  $= 0.89$ . For Mediterranean sites:  $m1 = 0.12\pm 0.84$ ;  $m2 = 3.74\pm 1.09$ ;  $m3 = -5.28\pm 0.19$  and  
1496  $m4 = 0.97\pm 0.41$  with  $R^2 = 0.70$ . The constant uncertainties are  $\pm 1\sigma$ .

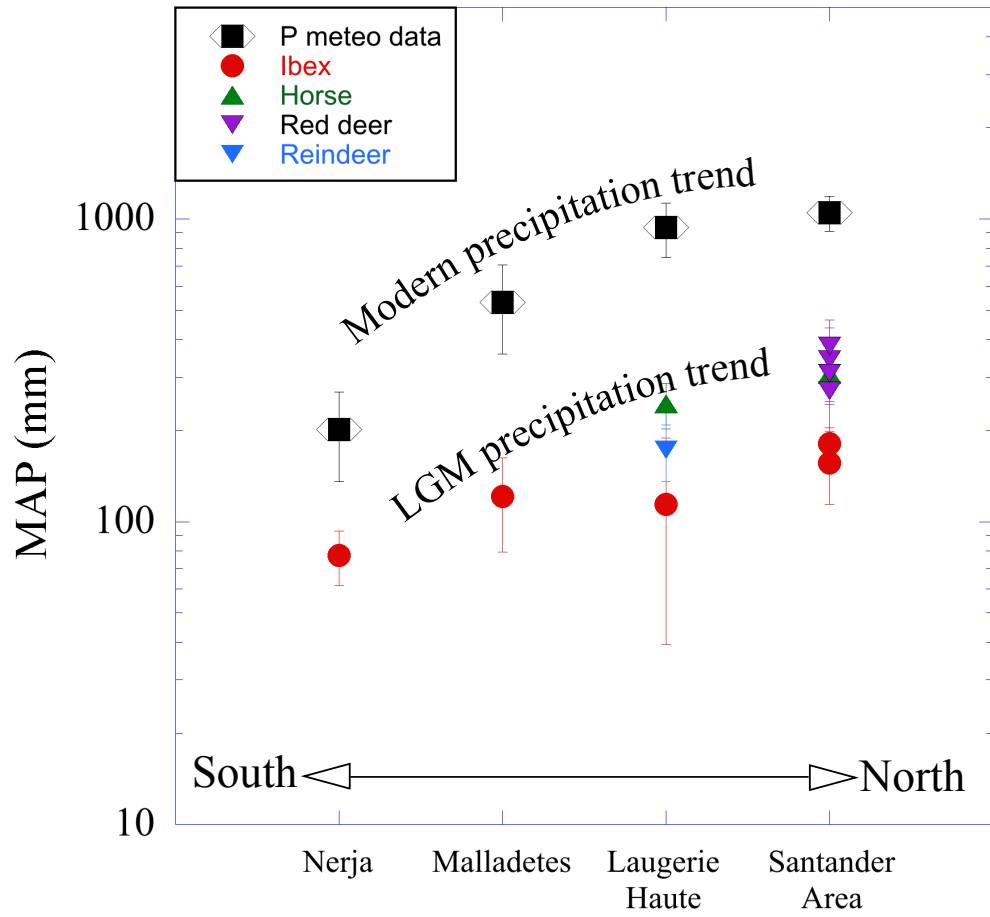
1497

1498 Figure 7: Modern and reconstructed MAAT (°C) of the sampled archaeological sites. Modern  
1499 cities (Cestas-Pierroton for Laugerie-Haute, Santander for northern Spain, Valencia for  
1500 Malladates and Almeria for Nerja) in the vicinity of studied sites were ranked according  
1501 to a decreasing MAAT that roughly follow a S–N trend. See Table 2 for the output of  
1502 calculation. Temperatures were calculated assuming an oxygen isotope composition of  
1503 oceanic surface waters of +0.8‰ (VSMOW).

