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# Environmental conditions in the Massif Central during the Upper Palaeolithic using stable isotope tracking ( $^{13}\text{C}$ , $^{15}\text{N}$ ) of bone collagen from large herbivores

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**ABSTRACT:** The environmental conditions experienced by hunter-gatherers during the second part of the Upper Palaeolithic (ca. 28 000–15 000 cal BP) are poorly known in the mid-elevation volcanic mountains of the Massif Central in southern France. The stable isotope ratios of carbon and nitrogen ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) in bone collagen of large herbivores can track their diet and habitat, reflecting local abiotic conditions (temperature, aridity, altitude). Due to poor preservation of skeletal organic matter in the region, new radiocarbon dating was conducted on a limited number of quality-controlled collagen samples, based on a minimum carbon content of 30%. They document three main phases of occupation corresponding to the Final Gravettian, the Badegoulian and the Magdalenian, each of which is represented in different regions of the Allier and Loire valleys. Over time, a decrease in horse  $\delta^{15}\text{N}$  values, the best documented species of large herbivores, is found between the Final Gravettian (ca. 26 700–25 600 cal BP), around the Last Glacial Maximum and the Badegoulian (ca. 21 900–19 200 cal BP), followed by an increase in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values during the Magdalenian (ca. 19 100–16 600 cal BP). During the Badegoulian, the  $\delta^{15}\text{N}$  values of the horses were lower than those of their counterparts in southwestern France, testifying to harsh climatic conditions favourable to a tundra-like landscape, also reflected in the higher horse and reindeer  $\delta^{13}\text{C}$  values in the Allier valley compared to those in southwestern France. The relatively high  $\delta^{13}\text{C}$  and low  $\delta^{15}\text{N}$  values of a Final Gravettian wolf from the Allier valley suggests reindeer as a preferred prey, in line with their high abundance in the archaeological sites. Game access, rather than climatic conditions or lithic resources, seems to have motivated human groups to occupy the Massif Central during the Upper Palaeolithic.

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**KEYWORDS:** environment; horse; ibex; reindeer; south-central France

## Introduction

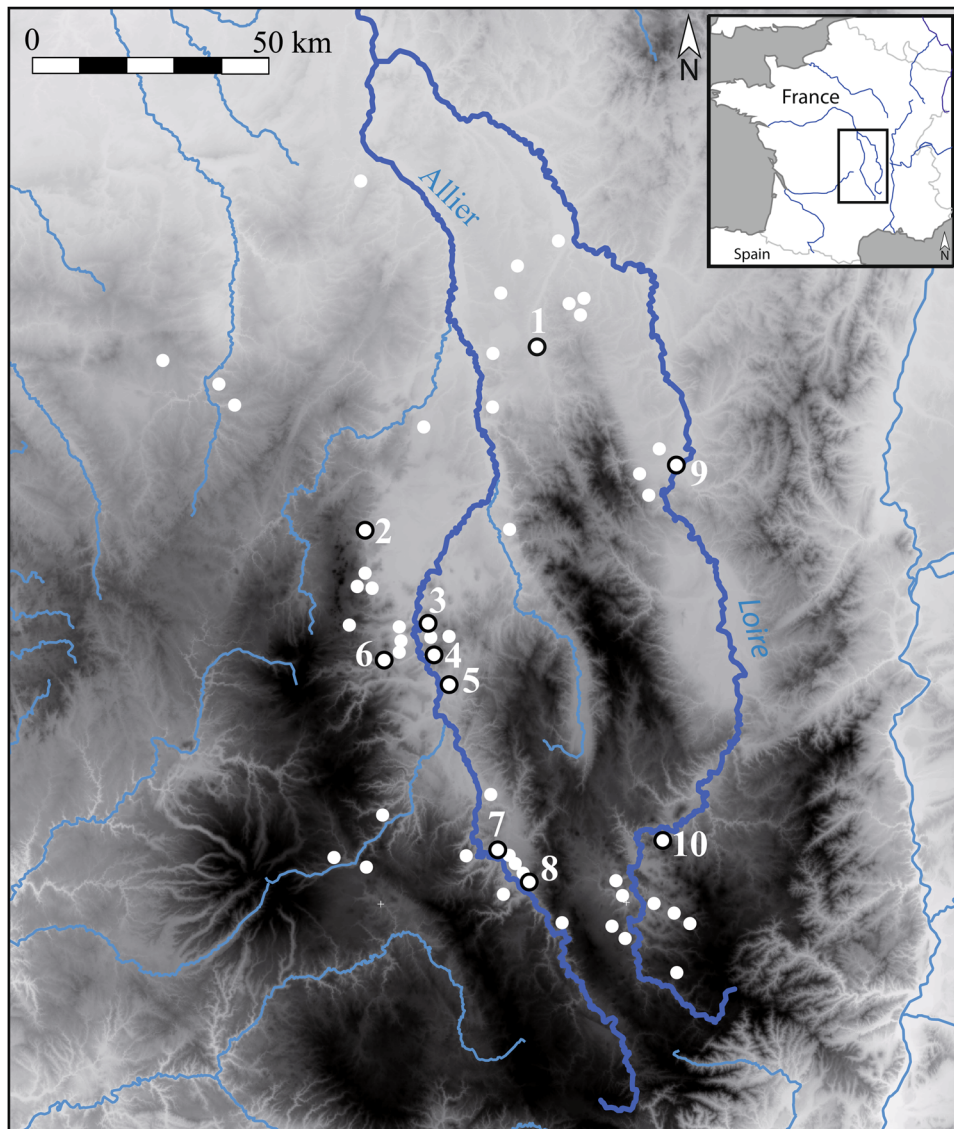
The Upper Palaeolithic societies of the Massif Central are unique in France in that they procured flint raw material from a region more than 250 km away, whereas elsewhere in France most of the lithic resources were of local origin (Masson, 1981). In addition, little is known about the settlement pattern of this large area, since sites dating before the Upper Magdalenian (16 000 cal BP) are rare despite reduced volcanic activity between ca. 29 000 and 13 500 cal BP (Raynal and Dugas, 1984; Vernet, 2013), and most of them have been identified as resulting from short-term occupations, unlike sites in southwestern France or in the Pyrenees. Upper Palaeolithic groups occupied the middle and upper valleys of the Loire and Allier rivers (Figure 1), as indicated by the distribution of the archaeological sites (sheltered, cave and open-air), never located above 820 m elevation in a context of mid-elevation volcanic mountains (300–1800 m asl). An integrated study of the exploitation of animal resources (e.g. hunting seasons based on teeth and antler study) has demonstrated the

absence of winter occupation, linked to the absence of humans and/or reindeer during the cold season (Fontana, 2022, 2005; Fontana et al., 2009). The same research demonstrated the absence of sites where hunting weapons and tools were manufactured from large reindeer antlers from male adults, although such remains have been identified at a few sites. Procurement and exploitation of antler material would have taken place during the seasonal occupation of territories outside the Massif Central. The lithic raw material originated primarily from the south of the Paris Basin (e.g. Masson, 1981; Delvigne et al., 2018), a potential winter territory for the Gravettian and Magdalenian groups. These data have made it possible to propose a pattern of nomadic cycles and group mobility quite different from those of other regions south of the Loire (Fontana, 2017, 2022; Fontana et al., 2018). This raises several questions related to the exploited environments from the plain in the northern Allier to the southern Loire and Allier valleys. More specifically, could these contexts be inhospitable for human or even animal settlement during the last cold period of the Pleistocene, thus explaining the absence of winter occupations observed so far?

The environments of the Late Pleistocene remain poorly known in the Massif Central mountains (reaching 1885 m asl) and knowledge is based on palynological analysis of data

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**Figure 1.** Maps with locations of the selected sites in the Massif Central. 1 = Grotte des Fées, 2 = Blanzat, 3 = Pont de Longues, 4 = Lépétade-Chabasse, 5 = Le Bay, 6 = Thônes-Auzary, 7 = Le Blot, 8 = Abri du Rond, 9 = Vigne-Brun, 10 = Cottier. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

obtained in peaty, marshy and lacustrine contexts in sites located in the centre and south of the Massif. These data have documented an evolution of the vegetation cover, from 20 000 cal BP onwards, as in other French regions, with certain particularities such as the delay in development of tree cover during the Younger Dryas (Reille & de Beaulieu, 1988). However, little if anything is known regarding the difference between the environments of the northern Limagne plain and the southern high valleys, and more generally between the Massif Central and other documented regions, such as the southwestern border area, the mid-mountain region of French Jura and the northern Iberian Peninsula. Were these environments less suitable to human and animal settlement than other regions, and to what extent? To address these questions, we aimed to document the environmental conditions experienced by large animals in the middle and high valleys of the Loire and Allier rivers through their isotopic values obtained from bone collagen. Radiocarbon dating was conducted to decipher a more precise chronological framework and to establish to what extent isotopic differences or similarities could be associated with geographical (North vs South, altitude) and/or climatic contrasts. Finally, we consider how the environmental conditions reflected by large herbivores in the Massif Central differ from those of other isotopically documented

areas, such as the near southwestern region in France, and the mid-mountain region of the French Jura and northeastern Iberian Peninsula.

## Materials and Methods

Collagen isotopic tracking of diet components and habitat conditions has been extensively applied to large herbivores and carnivores of the late Pleistocene in Europe (reviews in Bocherens, 2015; Drucker, 2022). In brief, the carbon and nitrogen stable isotope ratios (expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) in tissues of a vertebrate depend on those that are present in their diet. The source of carbon for plants is atmospheric  $\text{CO}_2$ . Thus, the  $\delta^{13}\text{C}$  values of plants depend on the amounts of  $^{13}\text{C}$  in the atmosphere as well as assimilation of atmospheric  $\text{CO}_2$  through the process of photosynthesis (reviewed in Kohn, 2010; Diefendorf et al., 2010). In the open landscape and cold context of the late Pleistocene in northwestern Europe, the  $\delta^{13}\text{C}$  values of the plants are expected to be positively correlated with aridity and water use efficiency, the latter increasing with decreasing temperature and atmospheric  $p\text{CO}_2$  (e.g. Beerling et al., 1993).

