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Environmental context of the Magdalenian settlement in the Jura Mountains using stable isotope tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen from reindeer (*Rangifer tarandus*)

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ABSTRACT

The Jura Mountains are considered to be a region where phases of ice cap extension and retreat in response to climatic variation during the Upper Pleniglacial and Lateglacial (ca. 24,000–12,800 cal BP) are well reflected in the vegetation and animal spectrum composition. A new set of direct AMS radiocarbon dates of collagen from reindeer (*Rangifer tarandus*) bones found at archaeological sites indicated an almost continuous occupation of the Jura region since the end of Last Glacial Maximum, at ca. 24,000 cal BP, until its local disappearance around 14,000 cal BP. To investigate a possible change in reindeer ecology, isotopic analysis of carbon, nitrogen, sulfur in collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) were performed on the dated specimens. A decrease in the $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values of Jura reindeer was found at the beginning of the Lateglacial period around 16,300–15,600 cal BP. While the change in $\delta^{13}\text{C}_{\text{coll}}$ values was better explained by a change in diet composition with a decreasing input of lichens, the relative low $\delta^{15}\text{N}_{\text{coll}}$ values of the reindeer during the Lateglacial was consistent with a geographical pattern of soil maturity inherited from the Last Glacial Maximum. The same pattern was also seen in the $\delta^{15}\text{N}_{\text{coll}}$ values of the Lateglacial horse (*Equus* sp.) and red deer (*Cervus elaphus*) until ca. 14,000 cal BP. The decrease in reindeer $\delta^{15}\text{N}_{\text{coll}}$ around 16,300–15,600 cal BP and around 21,000–20,000 cal BP in the Jura region may be linked to the occupation of territories recently released by glaciers that formed during the Heinrich event 1 and the Last Glacial Maximum, respectively. The associated high $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{34}\text{S}_{\text{coll}}$ values found in two specimens indicate the occurrence of areas of high soil activity in a globally cold context. This might correspond to the occupation of refugia in the close surroundings of the Jura region. Such local refugia could explain the capacity of the reindeer to occupy rapidly the newly available territories during phase of glacier retreat. The intensification of the Magdalenian human settlement could have been favored by these local ecosystem expansions.

1. Introduction

The stable isotope signature of ancient bone collagen has been used for several decades for dietary and environmental reconstruction (e.g. review in Koch, 2007; Bocherens and Drucker, 2007). Although isotope signatures were originally used mostly to reconstruct trophic webs involving humans, large mammals have been employed more recently as trackers of change in ecology and environment in the analyzed species. The chronological evolution

of carbon-13 and nitrogen-15 (^{13}C and ^{15}N) abundance in collagen over the last 40,000 years, during the Upper Palaeolithic, has been studied in reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), horse (*Equus* sp.), large bovines (*Bos* or *Bison*) and woolly mammoth (*Mammuthus primigenius*) from Eurasia (e.g. Iacumin et al., 1997, 2000; Drucker et al., 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Stevens et al., 2008) and North America (Fox-Dobbs et al., 2008; Szpak et al., 2010). These studies have demonstrated a rather stable distribution in the collagen ^{13}C abundance among large herbivore species that is linked to diet specialization. Plant growth forms differ in the relative amount of carbon-13 they contain. For instance, lichens are systematically enriched in ^{13}C compared to vascular plants from the same ecosystem (e.g. Barnett,

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1994). Thus, high ^{13}C abundance in the collagen of ancient and modern reindeer may be interpreted as the predominant consumption of lichens, which are avoided by other herbivores due to its toxicity (e.g. Fizet et al., 1995; Drucker et al., 2003, 2010; Bocherens et al., 2011a). In contrast, the nitrogen-15 amounts in the collagen of the same individuals exhibit variation over time as a result of change in climatic conditions, such as aridity in Alaska (Fox-Dobbs et al., 2008; Szpak et al., 2010) and temperature in northwestern Europe (Drucker et al., 2003; Stevens et al., 2008). In the latter, the effect of temperature on ^{15}N abundance in large herbivores is thought to be indirect and conveyed by soil processes, particularly under permafrost influence. Regions where permafrost action was the most intense from the Last Glacial Maximum (LGM) deliver the lowest collagen ^{15}N abundance in large herbivores during the post-LGM period (Drucker et al., 2003, 2011b). From a chronological point of view, ^{15}N amounts in large herbivores collagen were found to increase with rising temperature, which triggered higher soil activity (Drucker et al., 2003, 2011a). These spatial and temporal patterns are comparable to modern ones in which ^{15}N amounts in surface soils rise with increasing distance from a glacier front due to soil development (Hobbie et al., 2005).

Higher soil maturity, reflected in higher ^{15}N amounts passed on to herbivores, has been recently hypothesized to lead to higher abundance of sulphur-34 in the collagen of deer as well (Drucker et al., 2011a). At a given period of time, some differences in the sulphur-34 abundance in deer collagen were observed that might be linked to local geology parameters (Drucker et al., 2011b). Thus, applied on terrestrial herbivore in continental context, sulphur-34 appears to be a promising tracker of home range that could complete the information delivered by the carbon-13 and nitrogen-15 measurements.