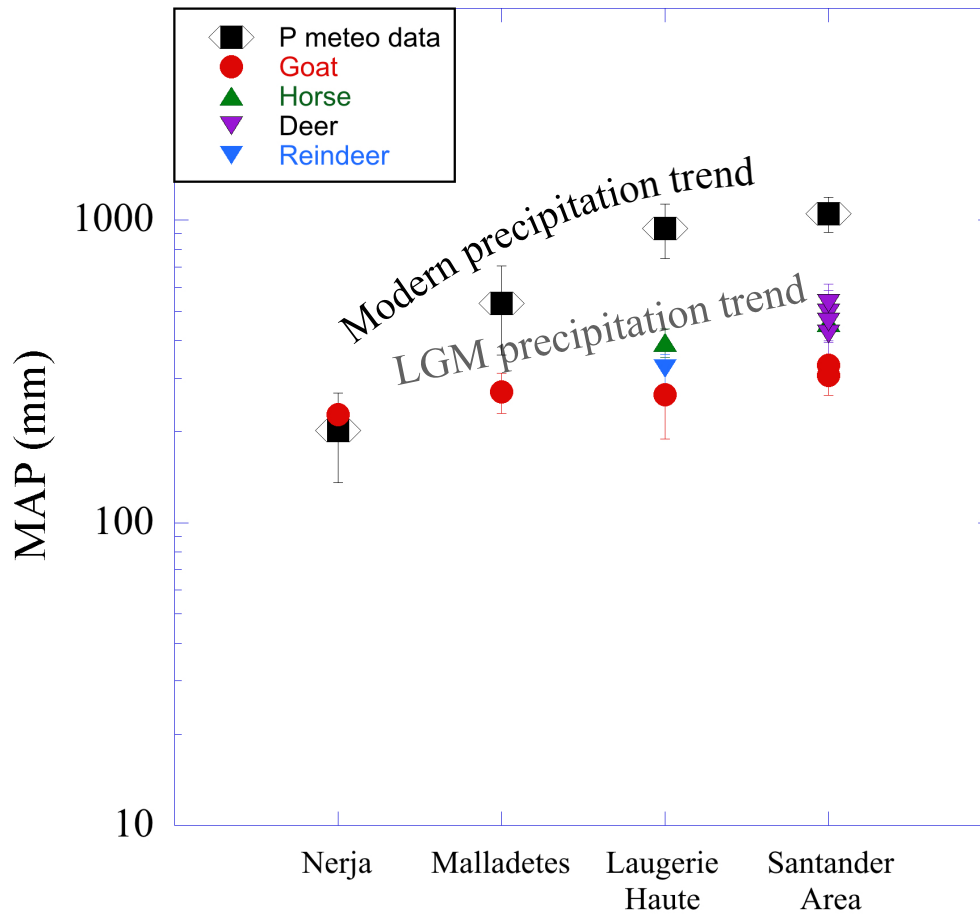




A)



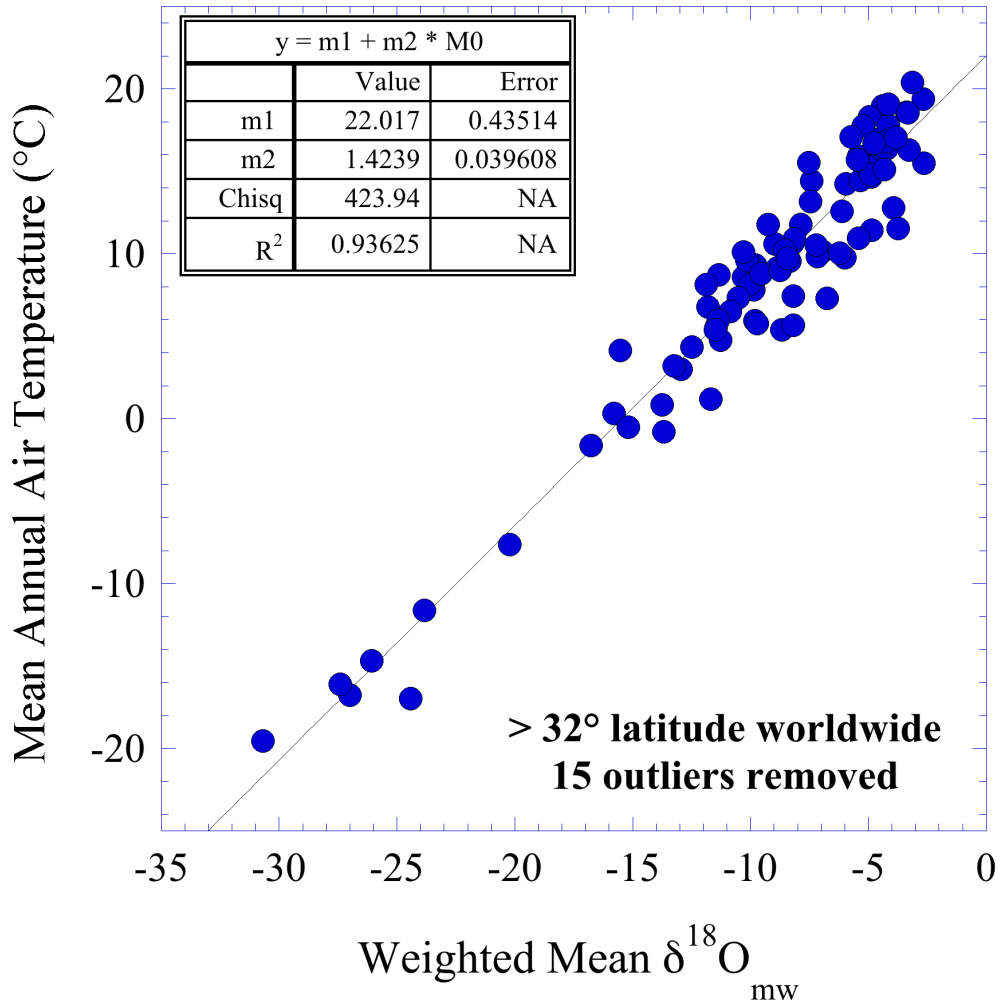
B)