Most plants obtain their nitrogen from the soil and their  $\delta^{15}\text{N}$  values depend on the nitrogen source (inorganic or organic

nitrogen), nitrogen uptake pathway (direct or mediated through mutualistic association), nitrogen availability (demand vs. supply) and pedogenic parameters (e.g. enhanced nitrogen cycling process) (reviewed in Amundson et al., 2003; Craine et al., 2009). In the context of limited nitrogen supply, plants benefiting from an association with mycorrhizae, such as shrubs and trees, have lower  $\delta^{15}\text{N}$  values than those that obtain their nitrogen without mutualistic assistance, as it is the case for graminoids (e.g. Högberg, 1997). Temperature and aridity should also influence the plants'  $\delta^{15}\text{N}$  values through their impact on soil nitrogen cycling, since microbial activity promotes nitrogen transformation that leads to  $^{15}\text{N}$  enrichment of the residual substrates finally available to plants (e.g. Högberg 1997, Craine et al., 2009). As a result, increasing mean annual precipitation and decreasing mean annual temperature result in decreasing plant  $\delta^{15}\text{N}$  values (Amundson et al., 2003). Hence, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in herbivore collagen reflect their habitat and local environment. Collagen  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of predators give information on the origin of diet protein and their trophic level, when considering the trophic isotopic enrichment of ca. 1‰ in  $^{13}\text{C}$  and ca. 3–5‰ in  $^{15}\text{N}$  (e.g. Minagawa and Wada, 1984; Bocherens and Drucker, 2003).

We sampled faunal remains from the occupations of 10 Upper Palaeolithic sites in the Massif Central: Vigne-Brun in the Loire Valley (Digan, 2003; Digan et al., 2008), Grotte des Fées (Delporte, 1955; Zilhão et al., 2008), Blanzat (Pomerol, 1888; Surmely et al., 2008), Le Bay (Surmely, 2000; Angevin and Surmely, 2013), Pont de Longues (Surmely, 1998; Fontana, 2000a), Lépétade-Chabasse (Angevin and Surmely, 2013) and Thônes-Auzary (Delporte, 1970; Surmely, 2000) in the Limagne plain in the Allier river valley, Abri du Rond (Boule and Vernière, 1899; Delporte and Virmont, 1983; Fontana et al., 2018; Delvigne et al., 2019) and Le Blot (Delporte, 1966; Bosselin, 1992; Chauvière and Fontana, 2005; Surmely and Hays, 2011; Delvigne et al., 2019) further south in the Allier river valley, and, at a comparable latitude, Cottier (Evin, 1976; Lafarge, 2014) in the Loire river Valley (Figure 1). We selected bone and tooth samples of reindeer (*Rangifer tarandus*,  $n=25$ ), horse (*Equus* sp.,  $n=49$ ), ibex (*Capra ibex*,  $n=6$ ) and wolf (*Canis lupus*,  $n=2$ ) from the occupation levels attributed to the Châtelperronian, Early and Final Gravettian, Badegoulian and Magdalenian cultural periods (Table 1).

Preference was given to the compact part of long bones for reindeer and ibex, for two main reasons. First, in these sites, as in Palaeolithic sites in general, dental remains are far less numerous than bone remains (with a few exceptions, such as open-air sites where the organic remains are very poorly preserved). Furthermore, selecting a dental sample is problematic in that it damages the tooth, while it is a crucial element for determining the age of the specimen and even the hunting season of the game. Note that tooth roots were sampled in the case of horse due to the long-term growth of their hypsodont teeth, providing a time range record comparable to bone collagen. Moreover, for the wolf (Le Blot), two pieces of the same specimen were considered, one from the root of a canine and the other from the associated mandible.

Collagen preparation and isotopic measurements were conducted at Institut des Sciences de l'Évolution (ISEM) of Montpellier 2 University (France). Prior to extracting collagen, elemental analysis was applied to the crushed samples on a CHN-elemental analyser (Eurovector). The nitrogen content of modern and thus non-altered bones is  $4.3 \pm 0.6\%$  (Bocherens et al., 2005). As nitrogen is derived primarily from collagen in skeletal remains, we considered the threshold of 0.4% nitrogen content (ca. 1/10th of the organic matter), below which the sample was not further processed (Bocherens et al., 2005). The analytical precision of the N content measurement was  $\pm 0.1\%$ .

Collagen extraction was performed following the acid–base–acid method protocol inspired from Longin (1971) and modified by Bocherens et al. (1997). In brief, the extraction procedure includes an initial step of demineralization in 1 M HCl, a subsequent soak in 0.125 M NaOH at room temperature to remove humic contaminants (e.g. Guiry and Szpak, 2021) and solubilization in diluted HCl solution (pH 2) at 100 °C before the freeze-drying process. For the Le Blot site, some collagen samples were not obtained using the ISEM facilities but from the Radiocarbon Dating Laboratory at the University of Lyon before accelerator mass spectrometry (AMS) measurement at the Centre for Isotope Research (CIO) at the University of Groningen. These samples correspond to those dated with the double GrA (AMS) and Ly (collagen preparation) references.

Elemental analyses ( $C_{\text{coll}}$ ,  $N_{\text{coll}}$ ) and isotopic measurements ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) were performed on a CHN-elemental analyser (Eurovector) coupled to a VG-Optima continuous-flow ratio mass spectrometer. The isotopic ratios are expressed in permil (‰) using the “ $\delta$ ” (delta) value as follows:

$$\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1]$$

$$\delta^{15}\text{N} = [(^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{standard}} - 1]$$

The measurements were calibrated in reference to the international standards (V-PDB for carbon and AIR for nitrogen) using cane sucrose ( $\delta^{13}\text{C} = -11.0\%$ ), urea ( $\delta^{15}\text{N} = -0.33\%$ ) and alanine ( $\delta^{13}\text{C} = -23.5\%$ ,  $\delta^{15}\text{N} = -0.44\%$ ), as well as in-house reference materials (collagen of modern camel,  $\delta^{13}\text{C} = -16.0\%$ ,  $\delta^{15}\text{N} = +7.7\%$ ). Analytical error, based on within-run replicate measurement of laboratory standards (egg albumin, keratin, alanine amino acid, modern collagen), was  $\pm 0.1\%$  for  $\delta^{13}\text{C}$  and  $\pm 0.2\%$  for  $\delta^{15}\text{N}$ . The repeatability error for the amounts of C and N in collagen was less than 2%.

Quality control of collagen was estimated by screening the collagen yield following the minimum of 1% recommended by van Klinken (1999). For all samples, the chemical composition of collagen was considered, with C/N atomic ratio ( $C:N_{\text{coll}}$ ) ranging from 2.9 to 3.6 (DeNiro, 1985) and percentages of  $C_{\text{coll}}$  and  $N_{\text{coll}}$  above a conservative limit of 13% and 5% respectively (Ambrose, 1990). To select collagen for new radiocarbon dating, we exclusively considered samples with a carbon content  $\geq 30\%$  (van Klinken, 1999; van der Plicht and Palstra, 2016). Secured collagen samples were sent to the AMS radiocarbon facility of the Centre for Isotope Research at the University of Groningen. Results were calibrated using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020).

## Results

### Collagen preservation

The elemental analysis on bone and dentine revealed a large range of N content from 0.0 to 3.8% (Table 2). At La Vigne-Brun, none of the tested horse dentine samples revealed any N content, and one sample could not be tested since it dissolved during the cleaning treatment (VB7 in Table 2). In the sole site of Le Blot, the N content of bone or dentine ( $N_{\text{bd}}$ ) spanned between 0.0 and 2.4%, testifying to the variable quantity of organic matter, primarily collagen, left in the skeletal remains. There is no apparent clear relationship between the geological context and the quantity of collagen preserved. Interestingly, the sites of Pont de Longues, Thônes, Abri du Rond and Cottier

**Table 1.** List of the selected sites with their geographical, archaeological and chronological contexts and samples selected for isotopic study. Calibration (cal BP, 2-sigma) were done using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020).

Site (map no.) with Lab code	Location	Type	Valley	Altitude (m)	Cultural attribution	AMS dating <sup>14</sup> C BP (source)	Reindeer	Horse	Ibex
Blanzat (2) BLZ	Blanzat, Puy-de-Dôme	RC	Allier	390	Magdalenian	Horse 12 870 ± 70 (3)		5 (dentine)	
Le Bay (5) LB	Les-Martres-de-Veyre, Puy-de-Dôme	OA	Allier	355	Magdalenian	Ibex, niv.1: 13 950 ± 50 (3) Bone, niv.2: 14 250 ± 60 (6)		5 (bone)	
Pont de Longues (3) PL	Les-Martres-de-Veyre, Puy-de-Dôme	OA	Allier	340	Magdalenian	Horse, niv.6: 11 920 ± 50 Beta-110598 (2)	5 (bone)	6 (bone)	
Lépétade-Chabasse (4) LPT	Vic-le-Comte, Puy-de-Dôme	OA	Allier	345	Magdalenian?	Reindeer, niv.6: 12 290 ± 60 Beta-124232 (2) Bone: 14 310 ± 60 (6)	2 (bone)	4 (dentine)	
Thônes-Auzary (6) THN	Puy-de-Dôme Grandeyrolles, Puy-de-Dôme	RC	Allier	820	Middle Magdalenian	Ibex: 13 950 ± 50; Horse: 15 100 ± 60 (3)		4 (dentine)	2 (bone)
Abri du Rond (8) AR	Saint-Arcons-d'Allier, Haute-Loire	RC	Allier	540	Final Gravettian?		4 (bone)	1 (bone)	
Cottier (10) COT	Retournac, Haute-Loire	CA	Loire	550	Badegoulian	Reindeer, niv II: 17 910 ± 70 Beta-377946 (7)	1 (bone)	4 (dentine)	4 (bone)
Le Blot (7) BLO	Cerzat, Haute-Loire	RC	Allier	490	Badegoulian	Horse, niv.9: 17 850 ± 80 GrA-17339 (1)		4 (dentine)	
					Badegoulian	Horse, niv.15: 18 000 ± 80 GrA-17337 (1)	4 (bone)	2 (dentine)	
					Final Gravettian	Reindeer, niv.22: 21 330 ± 210 GrA-19741 (5)	1 (bone)	1 (bone)	
					Final Gravettian	Reindeer, niv.23: 21 510 ± 220 GrA-19742 (5)	2 (bone)	1 (bone)	
					Final Gravettian	Reindeer, niv.24: 22 030 ± 230 GrA-19744 (5)	1 (bone)	1 (bone)	
					Final Gravettian	Reindeer, niv.27: 22 190 ± 220 GrA-19905 (5)	3 (bone)	2 (bone)	
					Final Gravettian	niv.30 (no data)	1 (bone)	1 (bone)	
					Final Gravettian	Reindeer, niv. 32: 21 870 ± 200 GrA-19745 (5)	1 (bone)	7 (dentine)	
La Vigne-Brun (9) VB	Villerest, Loire	OA	Loire		Early Gravettian	Bone, level B5: 39 150 ± 600 OxA-13622 (4)		1 (bone)	
Grotte des Fées (1) CHP	Châtel Perron, Allier	CA	Allier	250	Castelperronian?	Bone, level B5: 39 240 ± 380 OxA-14320 (4)			
					Castelperronian?	Bone, level B5: 40 650 ± 600 OxA-13621 (4)			

Abbreviations: CA, cave; OA, open air; RC, rockshelter.