By the end of the Upper Palaeolithic, during the Lateglacial period that extended from ca. 18,000 to 11,600 cal BP, a rapid oscillation from a cold episode (GS-2a event, ca. 18,000–14,700 cal BP) to a warm episode (GI-1e to GI-1a event, ca. 14,700–12,800 cal BP) was experienced by the ecosystems at a global scale (e.g. Lowe et al., 2008). This global first warming event succeeded thousands of years of cold conditions of the post-LGM period and allowed the development of boreal forest following grassland colonization (e.g. Amman and Lotter, 1989; De Beaulieu et al., 1994). A first major change in the large herbivore community occurred with the extinction or retreat of some emblematic species of the Pleniglacial, including reindeer (*R. tarandus*). Reindeer played a central role in human subsistence during the Upper Palaeolithic, and during most of the Lateglacial, it was one of the most important deer prey hunted by the human groups of the Magdalenian culture (e.g. Grayson et al., 2001). This taxon, however, was later replaced by the red deer (*C. elaphus*),

whose population significantly extended with the warming conditions (e.g. Bridault and Chaix, 2009). Thus, the chronology of the extinction of the reindeer has been intensively examined at the local scale especially in France (e.g. Bridault et al., 2000; Oberlin and Pion, 2009; Szmjdt et al., 2009; Drucker et al., 2011c). In the Jura Mountains in eastern France, reindeer have been shown to disappear around 14,000 cal BP (Bridault et al., 2000; Oberlin and Pion, 2009), ca. 2000 years after the local extinction of the woolly mammoth and the woolly rhinoceros (Bridault and Chaix, 2009). Similarly, the hypothesis of reindeer occurrence later than ca. 14,000 cal BP in the western French Pyrenees (e.g. Delpéch, 1983; Altuna et al., 1991) has not been confirmed so far by direct radiocarbon dating of bones from the Dufaure and Duruthy sites (Costamagno et al., 2009).

In this work, the aim is to examine the ecology of reindeer in the Jura Mountains during the key period of the Lateglacial using the stable isotope composition (carbon-13, nitrogen-15 and sulphur-34) of collagen combined with direct radiocarbon dating. The occupation of deglaciated territories with low soil activity is expected to provide low ^{15}N and possibly low ^{34}S amounts, while the context of global warming should be associated with increasing ^{15}N and ^{34}S abundance due to rising temperature. Moreover, changes in temperature are also expected to trigger changes in vegetation availability that could be reflected in the ^{13}C amounts of reindeer. This study presents a chronological record of variation in reindeer collagen stable isotopes for the Jura region in order to better understand the control parameters that occur during colonization in a periglacial context.

2. Material and methods

Bones of reindeer (*R. tarandus*) from the Jura region were selected from archaeological sites that contained Magdalenian artefacts (Table 1; Fig. 1): Baume Noire (Fréttigny; David, 1996), Chaumoiso-Boivin (Blois-sur-Seille; Cupillard, 2008), Grotte Grappin (Arlay; Cupillard and Welté, 2006, 2009), and La Baume (Gigny-sur-Suran; Campy et al., 1989; Fabre, 2010) and Les Cabônes (Ranchot; Cupillard and David, 1995). The selection of the bone was primarily oriented toward samples that could be taxonomically identified as reindeer. The number of bone fragments bearing cut-marks varied from ca. 30% to 50% of the studied material depending on the site. Thus, due to this relatively low frequency, special attention has been paid to retain bones showing fracture patterns clearly specific of human modification. Exceptions are the astragalus and navicular bones from the site of Arlay.

Analyses of carbon-13 and nitrogen-15 abundance ($n = 14$) as well as of direct AMS radiocarbon dating ($n = 13$) were conducted, thereby doubling the dataset published in Drucker et al. (2009) for

Table 1

List of the studied archaeological sites from the Jura Mountains with their geographical location, altitude, laboratory code and code number in Fig. 1.

Site	Locality	District	Region	Altitude (m)	Lab code	N° in Fig. 1
Kastelhöhle	Himmelried	Solothurn	Swiss Jura	397		1
Rochedane	Villars-sous-Dampjoux	Doubs	French Jura	355	RCD-	2
Baume Noire	Fréttigny	Haute-Saône	French Jura	345	FRT-	3
Les Cabônes	Ranchot	Jura	French Jura	216	RAN-	4
Grotte Grappin	Arlay	Jura	French Jura	225	ARL-	5
Chaumoiso-Boivin	Blois-sur-Seille	Jura	French Jura	475	BLS-	6
Mollendruz	Mont-la-Ville	Vaud	Swiss Jura	1088	ALP-10	7
La Baume	Gigny-sur-Suran	Jura	French Jura	480	GIS-	8
La Croze	Saint-Martin-du-Mont	Ain	French Jura	260		9
La Colombière	Neuville-sur-Ain	Ain	French Jura	275		10
Abri Gay	Poncin	Ain	French Jura	260		11
La Chênélaz	Hostias	Ain	French Jura	900	ALP-1	12
Les Hoteaux	Rosillon	Ain	French Jura	350	ALP-7	13
La Garenne	Vénérieu	Isère	French Jura	335	ALP-6	14
Les Romains	Virignin	Ain	French Jura	278		15