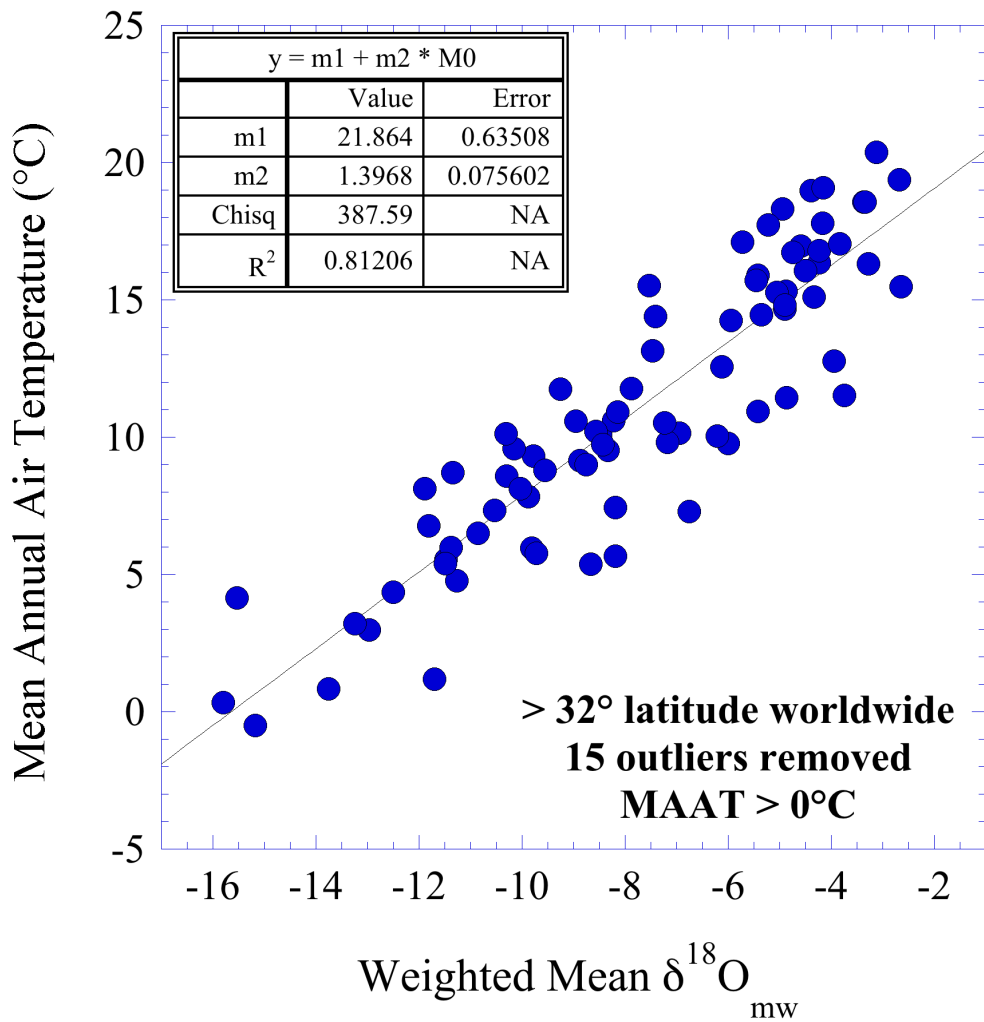