1 = <https://www.arar.mom.fr/banadora/>; 2 = Fontana, 2000b; 3 = Summely, 2000; 4 = Gravina et al., 2005; 5 = Summely and Hays, 2011; 6 = Angevin and Summely, 2013; 7 = Lafarge, 2014.

**Table 2.** Results of elemental analyses of bone or dentine ( $N_{bd}$ ) and collagen ( $C_{coll}$ ,  $N_{coll}$ ) and stable isotope analyses of collagen ( $\delta^{13}C_{coll}$ ,  $\delta^{15}N_{coll}$ ) of reindeer (*Rangifer tarandus*), horse (*Equus sp.*), ibex (*Capra ibex*) and wolf (*Canis lupus*).

Lab code	Species	Piece	Excavation reference	$N_{bd}$ (%)	Coll yield (%)	$C_{coll}$ (%)	$N_{coll}$ (%)	$N_{yield}$ (%)	C:N <sub>coll</sub>	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)	Age $^{14}C$ BP	Calibrated age, cal BP (2 $\sigma$ )
BLZ-1	Horse	Lower tooth	63.042-43	0.3	na	na	na	na	na	na	na		
BLZ-2	Horse	Incisor	63.042-7	1.5	2.9	40.1	14.7	28.7	3.2	-20.6	4.0		
BLZ-3	Horse	Lower tooth	63.042-65	1.5	2.6	41.1	15.4	26.9	3.1	-21.0	3.1		
BLZ-4	Horse	Incisor	63.042-6	1.7	8.1	44.1	16.2	76.8	3.2	-21.0	3.0	13 350 ± 70 GrA-27337*	16 290–15 820
BLZ-5	Horse	Lower tooth	63.042-59	1.0	3.8	38.6	14.8	56.0	3.0	-21.1	3.1		
LB1	Horse	Metatarsal III	No reference	0.2	na	na	na	na	na	na	na		
LB2	Horse	Humerus	No reference	0.7	1.5	34.6	13.6	29.7	3.0	-20.9	4.0		
LB3	Horse	Long bone	No reference	1.0	1.4	36.0	14.1	20.0	3.0	-20.8	4.3		
LB4	Horse	Long bone	No reference	1.6	1.7	37.4	14.0	15.3	3.1	-20.7	4.7		
LB5	Horse	Long bone	no reference	1.5	2.4	35.4	13.4	21.4	3.1	-21.3	3.8	14 090 ± 80 GrA-26870*	17 380–16 970
PL1	Horse	Phalanx III	PDL98H7SERB	1.2	<b>0.4</b>	<b>2.8</b>	<b>1.0</b>	<b>0.4</b>	<b>3.2</b>	(-22.9)	(0.2)		
PL2	Horse	Phalanx I	PDL98C8C6H5	0.8	0.0	na	na	na	na	na	na		
PL3	Horse	Metatarsal	PDL98H81/4SEC.6	2.0	0.0	na	na	na	na	na	na		
PL4	Horse	Phalanx II	PDL98C8C6H5	1.3	<b>0.2</b>	26.0	9.1	<b>1.3</b>	3.3	(-19.7)	(0.9)		
PL5	Horse	Phalanx I	PDL98C81/4SOSA	1.2	<b>0.4</b>	nd	nd	nd	nd	nd	nd		
PL6	Horse	Radius	PDL98G8C6H5	0.7	0.0	na	na	na	na	na	na		
PL7	Reindeer	Metacarpal	PDL98H9INESR4	0.7	<b>0.4</b>	<b>1.6</b>	nd	nd	nd	(-23.1)	(-0.6)		
PL8	Reindeer	Talus	PDL98H91/4NESR	0.8	<b>0.3</b>	na	na	na	na	na	na		
PL9	Reindeer	Talus	PDL98H9C6H	1.0	<b>0.2</b>	na	na	na	na	na	na		
PL10	Reindeer	Scapula	PDL98H91/4NESR	2.1	<b>0.5</b>	na	na	na	na	na	na		
PL11	Reindeer	Phalanx II	PDL98H81/4SE	1.4	<b>0.4</b>	<b>11.7</b>	<b>4.3</b>	<b>1.2</b>	3.2	(-17.6)	(-1.6)		
LPT1	Horse	Lower tooth	N.3, niv I-Nord	1.2	1.8	33.8	13.4	20.5	2.9	-21.2	3.4		
LPT2	Horse	Lower tooth	N.2, niv III	1.2	1.1	35.6	13.1	12.1	3.2	-21.2	4.1		
LPT3	Horse	Lower tooth	N.5, niv II	0.7	<b>0.4</b>	36.4	13.0	<b>7.7</b>	3.3	(-20.7)	(3.2)		
LPT4	Horse	Lower tooth	N.7, niv II	1.1	1.4	32.1	13.1	16.4	2.9	-20.1	4.0		
LPT5	Reindeer	Metacarpal	N.2, niv IV	1.3	2.3	36.9	14.3	25.1	3.0	-19.5	3.3	14 650 ± 70 GrA-27251*	18 210–17 610
LPT6	Reindeer	Metatarsal	N.3, niv II-1	0.2	na	na	na	na	na	na	na		
THN1	Horse	Upper tooth	69-15-4	1.5	3.8	40.9	15.7	39.5	3.0	-20.1	3.0	15 260 ± 70 GrA-27246*	18 750–18 280
THN2	Horse	Lower tooth	No reference	1.3	2.8	43.3	15.9	34.8	3.2	-20.1	3.2	15 310 ± 70 GrA-27245*	18 800–18 290
THN3	Horse	Incisor	No reference	1.6	2.8	40.2	15.2	26.4	3.1	-20.2	4.9		
THN4	Horse	Lower tooth	No reference	0.9	1.4	42.9	15.1	24.2	3.3	-20.4	2.9		
THN5	ibex	Phalanx II	cll I 6	1.2	2.1	36.4	13.0	22.5	3.3	-19.8	4.1		
THN6	ibex	Phalanx II	No reference	2.1	3.0	41.6	15.1	21.7	3.2	-19.6	3.3	13 200 ± 60 GrA-27243*	16 040–15 650
AR1	Reindeer	Jawbone	899.2	0.1	na	na	na	na	na	na	na		
AR2	Reindeer	Tibia	899.7	1.1	3.6	41.6	15.4	50.2	3.2	-18.3	4.0		
AR3	Reindeer	Metatarsal	899.8	1.8	5.8	43.5	16.2	52.6	3.1	-18.5	3.5		
AR4	Reindeer	Metatarsal	899.315	2.4	9.6	40.0	16.1	64.1	2.9	-19.3	4.9	21 510 ± 110 GrA-27242*	25 990–25 670
AR5	Horse	Metatarsal	899.306	0.3	na	na	na	na	na	na	na		
AR6	Horse	Tooth	899.307	1.0	2.1	37.8	15.0	30.8	2.9	-19.9	5.3		
AR7	Horse	Tooth	899.304	0.4	<b>0.6</b>	30.2	17.4	25.8	<b>2.0</b>	(-23.8)	(1.2)		
AR8	Horse	Tooth	899.309	0.8	2.3	42.7	15.4	44.0	3.2	-20.4	1.9	21 530 ± 110 GrA-27237*	26 000–25 680
AR9	Horse	Tooth	899.308	0.5	1.7	39.0	15.4	51.5	3.0	-20.2	4.2		
COT1	Reindeer	Maxillary	63.1.56	2.7	11.5	37.8	14.4	61.1	3.1	-19.7	2.8	16 310 ± 80 GrA-27249*	19 900–19 500
COT2	ibex	Metacarpal	64.45.25	0.4	<b>0.3</b>	<b>14.1</b>	<b>5.2</b>	<b>4.1</b>	3.2	(-21.6)	(0.0)		

(Continued)

Table 2. (Continued)