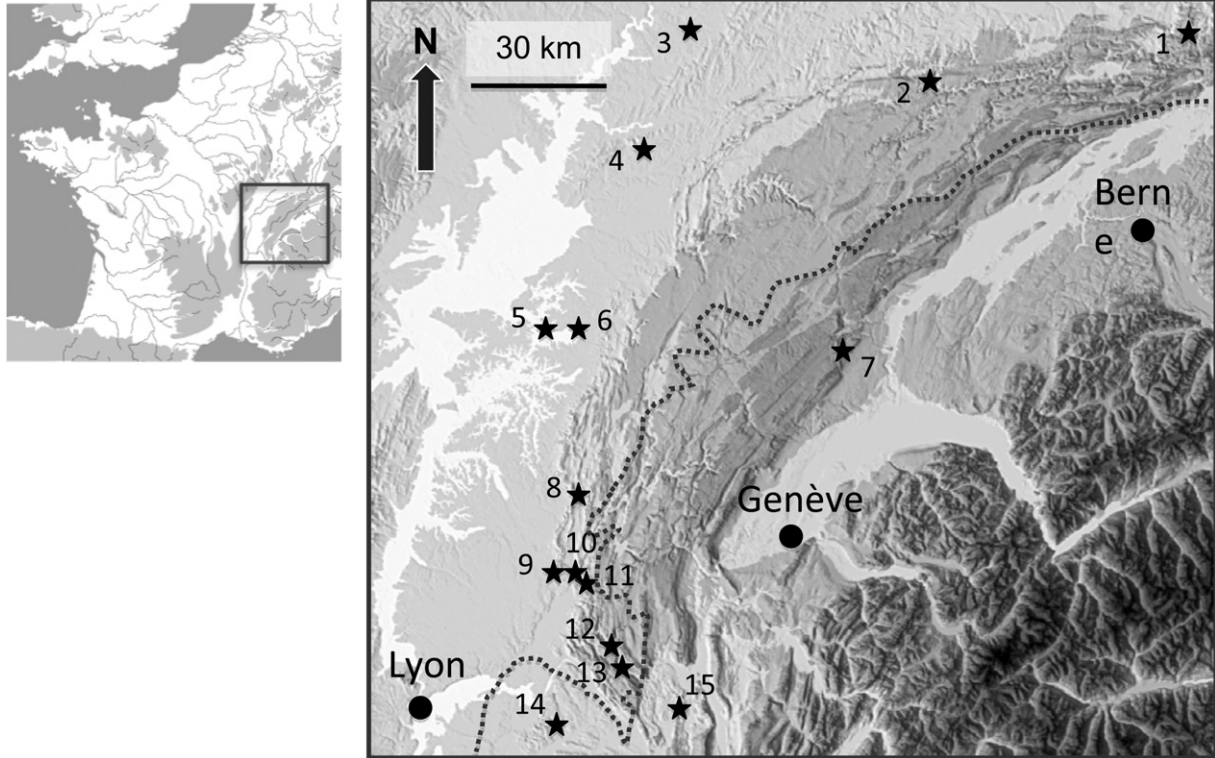


Fig. 1. Geographical location of the archaeological sites in the Jura Mountains where originated the reindeer samples considered for isotopic analysis. In Swiss Jura: 1 = Kastelhöhle – Himmelried (Solothurn), 7 = Mollendruz – Mont-la-Ville (Vaud). In French Jura: 2 = Rochedane – Villars-sous-Dampjoux (Doubs), 3 = Baume Noire – Frétigny (Haute-Saône), 4 = Les Cabônes – Ranchot (Jura), 5 = Grotte Grappin – Arlay (Jura), 6 = Chaumoiso-Boivin – Blois-sur-Seille (Jura), 8 = La Baume – Gigny-sur-Suran (Jura), 9 = La Croze – Saint-Martin-du-Mont (Ain), 10 = La Colombière – Neuville-sur-Ain (Ain), 11 = Abri Gay – Poncin (Ain), 12 = La Chênélaz – Hostia (Ain), 13 = Les Hoteaux – Rossillon (Ain), 14 = La Garenne – Vénérieu (Isère), 15 = Les Romains – Virignin (Ain).

the Jura Mountains. Sulphur-34 abundance was measured for a few collagen samples published by Drucker et al. (2009), in addition to most of the new ones produced for this work. Three directly dated reindeer of the early post-LGM from the site Kastelhöhle in the Swiss Jura, which benefited from carbon-13 and nitrogen-15 analysis (Bronk Ramsey et al., 2002; Stevens et al., 2008), were considered for chronological comparison with the results from the Jura Mountains. Direct AMS radiocarbon (^{14}C) dating was performed on a sub-sample of the bones selected for stable isotope analysis. The results were calibrated at 2 sigma based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009).