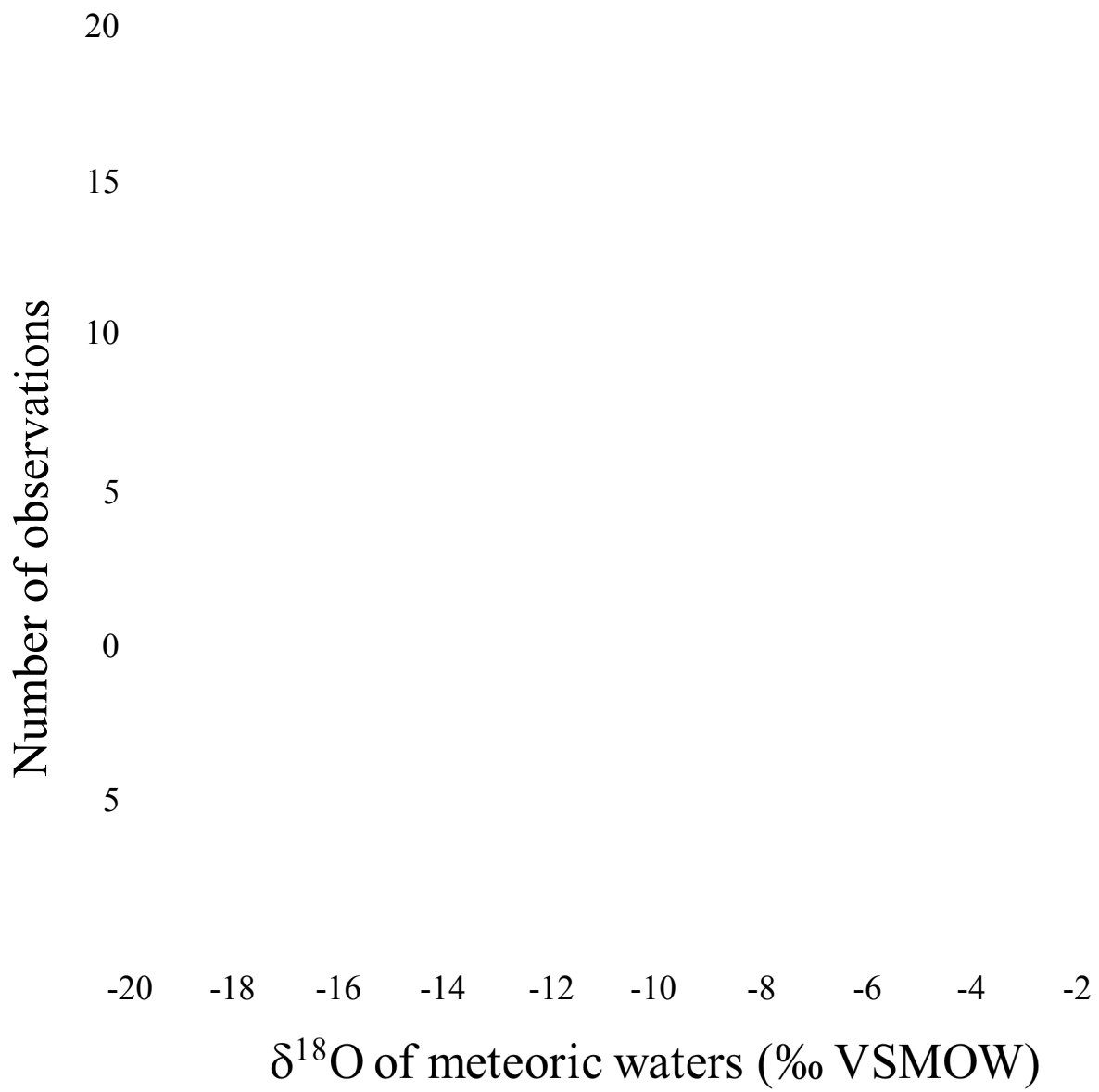