Lab code	Species	Piece	Excavation reference	N <sub>bd</sub> (%)	Coll yield (%)	C <sub>coll</sub> (%)	N <sub>coll</sub> (%)	N <sub>yield</sub> (%)	C:N <sub>coll</sub>	δ <sup>13</sup> C <sub>coll</sub> (‰)	δ <sup>15</sup> N <sub>coll</sub> (‰)	Age <sup>14</sup> C BP	Calibrated age, cal BP (2σ)
COT3	Ibex	Phalanx II	64.45.47	3.8	10.6	38.8	14.5	40.6	3.1	-19.6	2.6	15 910 ± 80 GrA-27250*	19 450–18 980
COT4	Ibex	Phalanx I	64.45.22	1.3	nd	35.6	13.7	nd	3.0	-19.2	5.2		
COT5	Ibex	Metatarsal	64.45.43	3.1	9.3	39.7	15.1	45.3	3.1	-19.5	4.8		
BLO1	Horse	Upper tooth	B67 J4 100, niv.9	1.0	1.7	34.8	13.4	23.4	3.0	-20.3	2.3		
BLO2	Horse	Upper tooth	B68 J4 168, niv.9	1.1	<b>0.2</b>	na	na	na	na	na	na		
BLO3	Horse	Upper tooth	B67 J4 64, niv.9	0.6	1.3	35.8	13.4	29.3	3.1	-20.4	2.1		
BLO9	Horse	Tooth	B67 K4 11, niv.9	nd	nd	29.9	10.9	nd	3.2	-20.9	1.5	17 850 ± 80 GrA-17339	21 970–21 400
BLO4	Horse	Upper tooth	B70 K6 116, niv.15	0.9	<b>0.8</b>	32.4	12.7	11.3	3.0	(-21.2)	(1.3)		
BLO10	Horse	Tooth	B70 J8 15 41, niv.15	nd	nd	29.5	11.0	nd	3.1	-20.9	1.4		
BLO5	Reindeer	Metacarpal	B81 I4 802, niv.15	2.3	<b>0.3</b>	25.9	9.2	<b>1.2</b>	3.3	(-19.5)	(3.0)		
BLO6	Reindeer	Talus	B82 J4 1994-48, niv.15	2.4	<b>0.8</b>	35.0	12.1	<b>3.8</b>	3.4	(-19.6)	(5.1)		
BLO7	Reindeer	Metatarsal	B81 L3 1561, niv.15	0.1	nd	na	na	na	na	na	na		
BLO8	Reindeer	Metatarsal	B80 H2 823, niv.15	1.6	<b>0.0</b>	na	na	na	na	na	na		
BLO25	Horse	Ulna	B68 H2 81, niv.22	1.1	1.5	38.2	14.1	19.0	3.2	-20.6	2.2		
BLO27	Reindeer	Long bone	B68 I2, niv.22	nd	nd	40.4	16.0	nd	2.9	-18.5	2.9	21 330 ± 210 GrA-19741	25 980–25 200
BLO20	Horse	Calcaneus	B69 J74, niv.23	0.5	1.1	37.3	14.2	29.4	3.1	-20.2	3.1		
BLO28	Reindeer	Long bone	B69 I1 69, niv.23	nd	nd	34.2	15.9	nd	<b>2.5</b>	(-18.7)	(-0.2)		
BLO21	Reindeer	Metacarpal	B69 F3 2, niv.23	2.0	4.3	42.4	15.6	33.5	3.2	-19.7	4.4		
BLO26	Horse	Long bone	B70 I4 209, niv.24	1.4	1.4	39.7	14.9	14.8	3.1	-20.0	3.7		
BLO29	Reindeer	Long bone	B70 I1 196, niv.24	nd	nd	33.1	12.2	nd	3.2	-18.9	3.9	22 030 ± 230 GrA-19744	26 930–25 890
BLO22	Horse	Long bone	B96 H0 115, niv.26sol27	0.2	na	na	na	na	na	na	na		
BLO24	Reindeer	Metatarsal	niv.26sol27	2.2	3.8	43.1	15.8	27.8	3.2	-19.2	4.1		
BLO19	Horse	Radius	B70 K3 27 344, niv.27	0.0	na	na	na	na	na	na	na		
BLO30	Reindeer	Long bone	B70 J3 490, niv.27	nd	nd	30.7	11.1	nd	3.2	-18.9	3.7	22 190 ± 220 GrA-19905	27 030–25 960
BLO23	Reindeer	Metatarsal	B75 I3 27 1150, niv.27	1.5	1.4	40.3	15.0	14.2	3.1	-18.8	3.5		
BLO14	Reindeer	Radius/ulna	B77 K4 30 732, niv.30	1.1	1.6	35.4	12.8	18.2	3.2	-19.3	4.3		
BLO15	Horse	Femur	B76? 831, niv.30	0.4	<b>0.4</b>	31.8	12.3	11.4	3.0	(-21.3)	(1.8)		
BLO31	Reindeer	Long bone	B77 J13 1718, niv.32	nd	nd	27.4	10.1	nd	3.2	-18.8	3.6	21 870 ± 200 GrA-19745	26 780–25 780
BLO16	Wolf	Jawbone	B76 K3 804, niv.30	1.0	1.6	41.9	15.2	24.0	3.2	-18.7	7.6		
BLO17	Wolf	Canine root	B76 K3 804, niv.30	1.4	4.5	39.8	14.6	46.6	3.2	-18.7	9.5		
VB1	Horse	Upper tooth	VB78 P16 220	0.0	na	na	na	na	na	na	na		
VB2	Horse	Lower tooth	VB O16 290	0.0	na	na	na	na	na	na	na		
VB3	Horse	Lower tooth	VB J18 95, str.KL19	0.0	na	na	na	na	na	na	na		
VB4	Horse	Lower tooth	VB78 L18 258, str.KL19	0.0	na	na	na	na	na	na	na		
VB5	Horse	Lower tooth	VB80 J20 103, str.KL19	0.0	na	na	na	na	na	na	na		
VB6	Horse	Lower tooth	mand Q9, str.OP10	0.0	na	na	na	na	na	na	na		
VB7	Horse	Upper tooth	P10 312, str.OP10	nd	na	na	na	na	na	na	na		
CHP1	Horse	Tibia	B5	2.1	2.6	37.6	13.7	16.8	3.2	-20.2	6.3	40 030 ± 500 GrA-27247*	44 230–42 670

Notes: Numbers in bold indicate potential problem with collagen quality, and values in parentheses indicate data not considered as reliable enough for further interpretation. Radiocarbon results were calibrated using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020). \* Radiocarbon dating from this work. Abbreviations: na, not applicable; nd, not determined.

are those with a minimum N content of 2% in bone or dentine, while differing in altitude, geological context, and being either open air, rockshelter or cave. Cottier is the only site where  $N_{bd}$  content above 2.5% was measured, while its altitude (550 m asl) is not that different from most of the others (250–540 m asl), except for Thônes (820 m asl), and therefore does not point toward a positive effect of higher elevation on organic matter preservation in animal remains. Altogether, 15 bone or dentine samples did not contain the minimum of 0.4% N considered necessary for collagen extraction. Moreover, three bone samples from Pont de Longues did not yield collagen despite a N content above 0.4%.

The collagen carbon and nitrogen content ranged from 1.6 to 44.1% and 1.0 to 17.4% respectively (Table 2). It is noteworthy that one reindeer from Pont de Longues with a  $C_{coll}$  content below 2% could not be analysed for  $N_{coll}$ . One horse bone from Pont de Longues delivered the extract with the lowest  $C_{coll}$  and  $N_{coll}$  of 2.8 and 1.0% respectively. For all the samples from this site ( $n=11$ ), despite an  $N_{bd}$  content above 0.4%, the extraction yield (Coll yield) was not greater than 0.5%, leading to collagen in too low quantity to be further analysed ( $n=4$ ).

Regarding the C: $N_{coll}$  ratio, all extracts gave results between 2.9 and 3.4 except for one sample from Le Blot (2.5) and one sample from Abri du Rond (2.0) (Table 2). Interestingly, the sample from Le Blot corresponds to one of the previously dated samples (GrA-19742). If no clear pattern appeared when plotting the  $C_{coll}$  and  $N_{coll}$  content against the bone or dentine N content, a decreasing exponential trend appeared below 1% of extracted collagen when they were plotted against the extraction yield (Supporting Information Fig. S1A). We thus considered the extraction yield as a valuable quality control in our case study, in addition to the  $C_{coll}$  and  $N_{coll}$  content and atomic ratio.

We also explored the possibility of expressing the quantity of nitrogen in the extracted collagen in comparison to the expected quantity that should be retrieved based on the elemental measurement in bone and dentine. For this, we applied the following equation:

$$N_{yield} = (N_{coll} \times Coll_{yield}) / N_{bd}$$

A distinction was revealed for  $N_{yield}$  between sites, with open area sites delivering lower  $N_{yield}$  (0.4–29.7%,  $14.3 \pm 9.8\%$  on average) compared to rockshelter and cave sites (1.2–76.8%,  $31.0 \pm 17.9\%$  on average; Table 2, Supporting Information Fig. S2C). No such differences were found when considering the bone or dentine N content or collagen C content (Supporting Information Fig. S2A and S2B). Indeed, a poorer state of preservation that may be expected in a context of less protection from environmental conditions seems to be best reflected in  $N_{yield}$ .

When  $C_{coll}$  and  $N_{coll}$  were plotted against  $N_{yield}$ , the logarithmic correlation was even more robust than when plotted against  $Coll_{yield}$ . Below a threshold of  $N_{yield}$  of 10%, the chemical composition of collagen showed some alteration (Supporting Information Fig. S2C). On the other hand, if the sample with an out-of-range C:N ratio (2.0) was plotted among the samples delivering less than 1%  $Coll_{yield}$  (Fig. S1B), it clustered with samples with an  $N_{yield}$  above 10% (Fig. S1D). Hence,  $N_{yield}$ , which may have captured the process of collagen diagenesis, was a less good predictor of contamination than the extraction yield.

Based on the extraction yield (minimum of 1%), we ruled out one further sample from Pont de Longues, a site for which we finally had no reliable isotopic results, one horse from Lépétade-Chabasse, one horse from Abri du Rond, one ibex from Cottier, and three horses and two reindeer from Le Blot. In the case of

Abri du Rond, the excluded horse had a collagen containing 30.2% C but provided isotopic results obviously out of the range of other values found in the Massif Central for this species. For other specimens that we ruled out based on very low extraction yield, the isotopic data may have appeared consistent with those found for the same species in the same region, but they were nevertheless discarded from the interpretation for the sake of consistency. Altogether, we had a total of 46 collagen samples that met our quality control criteria.