For stable isotope analysis, collagen was extracted following a protocol based on Longin (1971) and modified by Bocherens et al. (1997). The extraction process includes a step of soaking in 0.125 M NaOH between the demineralization and solubilization steps to achieve the elimination of lipids. Elemental analysis (C_{coll} , N_{coll} , S_{coll}) and isotopic analysis ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) were conducted at the Department of Geosciences of Tübingen University using an NC2500 CHN-elemental analyzer coupled to a Thermo Quest Delta + XL mass spectrometer. The standard, internationally defined, is a marine carbonate (PDB) for $\delta^{13}\text{C}$ and atmospheric nitrogen (AIR) for $\delta^{15}\text{N}$. Analytical error, based on within-run replicate measurement of laboratory standards (albumen, modern collagen, USGS 24, IAEA 305A), is $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ values and $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ values. Samples were calibrated to $\delta^{34}\text{S}$ values relative to CDT of NBS 123 ($\delta^{34}\text{S} = 17.10\text{‰}$), NBS 127 ($\delta^{34}\text{S} = 20.31\text{‰}$), IAEA-S-1 ($\delta^{34}\text{S} = -0.30\text{‰}$) and IAEA-S-3 ($\delta^{34}\text{S} = 21.70\text{‰}$). The reproducibility is $\pm 0.4\text{‰}$ for $\delta^{34}\text{S}$ measurements, and the error on amount of S measurement is 5%. Reliability of the $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values can be established by measuring the chemical composition of collagen, with C/N_{coll} atomic

ratio ranging from 2.9 to 3.6 (DeNiro, 1985), percentage of C_{coll} and N_{coll} above 8% and 3%, respectively (Ambrose, 1990). The $\delta^{34}\text{S}$ values of samples for which the atomic C/S_{coll} and N/S_{coll} ratios were included in the range of 300–900 and 100–300, respectively, were retained (Nehlich and Richards, 2009; Bocherens et al., 2011b). In modern mammals, the collagen sulphur content was found to vary from 0.14 to 0.33% (Bocherens et al., 2011b), which generally fits the theoretical range of 0.14–0.29% based on DNA and amino acid sequence (Nehlich and Richards, 2009). In this study, selection included samples with a percentage of S_{coll} ranging from 0.14 to 0.24% based on the minimum and maximum values obtained on modern mammalian collagen (Aldrich collagen, modern elk and modern camel) measured in the same series.

3. Results and discussion

3.1. Chronological sequence of the reindeer in the Jura Mountains

The new AMS radiocarbon dating results of reindeer bone from the French Jura have delivered a long chronological sequence extending from ca. 14,600 to 23,000 cal BP (12,500 to 19,300 BP; Table 2). About half of these dates were comparable with previous results ranging from ca. 14,000 to 17,500 cal BP published in Bridault et al. (2000) and in Oberlin and Pion (2009) for the Lateglacial reindeer of the French Jura and northern Alps. This time range was coeval to the GI-1e and GS-2a events of NGRIP isotopic record stratigraphy (Lowe et al., 2008), which is classically considered to be a period of intense reoccupation of the Jura Mountains (Leesch et al., in press). AMS dating of a reindeer from the layer C of Grotte Grappin-Arlay, which is associated with possibly several successive Magdalenian occupations, provided an age close to 19,900 cal BP (Cupillard and

Table 2

List of the directly dated samples of reindeer (*Rangifer tarandus*) from the Jura Mountains with the archaeological record, result of AMS dating, chronological range and source of the data. The carbon and nitrogen composition of the collagen is given through atomic ratio (C/N_{coll}). The results were calibrated at 2 sigma based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009). 1 = Bronk Ramsey et al., 2002; 2 = Cupillard and Welté, 2006; 3 = Stevens et al., 2008; 4 = Drucker et al., 2009; 5 = Bridault et al., 2000. Magd. and Pal. stand for Magdalenian and Paleolithic, respectively.