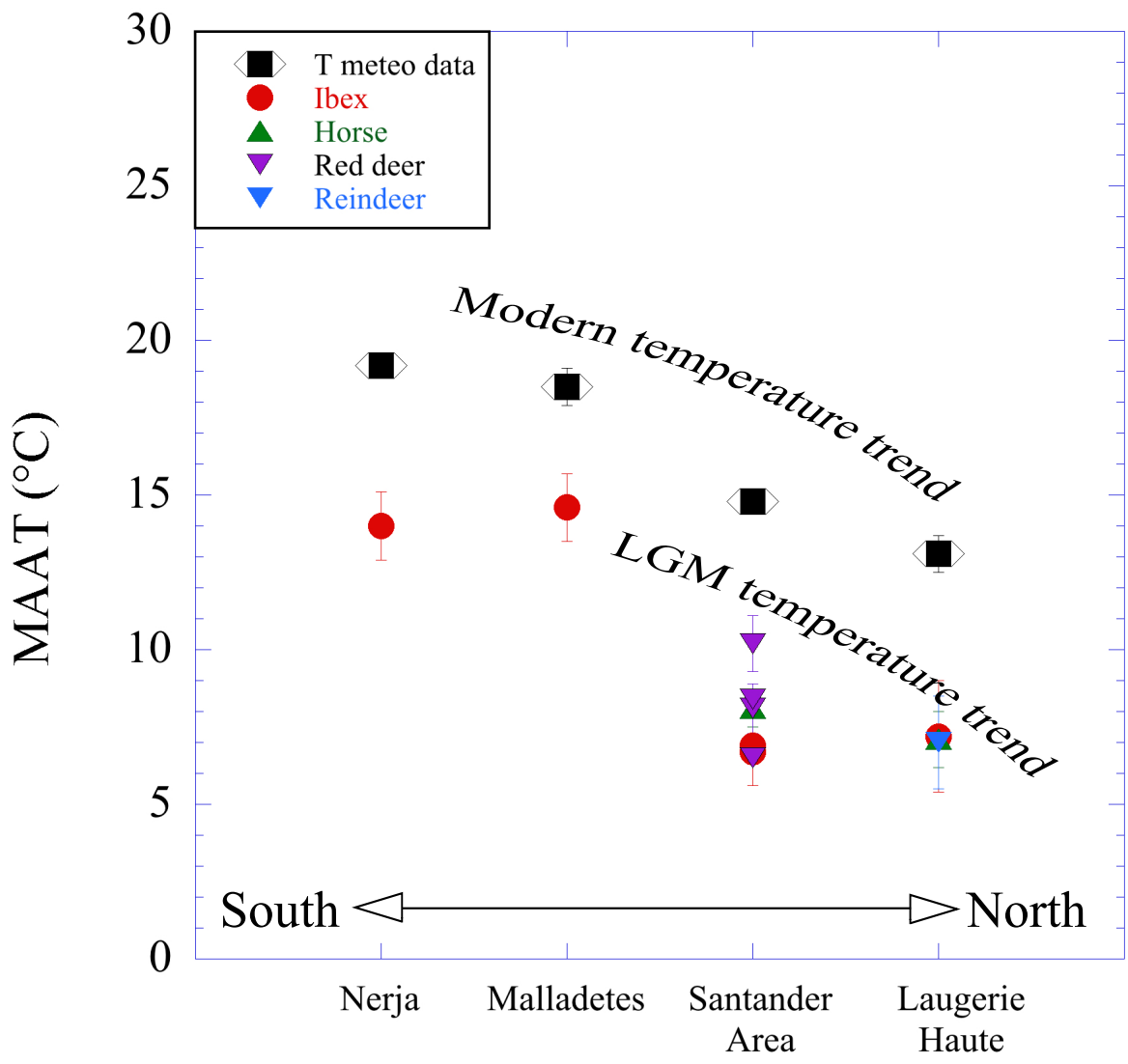
A)



B)