### Radiocarbon dating

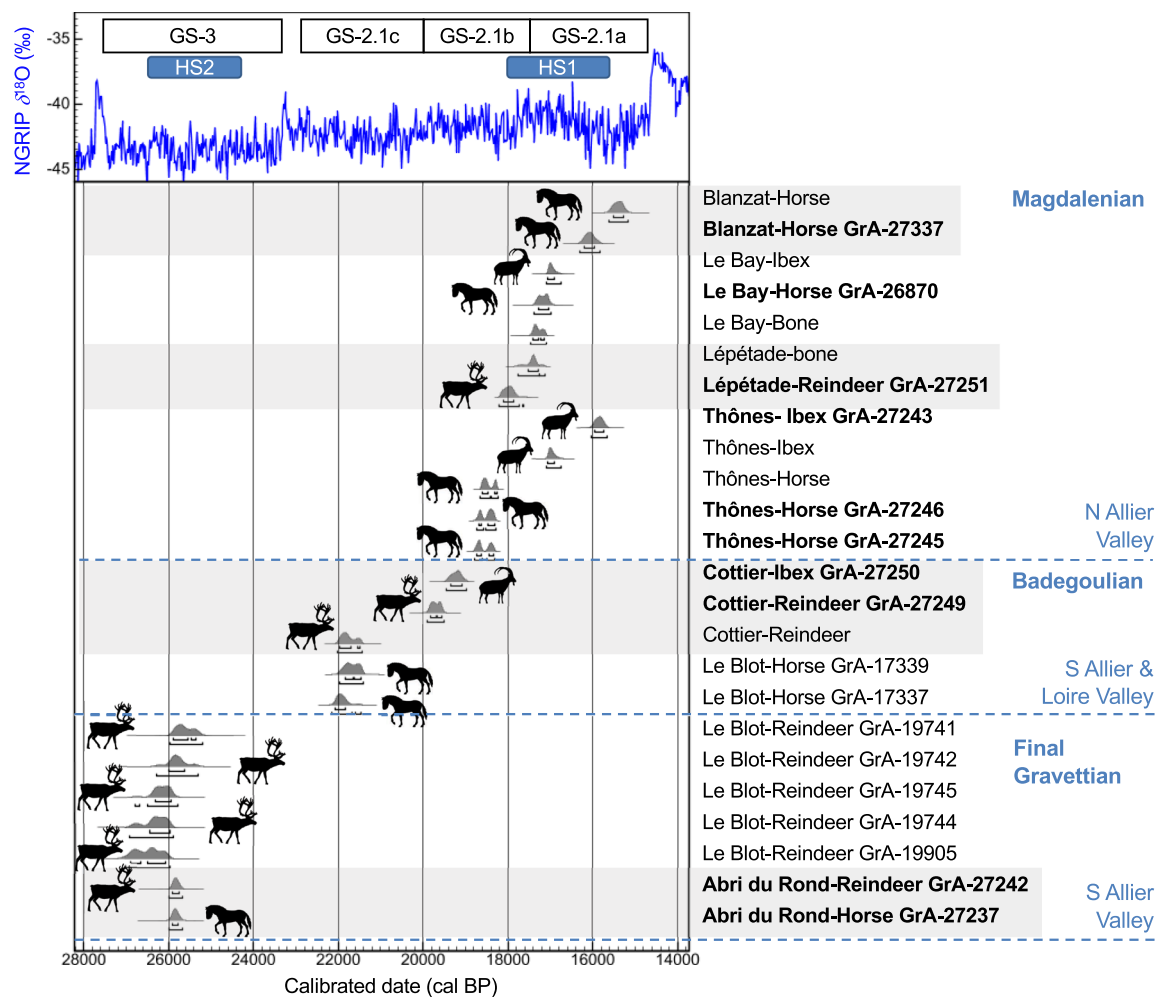
Altogether, eight new radiocarbon dates were obtained after a careful check of the collagen quality. For the sites where radiocarbon measurement had already been performed on bone collagen, the new results were consistent with the previous AMS data, as illustrated at Blanzat, Le Bay, Lépétade-Chabasse and Grotte des Fées (Tables 2 and 3; Figure 2; Supporting Information Fig. S3). At Thônes, the two additional dates on horse gave identical results to those obtained on the same species (late Greenland Stadial 2.1b; ca. 18 000–17 500 cal BP), while the new radiocarbon date on ibex extends the chronology of the site further in GS-2.1a (ca. 17 500–14 800 cal BP). At Cottier, the newly dated reindeer and ibex indicated occupation as late as the GS-2.1b (ca. 20 000–17 500 cal BP), while a previous dating on reindeer fitted the previous GS-2.1c (ca. 22 800–20 000 cal BP), still preceding the Magdalenian occupation of Thônes and Le Bay as expected from the cultural diagnosis. Finally, we obtained the first radiocarbon dates on animal remains at Abri du Rond, which confirmed an age contemporaneous to levels 22 and 23 of Le Blot, and consistent with attribution to the Final Gravettian (previously called Protomagdalenian). The exceptional stratigraphy of Le Blot allowed us to illustrate the GS-3 period (ca. 27 500–23 300 cal BP), together with the nearby site of Abri du Rond, and from after GS-3 to the first part of GS-2.1b, including the site of Cottier located in the adjacent Loire Valley for this last chrono-period. For the second part of GS-2-1b and GS-2.1a, we dealt with the northern part of the Allier Valley. Direct comparison between the north and south of the Massif Central was thus not possible.

### Stable isotopes

From the retained collagen, the horse  $\delta^{13}C$  and  $\delta^{15}N$  values ranged between  $-21.3$  to  $-19.9\%$  and from  $+1.4$  to  $+6.3\%$  respectively (Tables 2 and 3). The reindeer exhibited higher  $\delta^{13}C$  values than those of horse, ranging from  $-19.7$  to  $-18.3\%$ , while their  $\delta^{15}N$  values clustered in the range of horse values, from  $+2.8$  to  $+4.9\%$ . The  $\delta^{13}C$  and  $\delta^{15}N$  values of the ibex clustered in comparable ranges to those of the reindeer, varying from  $-19.8$  and  $-19.2\%$  and from  $+2.6$  to  $+5.2\%$  respectively. The wolf from Le Blot exhibited the same  $\delta^{13}C$  value in the jawbone and the canine root ( $-18.7\%$ ) but a higher  $\delta^{15}N$  value in the canine ( $+9.5\%$ ) than in the mandible ( $+7.6\%$ ).

When considering the sites located in the southern part of the Massif Central, the horse exhibited a decrease in  $\delta^{15}N$  values and, to a lesser extent, in  $\delta^{13}C$  values, between the Final Gravettian and the Badegoulian (Figure 3a and 3b; Supporting Information Fig. S4). This decrease in horse values was shown along the stratigraphy of Le Blot itself,  $\delta^{13}C$  and  $\delta^{15}N$  values ranging from  $-20.6$  to  $-20.0\%$  and  $+2.2$  to  $+3.7\%$ , respectively, during the Final Gravettian and from  $-20.9$  to  $-20.3\%$  and  $+1.4$  to  $+2.3\%$  during the Badegoulian. The horse specimens from the neighbouring site of Abri du Rond in the Allier Valley confirmed relatively high  $\delta^{13}C$  values and dispersed  $\delta^{15}N$  values ( $-20.4$  to  $-19.9\%$  and  $+1.9$  to  $+5.3\%$ ; Figure 3a).





**Figure 2.** Calibrated radiocarbon ages (cal BP, 2-sigma) for the dated animal bones from Abri du Rond, Le Blot, Cottier, Thômes-Auzary, Lépétade-Chabasse, Le Bay and Blanzat using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020) (dates in bold are from this study; see Tables 1, 2 and 3 for details). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3617)]

The reindeer revealed comparable isotopic ranges between both sites, with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values varying from  $-19.7$  to  $-18.5\text{‰}$  and from  $+2.9$  to  $+4.3\text{‰}$  at Le Blot, and from  $-19.3$  to  $-18.3\text{‰}$  and from  $+3.5$  to  $+4.9\text{‰}$  at Abri du Rond (Tables 2 and 3), respectively. The unique reindeer from the Badegoulian, during the early GS-2.1b, showed relatively low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $-19.7\text{‰}$  and  $+2.8\text{‰}$ , respectively; Figure 3b). This specimen comes from Cottier, a site at the same latitude as Le Blot and Abri du Rond but in the Loire Valley. However, it is difficult to infer local environmental conclusions based on the data from this one individual.

More recent phases were represented in the Magdalenian sites of Blanzat, Le Bay, Lépétade-Chabasse and Thômes all located in the northern part of the Massif Central. The horse samples from these sites showed the same range of  $\delta^{13}\text{C}$  values as the horse samples of Le Blot in the Badegoulian ( $-21.3$  to  $-20.1\text{‰}$ ), but they exhibited higher  $\delta^{15}\text{N}$  values ( $+2.9$  to  $+4.9\text{‰}$ ) (Figure 3c). With a  $\delta^{13}\text{C}$  of  $-19.5\text{‰}$  and a  $\delta^{15}\text{N}$  of  $+3.3\text{‰}$ , the reindeer from Lépétade-Chabasse clustered in the range of values found in the southern part of the Massif Central during previous periods. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the ibex from Thômes (from  $-19.8$  to  $-19.6\text{‰}$  and from  $+3.3$  to  $+4.1\text{‰}$ , respectively) also clustered close to the one observed at Cottier in the Badegoulian for the same species (from  $-19.6$  to  $-19.2\text{‰}$  and from  $+2.6$  to  $+5.2\text{‰}$ , respectively).

If we consider the results independent of their specific location, a decrease in the  $\delta^{15}\text{N}$  values of horse was observed after the Final Gravettian (ca. 27 000–25 000 cal BP) during

GS-3 with the Badegoulian contemporaneous to GS-2.1c and GS-2.1b (ca. 22 000–19 000 cal BP), before the values increased again during the Magdalenian over GS-2.1b and GS-2.1a (ca. 19 000–16 000 cal BP). However, these last  $\delta^{15}\text{N}$  values did not reach the one exhibited by the early Upper Palaeolithic horse from Grotte des Fées (ca. 43 450 cal BP,  $\delta^{15}\text{N}$ :  $+6.3\text{‰}$ ). It contrasted with the relative stability of the  $\delta^{13}\text{C}$  values that showed a clear dietary partitioning between the horse on the one hand and the reindeer and ibex on the other.

## Discussion

### Collagen preservation

Organic matter preservation of skeletal remains found in the Upper Paleolithic sites of the Massif Central is generally challenging. Bone and dentine collagen show a general poor condition of preservation both in quantity and in quality. None of the samples displayed more than half of the initial amount of organic matter, and, in most cases, less than half of the remaining organic matter could be retrieved as collagen during the extraction process (Table 2). Finally, the chemical composition of some extracted collagen does not meet the quality control criteria, as systematically found in the site of Pont de Longues. This is consistent with the poor macroscopic preservation of skeletal remains described from sites of the Massif Central (e.g. Fontana et al., 2018). Thus, particular

**Table 3.** Summary of the radiocarbon and stable isotope results on validated collagen based on this study. Calibration (cal BP, 2-sigma) were done using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020).