Site	N° lab	Sample	N° excavation	Level	Culture	C/N _{coll}	Age BP	N° date	Age cal BP	¹⁴ C source	
Abri Gay	—	tooth	M13/909	F2b	—	3.3	12,160 ± 60	Lyon-640(GrA9705)	13,819–14,189	5	
Rochedane	RCD-10800	metapodial	Ro70 220 47/28	D1	Late Magd.	3.2	12,420 ± 75	OxA-8030 (Ly-709)	14,107–15,001	5	
La Chênélaz	ALP-1	phalanx II	M6 2975	2	Upper Magd.	3.1	12,460 ± 65	OxA-8027 (Ly-703)	14,155–15,025	5	
Chaumois-Boivin	BLS 1	phalanx	31-11-A	1	Upper Magd.	3.3	12,530 ± 120	Ly-3280(Poz)	14,148–15,148	this work	
Les Romains	—	bone	H11 206	cIII	Upper Magd.	3.2	12,690 ± 60	GrA9709(Ly-642)	14,610–15,494	5	
Mollendruz	ALP-10	left scaphoid	—	c5 inf	—	3.0	12,780 ± 80	OxA-9460 (Ly-1135)	14,711–15,670	5	
Les Romains	—	bone	H11 176	cIIb	Upper Magd.	3.2	12,830 ± 60	GrA-9710(Ly-432)	14,937–15,688	5	
Les Hoteaux	ALP-7	antler	—	—	—	3.0	12,830 ± 75	OxA-9457(Ly-1132)	14,913–15,913	5	
Abri Gay	—	metatarsal	G18/123	F2d	Upper Magd.	2.9	12,980 ± 70	Ly-639(GrA-9720)	15,110–16,300	5	
Baume Noire	FRT-1	metacarpal	Fr-87-17-M3-297	M3	Upper Magd.	3.3	13,045 ± 75	Ly-3292(Poz)	15,172–16,400	this work	
La Garenne	ARL-6	bone	none	2b–2c	—	2.9	13,150 ± 110	OxA-8163(Ly-702)	15,226–16587	5	
Grotte Grappin	ARL-8	scapula	11 J1/1998-3-9	C	(Upper?) Magd.	3.1	13,450 ± 50	Ly-4865 (GrA)	16,297–16,882	this work	
Grotte Grappin	ARL-6	astragalus	44J-sect1/1998-3-384	C	(Upper?) Magd.	3.1	13,640 ± 60	Ly-3878(GrA)	16,591–16,980	this work	
Ranchot	RAN-10	coxal	Ran88 F12 lim260- 270	néant	Magdalenian	3.0	13,965 ± 101	Erl-9392	16,792–17,419	this work	
Grotte Grappin	ARL-11	metacarpal	70 J1/1998-3-14	C	(Middle?) Magd.	3.4	14,180 ± 50	Ly-4868 (GrA)	16,959–17,559	this work	
La Croze	—	metatarsal	R7	néant	Middle Magd.	3.2	14,260 ± 70	GrA-9704(Ly-638)	16,998–17,665	5	
La Colombière	—	antler	E7-6/27.7	—	—	3.2	14,390 ± 70	Lyon-644(GrA-9713)	17,164–17,849	5	
Grotte Grappin	ARL-14	navicular	118 J1/1998-3-380	C	(Middle?) Magd.	3.4	14,520 ± 50	Ly-4871(GrA)	17,363–17,937	this work	
Grotte Grappin	ARL-12	astragalus	83 J1/1998-3-364	C	(Middle?) Magd.	3.4	14,850 ± 50	Ly-4869(GrA)	17,770–18,516	this work	
Grotte Grappin	ARL-10	astragalus	65 J1/1998-3-357	C	(Middle?) Magd.	3.1	14,940 ± 60	Ly-4867(GrA)	17,946–18,532	this work	
Grotte Grappin	ARL-7	metapodial	322-J1/1998-3-105	C	(Middle?) Magd.	3.0	15,260 ± 70	Ly-3877(GrA)	18,079–18,698	this work	
Grotte Grappin	ARL-3	metapodial	30-R-2/1998-3-30	C	(Early?) Magd.	3.1	16,840 ± 110	Ly-3160(Poz)	19,579–20,320	2	
La Baume	GIS-2	phalanx I	16-F2-VI	VI	(Early?) Magd.	3.4	17,645 ± 110	Ly-3290(Poz)	20,523–21,411	this work	
Baume Noire	FRT-3	metacarpal	Fre86 E7-1-M5-405	M5	Upper Pal.	3.3	18,070 ± 80	Ly-5218(GrA)	21,289–22,008	this work	
Kastelhöhle	OxA-9737	bone	—	Mid.	Badegoulian	3.1	18,530 ± 150	Ox-A 9737	21,561–22,430	1	
Kastelhöhle	OxA-9739	bone	—	Horizon	Mid.	Badegoulian	3.4	19,200 ± 150	Ox-A 9739	22,428–23,395	1
Baume Noire	FRT-2	metapodial	Fre86 D8-42-M4	M4	Upper Pal.	3.0	19,310 ± 80	Ly-5217(GrA)	22,593–23,423	this work	
Kastelhöhle	OxA-9738	bone	—	Mid.	Badegoulian	3.5	19,620 ± 140	Ox-A 9738	22,933–23,896	1	

Welté, 2006, 2009; Cupillard et al., in press). This date corresponds to the time of the Jura ice sheet retreat between ca. 24,000 to 19,000 cal BP (Buoncrisiani and Campy, 2004) and thereby extends the possibility of human settlement in the region back to the GS-2b (Upper Pleniglacial). The other dates from reindeer samples of Arlay-level C ranged from ca. 17,700 to 18,600 cal BP, which confirms the earlier phase of formation of this level suggested by a previous AMS dating of a horse (ca. 18,500 years cal BP; Cupillard and Welté, 2006). It also fills partly the gap between the oldest AMS date from a reindeer of Arlay and its earliest Lateglacial counterparts of the Jura Mountains. The radiocarbon dates from La Baume at Gigny-sur-Suran and La Baume Noire at Frétingney overlap with an extent beyond dates from Kastelhöhle-Nord in the Swiss Jura (Bronk Ramsey et al., 2002; Terberger and Street, 2002; Sedlmeier, 2010). The occurrence of archaeological remains of reindeer from ca. 21,000–23,000 cal BP confirms the possible presence of human population in the Jura region shortly after the Last Glacial Maximum (LGM). Such an early occupation was also documented in western Germany through the radiocarbon dating of faunal remains from Wiesbaden-Igstadt (Terberger and Street, 2002). The chronological sequence obtained from reindeer remains from archaeological context in the Jura region supports the hypothesis that the ecosystems, including human populations, expanded rapidly after episodes of unfavorable environmental conditions during the Upper Pleniglacial (e.g. Terberger and Street, 2002; Blockley et al., 2006).