Site	Lab#	Level	<sup>14</sup> C dates BP	+/-	<sup>14</sup> C cal BP	Lithic scale	Taxon	Material	$\delta^{13}C_c$	$\delta^{13}C_{diet}$	$\Delta^{13}C_{leaf}$	P	$\delta^{18}O_c$	$\delta^{18}O_c$	$\delta^{18}O_{p\ calc.}$	$\delta^{18}O_{w\ cor.ice (1.2)}$	$\delta^{18}O_{w\ cor.ice (0.8)}$	T ( $\delta^{18}O_{sw} = 1.2$ )	T ( $\delta^{18}O_{sw} = 0.8$ )
					IntCal20 (92.9%)														
									% VPDB	% VPDB	(mm)	% VPDB	% VSMOW	% VSMOW	% VSMOW	% VSMOW	% VSMOW	(°C)	(°C)
El Cierro	EC-1B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.21	-24.55	17.99	336	-6.6	24.1	15.1	-10.4	-10.0	6.9	7.5
El Cierro	EC-2B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.12	-24.46	17.89	323	-6.1	24.5	15.5	-10.0	-9.6	7.4	8.0
El Cierro	EC-3B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.94	-24.28	17.71	298	-6.6	24.0	15.0	-10.5	-10.1	6.8	7.4
El Cierro	EC-4B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.42	-24.76	18.22	367	-5.9	24.8	15.8	-9.8	-9.4	7.7	8.3
El Cierro	EC-5B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.92	-24.26	17.69	296	-6.7	24.0	15.0	-10.5	-10.1	6.8	7.4
El Cierro	EC-17B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower D	-12.04	-25.38	18.86	463	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Cierro	EC-19B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-12.28	-25.62	19.11	505	-5.5	25.1	16.1	-9.5	-9.1	8.2	8.8
El Cierro	EC-20B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.06	-24.40	17.84	315	-4.8	25.9	16.9	-8.8	-8.4	9.2	9.8
El Cierro	EC-21B	G	15580	75	19011-18735	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 lower G	-10.46	-23.30	16.69	182	-6.3	24.3	15.3	-11.0	-10.6	6.1	6.7
El Cierro	EC-22B	G	15580	75	19011-18735	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower G	-10.67	-23.51	16.91	205	-6.0	24.7	15.7	-10.5	-10.1	6.7	7.3
El Cierro	EC-6B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.19	-24.53	17.97	333	-6.2	24.4	15.5	-10.1	-9.7	7.3	7.9
El Cierro	EC-7B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower D	-11.43	-24.77	18.22	367	-6.3	24.3	15.3	-10.2	-9.8	7.2	7.8
El Cierro	EC-9B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.43	-23.77	17.18	236	-6.0	24.7	15.7	-9.9	-9.5	7.7	8.3
El Cierro	EC-10B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.48	-24.82	18.28	375	-6.6	24.1	15.1	-10.4	-10.0	6.9	7.5
El Cierro	EC-11B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.58	-24.92	18.38	390	-6.4	24.3	15.3	-10.2	-9.8	7.2	7.8
El Cierro	EC-12B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-10.73	-24.07	17.50	272	-5.8	24.9	15.9	-9.7	-9.3	7.9	8.5
El Cierro	EC-13B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.10	-24.44	17.88	321	-6.0	24.7	15.7	-9.9	-9.5	7.7	8.3
El Cierro	EC-14B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-10.98	-24.32	17.75	304	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Cierro	EC-15B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-10.99	-24.33	17.77	306	-6.5	24.2	15.2	-10.4	-10.0	7.0	7.6
El Cierro	EC-23B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower G	-10.33	-23.17	16.56	169	-6.6	24.1	15.1	-11.2	-10.8	5.8	6.4
El Cierro	EC-24E	H	LGM	N/A	N/A	Upper Solutrean	<i>Capra pyrenaica</i>	M2 lower G	-8.93	-21.77	15.09	44	-6.4	24.3	15.3	-11.0	-10.6	6.0	6.6
El Pendo	PE-1B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2/M3? upper G	-10.66	-24.00	17.42	263	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Pendo	PE-2B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.80	-24.14	17.56	280	-5.5	25.2	16.2	-9.4	-9.0	8.3	8.9
El Pendo	PE-3B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper D	-10.52	-23.86	17.27	246	-5.4	25.3	16.3	-9.4	-9.0	8.4	9.0
El Pendo	PE-4B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.57	-23.91	17.33	252	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Pendo	PE-5B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.51	-23.85	17.26	244	-5.4	25.3	16.3	-9.3	-8.9	8.4	9.0
El Pendo	PE-6B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper D	-11.04	-24.38	17.81	312	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Pendo	PE-7B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper D	-10.90	-24.24	17.67	294	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Ruso	RU-2B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.50	-23.84	17.25	243	-3.7	27.1	18.0	-7.9	-7.5	10.5	11.1
El Ruso	RU-3B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper D	-10.59	-23.93	17.35	255	-4.3	26.5	17.4	-8.4	-8.0	9.8	10.4
El Ruso	RU-5B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-12.89	-26.23	19.75	622	-3.7	27.1	18.0	-7.8	-7.4	10.5	11.1