Site (Lab code)	Culture	AMS dating ( <sup>14</sup> C BP) (source)	<sup>14</sup> C species	$\delta^{13}\text{C}$ range (‰)	$\delta^{13}\text{C}$ mean (‰)	$\delta^{15}\text{N}$ range (‰)	$\delta^{15}\text{N}$ mean (‰)	<sup>13</sup> C, <sup>15</sup> N species	N	
Blanzat (BLZ)	Magdalenian	12 870 ± 70 (2)	Horse	-21.1 to -20.6	-20.9 ± 0.2	+3.0 to +4.0	+3.3 ± 0.5	Horse	4 (dentine)	
		15 610–15 160 cal BP 13 350 ± 70 GrA-27337 (7)	Horse							
Le Bay (LB)	Magdalenian	16 290–15 820	lbex							
		13 950 ± 50 (2)								
		17 100–16 730								
		14 090 ± 80 GrA-26870 (7) 17 380–16 970	Horse	-21.3 to -20.7	-20.9 ± 0.3	+3.8 to +4.7	+4.2 ± 0.4	Horse	4 (bone)	
Pont de Longues (PL) Lépétade-Chabasse (LPT)	Magdalenian Magdalenian?	14 250 ± 60 (5)	nd							
		17 470–17 080								
		niv.6: no collagen preserved	na	na	na	na	na	na	Horse, reindeer	0
		14 310 ± 60 (5)	nd	-21.2 to -20.1	-20.8 ± 0.6	+3.4 to +4.1	+3.8 ± 0.4	Horse	3 (dentine)	
		17 760–17 120	Reindeer	-19.5	na	+3.3	na	Reindeer	1 (bone)	
Thônes-Auzary (THN)	Magdalenian?	14 650 ± 70 GrA-27251 (7)	lbex	-19.8 to -19.6	-19.7 ± 0.1	+3.3 to +4.1	+3.8 ± 0.6	lbex	2 (bone)	
		18 210–17 610								
		16 040–15 650	lbex							
		13 950 ± 50 (2)								
Abri du Rond (AR)	Final Gravettian?	17 100–16 730	Horse	-20.4 to -20.1	-20.2 ± 0.1	+2.9 to +4.9	+3.5 ± 0.9	Horse	4 (dentine)	
		15 100 ± 60 (2)								
		18 650–18 230								
		15 260 ± 70 GrA-27246 (7)	Horse							
		18 750–18 280								
Cottier (COT)	Badegoulian	15 310 ± 70 GrA-27245 (7)	Reindeer	-19.3 to -18.3	-18.7 ± 0.5	+3.5 to +4.9	+4.1 ± 0.7	Reindeer	3 (bone)	
		18 800–18 290								
		21 510 ± 110 GrA-27242 (7) 25 990–25 670	Horse	-20.4 to -19.9	-20.2 ± 0.3	+1.9 to +5.3	+3.8 ± 1.7	Horse	3 (dentine)	
		26 000–25 680	lbex	-19.6 to -19.2	-19.5 ± 0.2	+2.6 to +5.2	+4.2 ± 1.4	lbex	3 (bone)	
Le Blot (BLO)	Badegoulian	15 910 ± 80 GrA-27250 (7)	Reindeer	-19.7	na	+2.8	na	Reindeer	1 (bone)	
		19 450–18 980								
		16 310 ± 80 GrA-27249 (7) 19 900–19 500	Horse	-20.9 to -20.3	-20.6 ± 0.3	+1.4 to +2.3	+1.8 ± 0.4	Horse	4 (dentine)	
		17 910 ± 70 Beta-377946 (6) 22 020–21 440	Horse							
Badegoulian	Badegoulian	17 850 ± 80 GrA-17339 (1)	Horse	-20.6 to -20.0	-20.3 ± 0.3	+2.2 to +3.7	+3.0 ± 0.8	Horse	3 (bone)	
		21 970–21 400								
		18 000 ± 80 GrA-17337 (1) 22 160–21 460	Reindeer	-20.6 to -20.0	-20.3 ± 0.3	+2.2 to +3.7	+3.0 ± 0.8	Reindeer	0	
Final Gravettian	Final Gravettian	21 330 ± 210 GrA-19741 (4)	Reindeer	-19.7 to -18.5	-19.0 ± 0.4	+2.9 to +4.4	+3.8 ± 0.5	Reindeer	8 (bone)	
		25 980–25 200								
		26 290–25 300								
Final Gravettian	Final Gravettian	21 510 ± 220 GrA-19742 (4)	Reindeer							
		22 030 ± 230 GrA-19744 (4)	Reindeer						(Continued)	

Table 3. (Continued)

Site (Lab code)	Culture	AMS dating ( <sup>14</sup> C BP) (source)	<sup>14</sup> C species	$\delta^{13}\text{C}$ range (‰)	$\delta^{13}\text{C}$ mean (‰)	$\delta^{15}\text{N}$ range (‰)	$\delta^{15}\text{N}$ mean (‰)	<sup>13</sup> C, <sup>15</sup> N species	N
		26 930–25 890							
	Final Gravettian	22 190 ± 220 GrA-19905 (4)	Reindeer						
	Final Gravettian	27 030–25 960							
	Final Gravettian	21 870 ± 200 GrA-19745 (4)	Reindeer						
	Final Gravettian	26 780–25 780							
La Vigne-Brun (VB)	Early Gravettian	No collagen preserved	na	na	na	na	na	Horse	0
Grotte des Fées	Castelperronian?	39 150 ± 600 OxA-13622 (3)	nd	-20.2	na	+6.3	na	Horse	1 (bone)
(CHP)		43 880–42 230							
		39 240 ± 380 OxA-14320 (3)	nd						
		43 160–42 380							
		40 030 ± 500 GrA-27247 (7)	Horse						
		44 230–42 670							
		40 650 ± 600 OxA-13621 (3)	nd						
		44 600–42 870							

Abbreviation: na, not applicable; nd, not determined.

1 = <https://www.atar.mom.fr/banadora/>; 2 = Surrmely, 2000; 3 = Gravina et al., 2005; 4 = Surrmely and Hays, 2011; 5 = Angevin and Surrmely, 2013; 6 = Lafarge, 2014; 7 = this work.

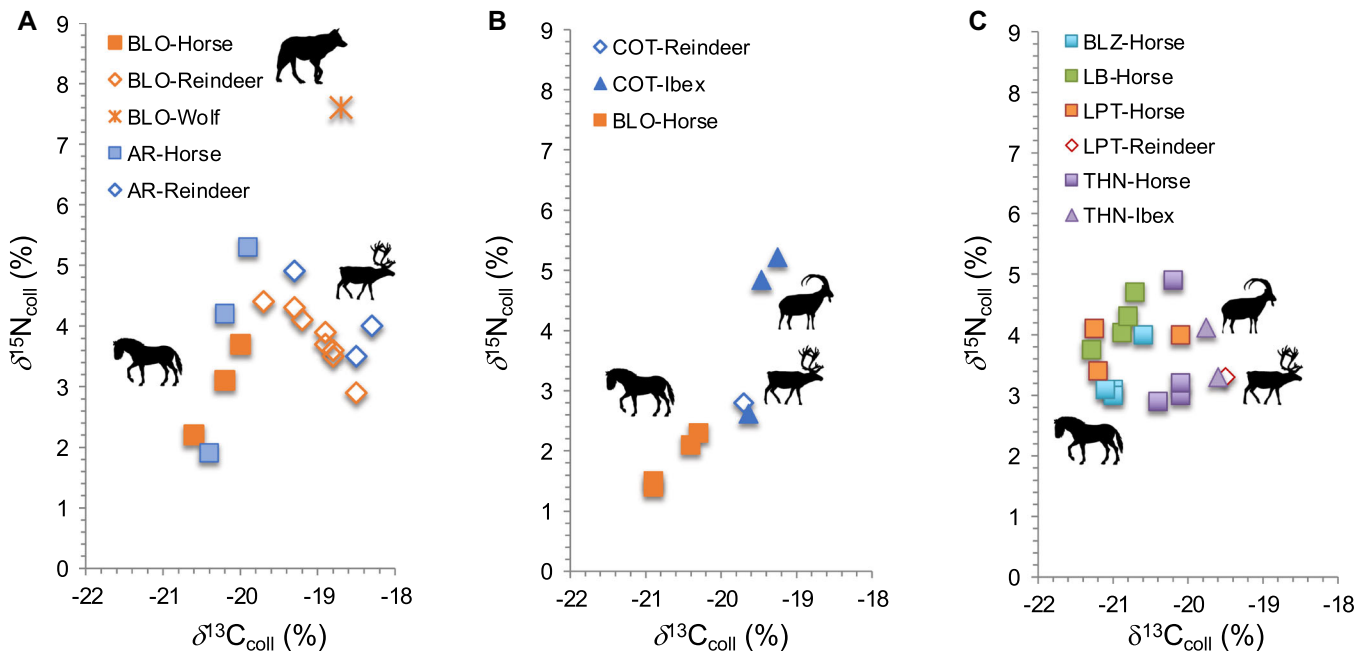
attention is required in the selection of samples for radiocarbon dating. Beyond the C:N ratio, the content of C and N in collagen should be scrutinized as well as the extraction yield which have served here as relevant quality indicators.