3.2. Change in reindeer ecology during the Lateglacial in the Jura Mountains

The $\delta^{13}\text{C}_{\text{coll}}$ values of the Jura reindeer from the Upper Pleniglacial to the Lateglacial period (ca. 24,000 to 14,000 cal BP) ranged

from -20.3 to -18.6‰ (Table 3, Fig. 2). A change in the reindeer $\delta^{13}\text{C}_{\text{coll}}$ values appeared over time with a range shift from -19.8 to -18.3‰ before ca. 16,300 cal BP to -20.3 to -19.4‰ afterward. This slight (0.7‰ in average) but statistically significant decrease (Mann-Whitney-Wilcoxon test, $p < 0.001$) occurred soon after the GS-2b to GS-2a transition, well prior to the GI-1e warming oscillation. It corresponds roughly to the start of marked decreases of $\delta^{18}\text{O}_{\text{ice}}$ values during the GS-2a or oldest Dryas. During the same period, a first phase of floral and faunal reorganization is evidenced, characterized by the expansion of pioneer shrubs (Argant et al., 2009) and the local extinction of the woolly mammoth and the woolly rhinoceros (Bridault and Chaix, 2009). Thus, a change in the reindeers' environment during the Lateglacial could explain their decrease in $\delta^{13}\text{C}_{\text{coll}}$ values as a consequence of a change in vegetation. Decline in lichen biomass was observed in modern ecosystems when conditions are favorable for the development of vascular plants (Cornelissen et al., 2001). A decreasing contribution of lichens to the diet of reindeer, as the result of the disappearance of the Pleniglacial steppe-tundra, could be a cause for decrease in the $\delta^{13}\text{C}_{\text{coll}}$ values of the Lateglacial reindeer (see also Drucker et al., 2011b). However, the ^{13}C abundance in plants can be influenced by various climatic conditions, among which mean annual precipitation is a dominant factor (Diefendorf et al., 2010; Kohn, 2010). As a result, a decrease in the ^{13}C abundance of reindeer collagen implies an increase in humidity. However, wetter conditions during winters are not apparent from the pollen record prior the beginning of GI-1e (Magny et al., 2006). Thus, a change in the diet of reindeer, which would have included decreasing amount of lichen, seems to be a more likely explanation for the decrease in their $\delta^{13}\text{C}_{\text{coll}}$ around 16,300 cal BP.

During the considered period (ca. 24,000 to 14,000 cal BP), the Jura reindeer exhibited $\delta^{15}\text{N}_{\text{coll}}$ values ranging from 0.8 to 5.3‰

Table 3
List of the directly dated samples of reindeer (*Rangifer tarandus*) from the Jura Mountains with the archaeological record, results of stable isotope analyses of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and source of the data. The carbon, nitrogen and sulphur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). 1 = Bronk Ramsey et al., 2002; 2 = Cupillard and Welté, 2006; 3 = Stevens et al., 2008; 4 = Drucker et al., 2009; 5 = Bridault et al., 2000.

Site	N° lab	Sample	C_{coll} (%)	N_{coll} (%)	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$ (‰)	$\delta^{15}\text{N}_{\text{coll}}$ (‰)	S_{coll} (%)	$\delta^{34}\text{S}_{\text{coll}}$ (‰)	$\text{C}/\text{S}_{\text{coll}}$ (%)	$\text{N}/\text{S}_{\text{coll}}$ (%)	^{13}C , ^{15}N source	^{34}S source
Abri Gay	—	tooth	42.6	15.0	3.3	-19.8	—	—	—	—	—	4	—
Rochedane	RCD10800	metapodial	37.2	13.7	3.2	-20.3	2.1	0.16	-2.8	621	196	4	this work
La Chênélaz	ALP-1	phalanx II	38.1	14.5	3.1	-19.9	1.9	0.19	-4.7	541	177	4	this work
Chaumois-Boivin	BLS 1	phalanx	41.6	14.7	3.3	-19.5	2.4	0.16	-1.9	715	217	this work	this work
Les Romains	—	bone	42.1	15.5	3.2	-19.9	2.3	—	—	—	—	4	—
Mollendruz	ALP-10	left scaphoid	36.9	14.6	3.0	-19.9	2.1	0.15	-6.5	639	217	4	this work
Les Romains	—	bone	43.5	15.8	3.2	-19.4	1.8	—	—	—	—	4	—
Les Hoteaux	ALP-7	antler	39.3	15.2	3.0	-20.0	2.2	—	—	—	—	4	—
Abri Gay	—	metatarsal	17.9	7.2	2.9	-19.7	0.8	—	—	—	—	4	—
Baume Noire	FRT 1	metacarpal	39.6	14.0	3.3	-19.5	3.7	0.18	6.2	600	182	this work	this work
La Garenne	ALP-6	bone	29.4	11.8	2.9	-19.5	3.3	0.16	-0.4	496	171	4	this work
Grotte Grappin	ARL 8	scapula	30.1	11.4	3.1	-18.6	2.7	—	—	—	—	this work	—
Grotte Grappin	ARL 6	astragalus	42.2	15.7	3.1	-19.1	2.8	0.16	-5.8	721	230	this work	this work
Ranchot	RAN-10	coxal	28.1	11.3	3.0	-19.1	3.9	—	—	—	—	this work	—
Grotte Grappin	ARL 11	metacarpal	41.0	14.1	3.4	-19.0	3.4	—	—	—	—	this work	this work
La Croze	—	metatarsal	44.7	16.2	3.2	-19.4	5.3	—	—	—	—	4	—
La Colombière	—	antler	42.6	15.4	3.2	-19.4	3.8	—	—	—	—	4	—
Grotte Grappin	ARL 14	navicular	42.7	14.8	3.4	-19.0	3.0	—	—	—	—	this work	—
Grotte Grappin	ARL 12	astragalus	41.1	13.9	3.4	-19.3	3.4	0.23	0.8	473	137	this work	this work
Grotte Grappin	ARL 10	astragalus	38.7	14.7	3.1	-19.3	3.2	—	—	—	—	this work	—
Grotte Grappin	ARL 7	metapodial	41.3	15.9	3.0	-19.3	2.0	0.15	-3.7	725	239	this work	this work
Grotte Grappin	ARL 3	metapodial	39.0	14.9	3.1	-19.0	2.0	0.18	-0.3	566	185	this work	this work
La Baume	GIS 2	phalanx I	42.3	14.7	3.4	-19.8	3.2	0.16	-4.1	720	214	this work	this work
Baume Noire	FRT-3	metacarpal	41.0	14.4	3.3	-19.0	4.8	0.14	6.0	782	236	this work	this work
Kastelhöhle	Ox-A 9737	bone	—	—	3.1	-18.5	2.9	—	—	—	—	1,3	—
Kastelhöhle	Ox-A 9739	bone	—	—	3.4	-18.4	3.4	—	—	—	—	1,3	—
Baume Noire	FRT-2	metapodial	38.4	15.0	3.0	-19.4	2.9	0.17	-1.5	603	202	this work	this work
Kastelhöhle	OxA-9738	bone	—	—	3.5	-18.3	3.1	—	—	—	—	1,3	—