El Ruso	RU-6B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.58	-23.92	17.33	253	-4.6	26.1	17.1	-8.7	-8.3	9.4	10.0
El Ruso	RU-7B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.84	-24.18	17.60	285	-4.9	25.8	16.8	-8.9	-8.5	9.0	9.6
El Ruso	RU-8B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M1 upper G	-10.11	-23.45	16.84	198	-5.6	25.1	16.1	-9.6	-9.2	8.1	8.7
Hornos de la Peña	HP-1e	B	18450	520	23425-21038	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.52	-24.86	18.31	380	-7.4	23.2	14.3	-11.2	-10.8	5.9	6.5
Hornos de la Peña	HP-4B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-9.64	-22.48	15.84	103	-6.7	23.9	14.9	-11.4	-11.0	5.5	6.1
Hornos de la Peña	HP-5B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-9.98	-22.82	16.19	134	-6.8	23.9	14.9	-11.4	-11.0	5.5	6.1
Hornos de la Peña	HP-6B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-10.00	-22.84	16.21	136	-5.3	25.4	16.4	-9.8	-9.4	7.7	8.3
Hornos de la Peña	HP-7e	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 upper D	-10.71	-23.55	16.95	210	-6.1	24.5	15.6	-10.7	-10.3	6.5	7.1
Hornos de la Peña	HP-7b	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 upper D	-10.92	-23.76	17.16	233	-6.1	24.6	15.6	-10.7	-10.3	6.5	7.1
Hornos de la Peña	HP-8B	B	18450	520	23425-21038	Lower Magdalenian	<i>Equus caballus</i>	M3 lower D	-10.78	-24.28	17.71	299	-5.9	24.8	15.8	-9.8	-9.4	7.8	8.4
Hornos de la Peña	HP-9B	B	18450	520	23425-21038	Lower Magdalenian	<i>Equus caballus</i>	M3 lower G	-10.90	-24.40	17.84	315	-6.3	24.4	15.4	-10.3	-9.9	7.1	7.7
Hornos de la Peña	HP-11B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 upper D	-9.90	-22.74	16.11	126	-7.2	23.5	14.5	-11.9	-11.5	4.9	5.5
Hornos de la Peña	HP-12B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 upper D	-10.40	-23.24	16.63	176	-5.3	25.4	16.4	-9.9	-9.5	7.7	8.3
Hornos de la Peña	HP-13B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 lower D	-9.97	-22.81	16.17	133	-7.4	23.2	14.3	-12.1	-11.7	4.5	5.1
Hornos de la Peña	HP-14B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M2 lower D	-10.22	-23.06	16.44	158	-5.2	25.5	16.5	-9.7	-9.3	7.9	8.5
Laugerie-Haute E.	LH-2B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Capra pyrenaica</i>	M2 upper G	-9.24	-22.08	15.42	69	-4.4	26.3	17.3	-8.9	-8.5	9.1	9.7
Laugerie-Haute E.	LH-3B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Capra pyrenaica</i>	M2 lower D	-10.82	-23.66	17.06	222	-6.2	24.4	15.4	-10.9	-10.5	6.3	6.9
Laugerie-Haute E.	LH-4B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.45	-22.85	16.22	137	-5.5	25.2	16.2	-10.1	-9.7	7.4	8.0
Laugerie-Haute E.	LH-5B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower D	-10.17	-22.57	15.93	111	-4.5	26.2	17.2	-8.9	-8.5	9.0	9.6
Laugerie-Haute E.	LH-6B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M2 lower D	-9.87	-22.27	15.62	85	-7.4	23.3	14.3	-12.1	-11.7	4.5	5.1
Laugerie-Haute E.	LH-7B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-9.70	-22.10	15.44	70	-6.2	24.4	15.4	-10.9	-10.5	6.3	6.9
Laugerie-Haute E.	LH-8B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.56	-22.96	16.34	148	-5.3	25.4	16.4	-9.8	-9.4	7.7	8.3
Laugerie-Haute E.	LH-14B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.19	-22.59	15.95	112	-5.5	25.2	16.2	-10.0	-9.6	7.5	8.1
Laugerie-Haute E.	LH-15B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M2 lower G	-10.14	-22.54	15.89	108	-7.4	23.2	14.2	-12.2	-11.8	4.4	5.0
Laugerie-Haute E.	LH-9B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Saiga tatarica</i>	M3 upper G	-10.55	-22.95	16.33	147	-5.0	25.7	16.7	-9.5	-9.1	8.3	8.9
Laugerie-Haute E.	LH-13B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Rupicapra rupicapra</i>	M3 lower G	-9.52	-22.36	15.71	92	-5.6	25.1	16.1	-10.2	-9.8	7.2	7.8
Laugerie-Haute E.	LH-10B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Equus caballus</i>	M3 upper D	-10.59	-24.09	17.51	274	-6.3	24.3	15.3	-10.3	-9.9	7.0	7.6
Laugerie-Haute E.	LH-11B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Equus caballus</i>	M3 upper D	-10.10	-23.60	17.00	215	-7.0	23.6	14.7	-11.0	-10.6	6.0	6.6
Laugerie-Haute E.	LH-12B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Capra pyrenaica</i>	M3 lower G	-9.66	-22.50	15.86	105	-7.0	23.6	14.7	-11.7	-11.3	5.1	5.7
Laugerie-Haute E.	LH-16B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-9.92	-23.26	16.64	178	-7.7	22.9	14.0	-10.7	-10.3	6.5	7.1
Laugerie-Haute E.	LH-17B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-10.18	-23.52	16.92	206	-6.9	23.7	14.7	-9.8	-9.4	7.8	8.4
Laugerie-Haute E.	LH-18B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-9.47	-22.81	16.18	13							