### Chronological trend for reindeer (ca. 40 000–14 000 cal BP)

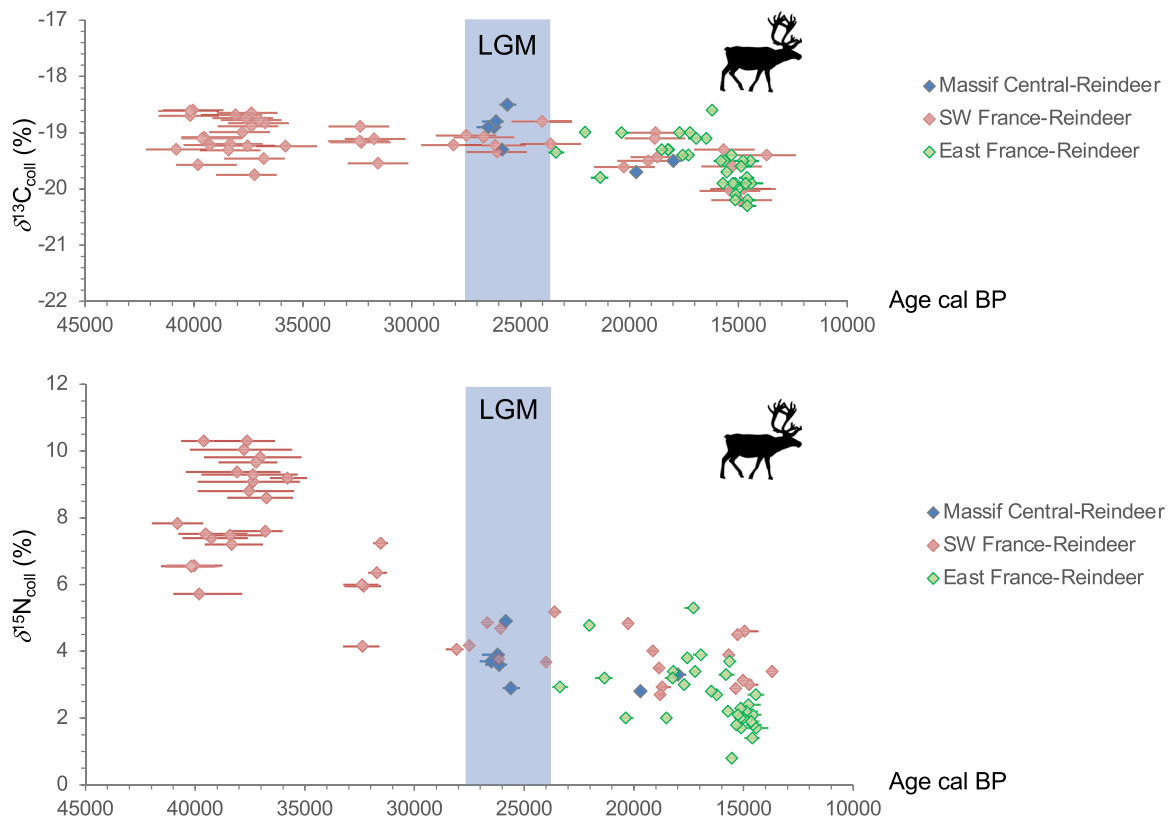
In some cases, the mediocre state of preservation of bone collagen may impact the reliability of previous radiocarbon dating, as in the site of Le Blot where one dated specimen of the Final Gravettian displays a C:N ratio of less than 2.9. In contrast, the high chemical quality of the dated collagen from Abri du Rond (C content >30%, C:N ratio of 2.9 and 3.2) secures the attribution of the occupation to the Final Gravettian (also named Protomagdalenian), a chrono-culture that has been identified in a limited number of sites in France (Le Blot in the Massif Central, Abri Pataud, Laugerie-Haute Est and Les Peyrugues in southwestern France; reviewed in Rigaud, 2008). Our new data corpus reflects the human subsistence activity in the northern part and southern part of the Massif Central, essentially along the Allier Valley, following diachronic periods during and after GS-3. We consider here GS-3, from ca. 27.5 to 23.3 ka according to the NGRIP record (Lowe et al., 2008), as equivalent to the Last Glacial Maximum (LGM) following the definition of Hughes and Gibbard (2015), in contrast to the LGM period between ca. 26.5 and 20–19 ka as defined by Clark et al. (2009).

The dated reindeer from the Massif Central can be added to the set of dated specimens of southwestern France (Aquitaine Basin; reviewed in Drucker, 2022) and eastern France (French Jura and northwestern Alps; Drucker et al., 2009, 2012). The dramatic change in  $\delta^{15}\text{N}$  values over time contrasts with the relative stability of the  $\delta^{13}\text{C}$  values (Figure 4). The highest  $\delta^{15}\text{N}$  values are reached in southwestern France between ca. 40 800 and 35 700 years cal BP, at the site of Castanet (+7.6 to +10.3‰) and Abri Pataud (+5.7 to +7.8‰) for reindeer found in an early Aurignacian context. Then, a decrease can be assumed by a more limited number of samples before the  $\delta^{15}\text{N}$  values stabilize between +2.7 and +5.2‰ during the LGM (or GS-3) and later. Possible reasons for the relatively higher  $\delta^{15}\text{N}$  values during the pre-LGM Palaeolithic are discussed in Bocherens et al. (2014), among which higher aridity could be the main driving factor. Finally, the more limited amount of data for the Massif Central reindeer suggests higher  $\delta^{13}\text{C}$  values than in southwestern France for comparable  $\delta^{15}\text{N}$  values during the LGM. This could be an indication of the higher aridity and/or lichen availability (e.g. lacumin et al., 2000; Drucker et al., 2011), reflecting more tundra-like conditions, in the Massif Central.

In eastern France, the available record is limited to the post-LGM period during the phase of animal and human recolonization after retreat of the mountain glaciers (reviewed in Cupillard et al., 2015). The decrease in  $\delta^{15}\text{N}$  values is interpreted to be the result of habitat extension to territories recently freed from glaciers and the impact of permafrost (Drucker et al., 2012). Low nitrogen availability and limited microbial activity in recently exposed soils, as well as low mycorrhization of plants close to the glacier front lead to <sup>15</sup>N-depleted soils and plants (e.g. Hobbie et al., 2005). Relatively lower  $\delta^{13}\text{C}$  values by the end of GS-2.1a, around 15 000 cal BP, is attributed to lower lichen availability and/or increased browsing, since both lichen and grasses display higher  $\delta^{13}\text{C}$  values than other plants in modern peri-arctic ecosystems (reviewed in Drucker, 2022). The corpus of directly dated reindeer data in the Massif Central is still too limited to infer comparable habitat re-extension and/or change in the foraging habits after the LGM on a precise chronological basis.



**Figure 3.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone or dentine collagen ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) of: wolf (*Canis lupus*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from Le Blot (BLO) and Abri du Rond (AR) during the Final Gravettian (A); reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and ibex (*Capra ibex*) from Cottier (COT) and Le Blot (BLO) during the Badegoulian (B); and reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and ibex (*Capra ibex*) from Blanzat (BLZ), Lépétade-Chabasse (LPT) and Thônes (THN) during the Magdalenian (C). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]



**Figure 4.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone or dentine collagen ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) directly dated from reindeer (*Rangifer tarandus*) from the Massif Central (this work), southwestern (SW) France (reviewed in Drucker, 2022) and East France (Drucker et al., 2009, 2012). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

#### Cultural phases in comparison with southwestern France and northeastern Iberian Peninsula

During the early Upper Palaeolithic, the relatively high  $\delta^{15}\text{N}$  values of the horse from Grotte des Fées (+6.3‰) are comparable with those found for the same species in southwestern France (from +4.2 to +6.5‰; Table 2; Supporting

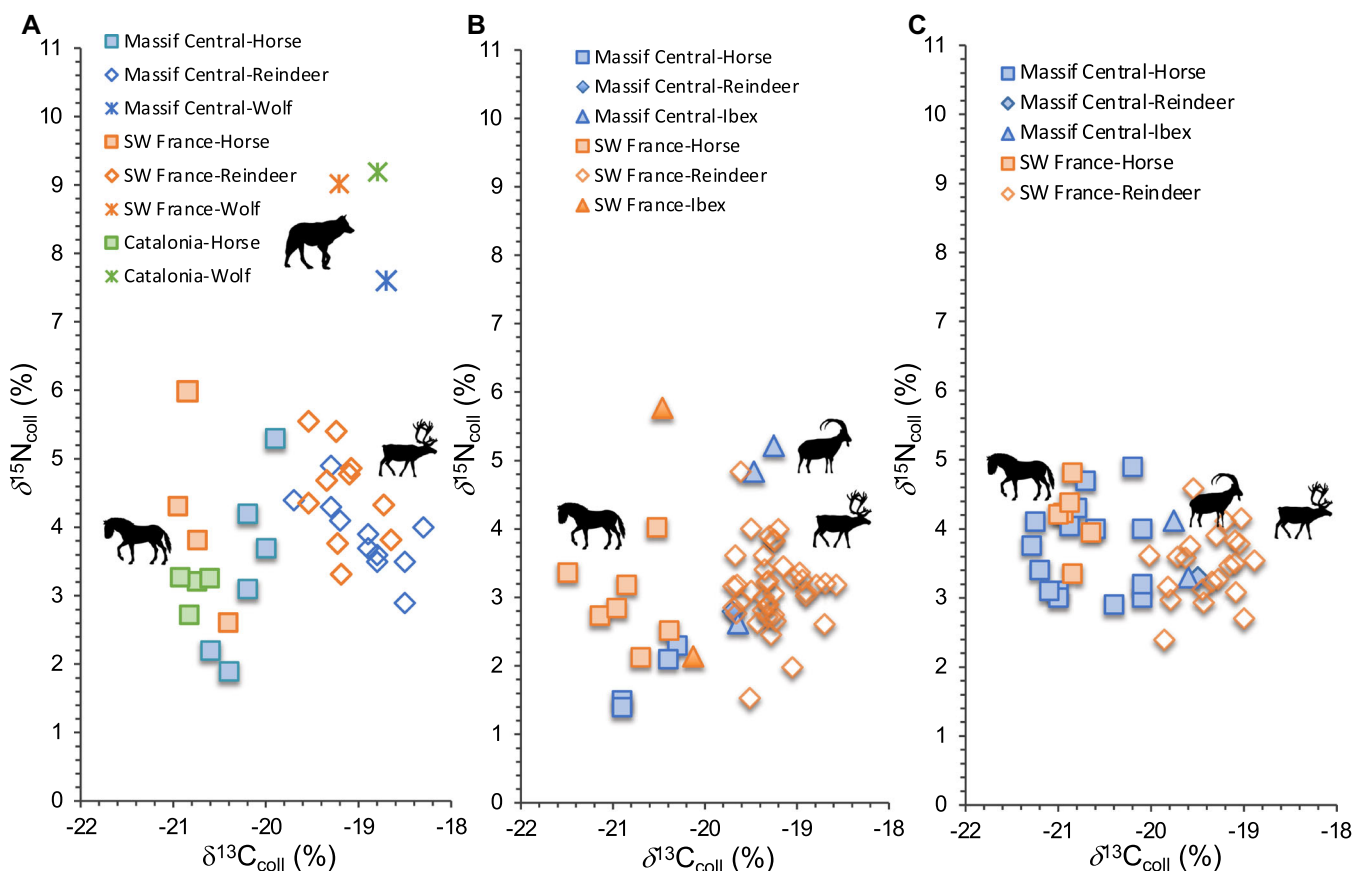
Information Fig. S5). These values are consistent with  $^{15}\text{N}$ -enriched collagen of large mammals observed during the pre-LGM in comparison with the LGM and late Pleniglacial periods in several regions of northwestern Europe, such as southwestern France ( $\delta^{15}\text{N} > +6\text{‰}$ ; Drucker et al., 2003; Drucker, 2022), Germany (Stevens et al., 2008) and British

Isles (Stevens and Hedges, 2004). In contrast, relatively more stable  $\delta^{15}\text{N}$  values of large herbivores over time have been observed in southern European regions, such as southern Italy (Iacumin et al., 1997) and northwestern Spain (Stevens et al., 2014; Domingo et al., 2015; Jones et al., 2020). Lower  $\delta^{15}\text{N}$  values in large herbivores during the LGM in northwestern Europe are attributed to the consequences of the cold conditions on the pedogenic activities of soils (Drucker et al., 2003; Stevens and Hedges, 2004).