(Table 3; Fig. 3). Until ca. 15,600 cal BP, most of the reindeer $\delta^{15}\text{N}_{\text{coll}}$ values varied between 2.7 and 3.9‰. However, some specimens provided values that were higher (4.8 and 5.3‰, $n = 2$) or lower (2.0‰, $n = 2$), respectively. Although one of the ^{15}N -enriched reindeer originates from the site of La Croze (Drucker et al., 2009), for which no other data were available, the other one was retrieved

from the site of Frétigney, a site from which two other bones were analyzed that had $\delta^{15}\text{N}_{\text{coll}}$ values within the typical 2.7–3.9‰ range. The outliers therefore do not seem to be site dependent. The same can be concluded for the two low $^{15}\text{N}_{\text{coll}}$ reindeer, which were dated from ca. 20,200 to 18,000 cal BP. Both were retrieved from the site of Grotte Grappin at Arlay where other reindeer bones

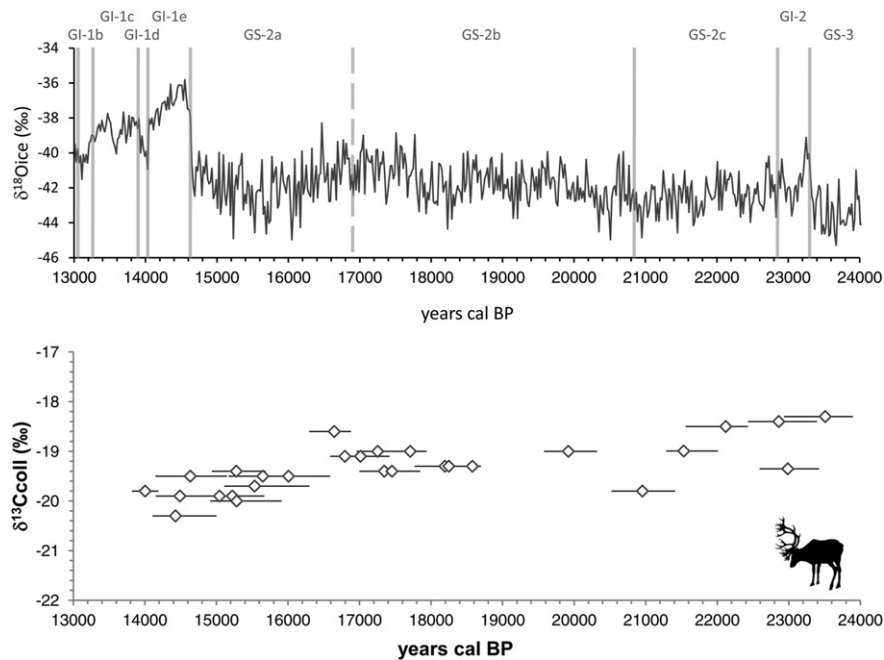


Fig. 2. The $\delta^{13}\text{C}_{\text{coll}}$ values of AMS dated reindeer (*Rangifer tarandus*) from the Jura Mountains against time. The AMS results were calibrated at based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009). Above are reported the NGRIP isotopic record stratigraphy (Lowe et al., 2008) and the retreat timing of the Jura ice sheet (Buoncristiani and Campy, 2004).