	MAP (mm)	MAP* (mm)	P (S.D.) (mm)	$\delta^{18}\text{Ow}$ ‰ VSMOW ( $\delta^{18}\text{Osw} = +1.2$ )	$\delta^{18}\text{Ow}$ ‰ VSMOW ( $\delta^{18}\text{Osw} = +0.8$ )	$\delta^{18}\text{Ow}$ (S.D.) ‰ VSMOW	MAAT (°C)	MAAT (S.D.) (°C)	T-EUROPE (°C) Skrzypek et al. 2011 ( $\delta^{18}\text{Osw} = +1.2$ )	T-EUROPE (°C) Skrzypek et al. 2011 ( $\delta^{18}\text{Osw} = +0.8$ )	S.D.	MAT anomaly (°C) ( $\delta^{18}\text{Osw} = +1.2$ )	MAT anomaly (°C) ( $\delta^{18}\text{Osw} = +0.8$ )	MAP anomaly (mm)
<b>Modern meteo data for cities close to the archaeological sites:</b>														
Almeria	202.0	N/A	66.2	-5.8		1.2	19.2	0.4						
Cestas-Pierroton	937.3	N/A	191.5	-5.8		0.7	13.1	0.6						
Santander	1049.9	N/A	140.3	-5.8		0.3	14.8	0.4						
Valencia	531.7	N/A	172.9	-5.2		0.7	18.5	0.6						
<b>MAP, MAT and their anomalies relative to present-days calculated for the studied archaeological sites:</b>														
<b>Nerja (≈Almeria)</b>														
<i>Capra</i>	78	228	16	-5.8	-5.4	0.8	N/A	N/A	13.4	14.0	1.1	-5.8	-5.2	-125
<b>Laugerie-Haute (≈ Cestas)</b>														
Caprinae	118	268	48	-10.4	-10.0	1.2	N/A	N/A	6.9	7.5	1.7	-6.2	-5.6	-819
Caprinae	120	270	39	-9.8	-9.4	0.5	N/A	N/A	7.8	8.4	0.7	-5.3	-4.7	-818
<i>Equus</i>	245	395	42	-11.9	-11.5	0.7	N/A	N/A	6.5	7.1	0.9	-6.6	-6.0	-693
Caprinae	105	255	n.a.	-11.7	-11.3	n.a.	N/A	N/A	5.1	5.7	N/A	-8.0	-7.4	-833
<i>Rangifer tarandus</i>	172	322	37	-10.8	-10.4	1.0	N/A	N/A	6.4	7.0	1.5	-6.7	-6.1	-765
<b>Malladetes (≈Valencia)</b>														
<i>Capra</i>	121	271	42	-5.4	-5.0	0.8	N/A	N/A	14.0	14.6	1.1	-4.5	-3.9	-411
<b>El Cierro (≈ Santander)</b>														
<i>Cervus elaphus</i>	363	513	79	-10.0	-9.6	0.6	N/A	N/A	7.6	8.2	0.8	-7.2	-6.6	-687
<i>Capra</i>	194	344	16	-10.8	-10.4	0.3	N/A	N/A	6.4	7.0	0.4	-8.4	-7.8	-856
<i>Cervus elaphus</i>	323	473	50	-10.1	-9.7	0.2	N/A	N/A	7.4	8.0	0.3	-7.4	-6.8	-727
<i>Capra</i>	169	319	n.a.	-11.2	-10.8	n.a.	N/A	N/A	5.8	6.4	N/A	-9.0	-8.4	-881
<b>El Pendo (≈ Santander)</b>														
<i>Cervus elaphus</i>	270	420	26	-9.8	-9.4	0.3	N/A	N/A	7.8	8.4	0.5	-7.0	-6.4	-780
<b>El Ruso (≈ Santander)</b>														
<i>Cervus elaphus</i>	310	460	156	-8.5	-8.1	0.7	N/A	N/A	9.6	10.2	0.9	-5.2	-4.6	-740
<b>Hornos de la Pena (≈ Santander)</b>														
<i>Cervus elaphus</i>	380	530	n.a.	-11.2	-10.8	n.a.	N/A	N/A	5.9	6.5	N/A	-8.9	-8.3	-670
<i>Capra &amp; Rupicapra</i>	157	307	43	-10.8	-10.4	0.9	N/A	N/A	6.3	6.9	1.3	-8.5	-7.9	-893
<i>Equus</i>	307	457	11	-11.1	-10.7	0.4	N/A	N/A	7.5	8.1	0.6	-7.3	-6.7	-743

MAP = Mean Annual Precipitation in mm

MAP\* = Mean Annual Precipitation in mm corrected from the LGM pCO<sub>2</sub> estimate

$\delta^{18}\text{Ow}$  = mean oxygen isotope composition of precipitations

$\delta^{18}\text{Osw}$  = mean oxygen isotope composition of oceanic surface waters

MAAT = Mean Annual Air Temperatures obtained from IAEA/WMO database

MAT = calculated Mean Air Temperatures at archaeological sites

MAT anomaly = anomaly in MAT relative to present-days

MAP anomaly = anomaly in MAP relative to present-days