During the Final Gravettian (ca. 26 700–25 600 cal BP), the  $\delta^{15}\text{N}$  values of horses and reindeer revealed comparable ranges between the Iberian Peninsula (Catalonia; Drucker et al., 2021), southwestern France and the Massif Central despite obvious geographical contrasts (Figure 5a). The more constrained range in  $\delta^{15}\text{N}$  values of the Catalonian horse may be due to the small sample size or a higher homogeneity in the ecotypes exploited by equids in the northeastern Iberian Peninsula. If access to variable elevations over relatively small distances may explain the contrasts in  $\delta^{15}\text{N}$  values among the Massif Central horses, it is unlikely to be the case in southwestern France (Laugerie-Haute and Abri Pataud sites). Interestingly, the reindeer and horse of the Massif Central show a similar range of  $\delta^{15}\text{N}$  values to those of southwestern France, while their  $\delta^{13}\text{C}$  are slightly shifted to higher values. This may reflect more arid conditions for the horses and/or greater access to lichen for reindeer, lichen exhibiting higher  $\delta^{13}\text{C}$  than those of vascular plants (reviewed in Drucker, 2022). In both cases, more tundra-like environmental conditions would characterize the Massif Central compared to southwestern France.

The wolf from Le Blot in the Massif Central is rather enriched in  $^{13}\text{C}$  compared to the wolf specimen of southwestern France and, to a lesser extent, of Catalonia (Figure 5a). Together with lower  $\delta^{15}\text{N}$  values, a diet with a higher reindeer contribution could be hypothesized for this specific specimen wolf from Le Blot. Indeed, reindeer is also the mostly most common found species in the archaeological occupation (more than 80% of the determined remains; Chauvière and Fontana, 2005; Fontana 2022). Their presence year-round as established for southwestern France could not be confirmed based on zooarchaeological evidence. The stable isotope results of this study do not rule out or confirm a migratory behaviour of the reindeer, since bone collagen averaged a long-term dietary record. Further incremental analysis on antler or teeth may help in this regard because it could capture the seasonal variability of foraging conditions and territories.

During the Badegoulian and early Magdalenian (ca. 22 500–19 100 cal BP), a general decrease in the  $\delta^{15}\text{N}$  values of large herbivores is seen, especially for reindeer in southwestern France and horse in the Massif Central (Figure 5b). The GS-2.1 phase is characterized by cold and increasingly arid conditions leading to the regression of glaciers in the Massif Central (Ancrenaz et al., 2022). The relatively lower  $\delta^{15}\text{N}$  values of horse could be attributed to a habitat encompassing recently deglaciated areas (Drucker et al., 2012), where pedogenic activity is still low and leads to lower  $\delta^{15}\text{N}$  values of the plants (e.g. Hobbie et al., 2005). Alternatively, the Massif Central horse may have experienced more diverse habitat during the LGM linked potentially to greater mobility due to harsh conditions during winter.



**Figure 5.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone or dentine collagen ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) of: wolf (*Canis lupus*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from the Massif Central (this work), southwestern (SW) France (Drucker et al., 2003; Vercoutère et al., 2014) and Catalonia (Drucker et al., 2021) during the Final Gravettian (A); reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and ibex (*Capra ibex*) from the Massif Central (this work) and southwestern (SW) France (reviewed in Drucker, 2022) during the Badegoulian and early Magdalenian (B); and reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and ibex (*Capra ibex*) from the Massif Central (this study) and southwestern (SW) France (reviewed in Drucker, 2022) during the later phases of the Magdalenian (C). [Color figure can be viewed at wileyonlinelibrary.com]

In the later phases of the Magdalenian (ca. 19 100–16 600 cal BP), the horses from the Massif Central show a similar range in  $\delta^{15}\text{N}$  values but a higher variability in  $\delta^{13}\text{C}$  values compared to southwestern France (Figure 5c). The altitude effect on plants could explain the higher  $\delta^{13}\text{C}$  values of horses from Thônes than in southwestern France and other Massif Central sites (Körner et al., 1991; Männel et al., 2007). As during the earlier part of the Magdalenian, some ibex specimens have  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values overlapping with those of reindeer from the Massif Central. The diet of modern ibex is dominated by grasses, in contrast to reindeer which is a mixed feeder (Parrini et al., 2009). However, they also consume leaves of shrubs in winter, as well as mosses and lichen in spring (Parrini et al., 2009) which could explain similar collagen isotopic values to reindeer. Surprisingly, the higher elevation expected for ibex foraging is not reflected by lower  $\delta^{15}\text{N}$  values than those of reindeer, but the limited number of data may not capture the elevation differences in the habitat of the two species.

Horses show a comparable pattern in the change of their  $\delta^{15}\text{N}$  values over GS-3 and GS2.1 in both the Massif Central and southwestern France: a high variability during GS-3 with values above +5‰, a general decrease with more constrained range during GS-2.1c, and a relative increase during GS-2.1b and 1.a with no values above +5‰. The decrease during GS-2.1c is more pronounced in the Massif Central, leading to an even more dramatic successive increase in the later phases of GS-2. This illustrates the more challenging environmental conditions of this region that were isotopically recorded by horse and reindeer through their diet, testifying to their presence over a substantial part of the year.

## Conclusions

Isotopic study of the bone collagen of large mammal remains from Upper Palaeolithic sites of the Massif Central was undertaken to better decipher the environmental conditions faced by human groups and their prey, mainly reindeer, in the upper and middle valleys of the Allier and Loire rivers. The results presented here indicate that generally harsher conditions prevailed in the southern Allier valley in the Massif Central than in the Dordogne and Lot region in southwestern France, as indicated by higher  $\delta^{13}\text{C}$  values of horses and reindeer. The importance of the tundra landscape, with arid conditions and high availability of terrestrial lichens, may have produced a seasonal peak of reindeer occurrence in this mountainous area of the Massif Central, which could have been a calving ground (Fontana, 2022). This may have motivated the human occupation of the Massif Central mountains for hunting purposes from the end of spring to late summer.

The small number and chronological position of the samples mean that it is not possible to identify differences in the environment between the southern high valleys and the northern Limagne plain, where horses were hunted to a greater extent. The overall harsher climatic conditions than in southwestern France may explain the lack of human occupation during winter in the whole Massif Central. However, it is likely that other factors also contributed to the decision to leave this region during the cold season, such as the supply of flint from the south of the Paris Basin and the gathering of large antlers from adult male reindeer (available from October) in adjacent areas (Fontana et al., 2018; Fontana, 2022). Nevertheless, this study demonstrates that the Upper Palaeolithic societies of the Massif Central on the one hand, and those of the Lot and Dordogne on the other, lived in distinct environments in terms of both climate and landscape. This information is fundamental in that it is coupled with a

difference in terms of group mobility and the availability of two key resources in the economic system (reindeer and good quality flint) between the Massif Central and southwestern France. Further isotopic analyses, particularly in the northern part of the Limagne plain, will provide further information on the annual nomadic cycle of human societies in the distinct context of the Massif Central.

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## Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Figure S1.** Carbon and nitrogen contents in bone or dentine collagen ( $C_{\text{coll}}$  and  $N_{\text{coll}}$ ) plotted against the collagen extraction yield (Coll yield) (A), atomic C:N ratios in bone or dentine collagen ( $C:N_{\text{coll}}$ ) plotted against the collagen extraction yield (Coll yield) (B), carbon and nitrogen contents in bone or dentine collagen ( $C_{\text{coll}}$  and  $N_{\text{coll}}$ ) plotted against collagen extraction yield expressed as quantity of nitrogen obtained as collagen compared with nitrogen content in bone or dentine ( $N_{\text{yield}}$ ) (C), and atomic C:N ratios in bone or dentine collagen ( $C:N_{\text{coll}}$ ) plotted against collagen extraction yield expressed as quantity of nitrogen obtained as collagen compared with nitrogen content in bone or dentine ( $N_{\text{yield}}$ ) (D).

**Figure S2.** Nitrogen content in bone or dentine ( $N_{\text{bd}}$ ) in rockshelters vs. open air sites (A), carbon content in bone or dentine collagen ( $C_{\text{coll}}$ ) in rockshelters vs. open air sites (B), and collagen extraction yield expressed as quantity of nitrogen obtained as collagen compared with nitrogen content in bone or dentine ( $N_{\text{yield}}$ ) in rockshelters vs. open air sites (C).

**Figure S3.** Calibrated radiocarbon ages for the dated animal bones from level B5 of la Grotte des Fées at Châtelperron using OxCal v.4.4 according to the IntCal20 calibration dataset (Reimer et al., 2020) (dates in bold from this study, others from Gravina et al., 2005; Table 1).

**Figure S4.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone or dentine collagen ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) directly dated from reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from in the Massif Central (this work).

**Figure S5.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone or dentine collagen ( $\delta^{13}\text{C}_{\text{coll}}$ ,  $\delta^{15}\text{N}_{\text{coll}}$ ) of the horse (*Equus* sp.) from Grotte des Fées (Massif Central; this work) and horse (*Equus* sp.), reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), giant deer (*Megaloceros giganteus*) and *Bos/Bison* from Roc-de-Combe, Saint-Césaire and Grotte XVI (SW France; Bocherens et al., 2014; Bocherens, 2015) during the early Upper Palaeolithic.

**Abbreviations.** AMS, accelerator mass spectrometry; AR, abri du Rond – Saint Arcons; BLO, Le Blot; BLZ, Blanzat; CA, cave;  $C_{\text{coll}}$ , carbon content in collagen;  $C:N_{\text{coll}}$ , atomic carbon-to-nitrogen ratio in collagen; CHP, Grotte des Fées– Châtelperron;  $\text{Coll}_{\text{yield}}$ , collagen yield; COT, Cottier;  $c_{\text{coll}}$ , carbon stable isotope ratio in collagen (expressed as delta values in per mill);  $\delta^{15}\text{N}_{\text{coll}}$ , nitrogen stable isotope

ratio in collagen (expressed as delta values in per mill); GI, Greenland Interstadial; GS, Greenland Stadial; HS, Heinrich Stadial; LB, Le Bay; LGM, Last Glacial Maximum; LPT, Lépétade-Chabasse;  $N_{bd}$ , nitrogen content in bone or dentine;  $N_{coll}$ , nitrogen content in collagen;  $N_{yield}$ , nitrogen yield; NGRIP, North Greenland Ice Core Project; OA, open air; PL, Pont de Longues; RC, rockshelter; THN, Thônes-Auzary; VB, La Vigne-Brun.

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