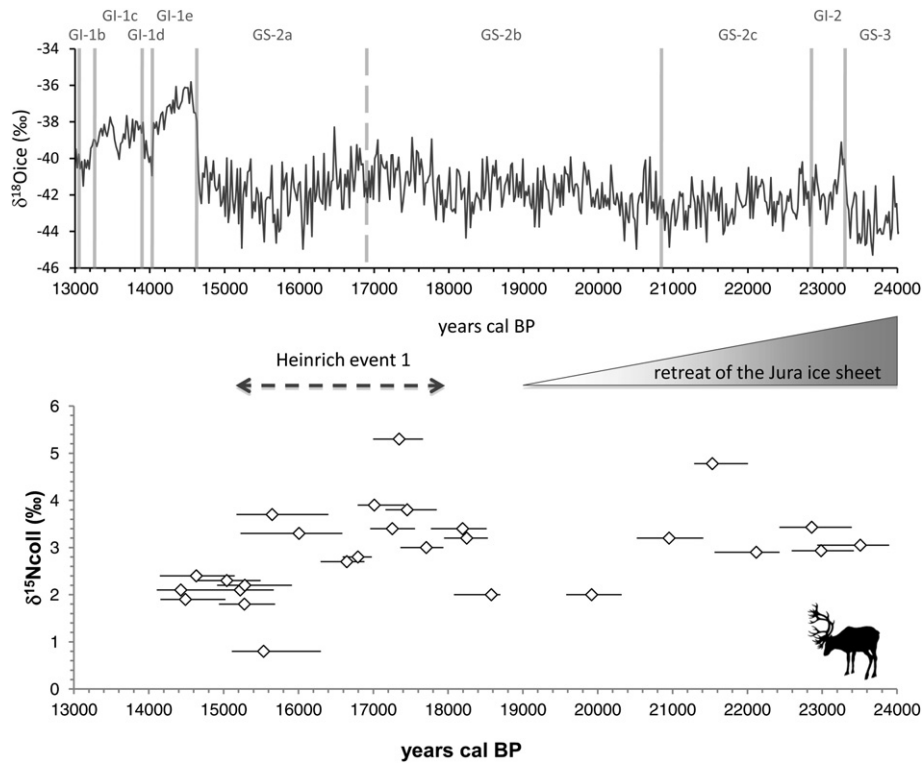


Fig. 3. The $\delta^{15}\text{N}_{\text{coll}}$ values of AMS dated reindeer (*Rangifer tarandus*) from the Jura Mountains against time. The AMS results were calibrated at based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009). Above are reported the NGRIP isotopic record stratigraphy (Lowe et al., 2008), the timing of the Jura ice sheet retreat (Buoncristiani and Campy, 2004) and the Heinrich event 1 (Elliot et al., 2002).

delivered the commonly found $\delta^{15}\text{N}_{\text{coll}}$ values of 2.7–3.4‰. The two low $\delta^{15}\text{N}_{\text{coll}}$ values from Arlay are consistent with those of the Jura reindeer present in the Jura Mountains after ca. 15,600 cal BP, all of them ranging from 0.8 to 2.4‰.

Variation in ^{15}N abundance, as in ^{13}C abundance, of reindeer collagen can originate from diet and/or environmental change. Reindeer are mixed feeders and consume a large range of vascular plants, including shrub leaves, forbs, and graminoids (e.g. Kelsall, 1968). Graminoids (grasses and sedges) have ^{13}C -depleted and ^{15}N -enriched abundance compared to the leaves of trees and shrubs (e.g. Barnett, 1994). This difference is reflected by isotopic divergences between modern reindeer and moose (*Alces alces*), the latter being specialized on browsing (consumption of leaves of trees and shrubs) (Drucker et al., 2010). Thus, a relative increase of browsing versus grazing in the dietary habit of the Lateglacial reindeer in the Jura Mountains could explain a decrease in their $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values during a time of shrub expansion (Argant et al., 2009). However, this tendency would be expected to be concomitant between the two isotopic trackers. This did not seem to be the case since lower $\delta^{13}\text{C}_{\text{coll}}$ values were observed around 16,300 cal BP, while the $\delta^{15}\text{N}_{\text{coll}}$ values remained as high as before. However, the scale of precision of the radiocarbon dating did not allow us to consider this apparent timing discrepancy as definitive evidence.

Previous studies dealing with variation in reindeer ^{15}N abundance have concluded that environment was the driving parameter (Stevens et al., 2008; Drucker et al., 2010, 2011b). Given the mountainous context of the study region, the contrast in altitude of the home range needs to be considered as well. However, higher altitude for reindeer habitat should be reflected by lower $\delta^{15}\text{N}_{\text{coll}}$ values but higher $\delta^{13}\text{C}_{\text{coll}}$ values. The weak correlation between the $^{13}\text{C}_{\text{coll}}$ and $^{15}\text{N}_{\text{coll}}$ amounts in the Jura reindeer during the Lateglacial (ca. 18,000–14,000 cal BP), however reflects the opposite tendency. Thus, other environmental parameters than change in

home range altitude should be considered when explaining variation in $\delta^{15}\text{N}_{\text{coll}}$ values of Jura reindeer.

Variation in $\delta^{15}\text{N}_{\text{coll}}$ values of Lateglacial reindeer in Europe was found to fit a predictable pattern of soil maturity advancement linked to the environmental conditions of the Last Glacial Maximum, such as the intensity of permafrost or the distance from the glacial front (Drucker et al., 2011b). Reduced activity of soil organisms due to harsh climatic conditions leads to lower ^{15}N amounts in soils, which is then passed on to plants and their consumers (see discussion in Drucker et al., 2003; Stevens and Hedges, 2004). As a matter of fact, lower $\delta^{15}\text{N}_{\text{coll}}$ values of Lateglacial reindeer were found for regions where the permafrost was the most intense and/or the proximity to a glacier the highest (Drucker et al., 2011b). Indeed, when considering the period spanning from 15,600 to 14,000 cal BP, the highest $^{15}\text{N}_{\text{coll}}$ amounts in Lateglacial reindeer were found in southwestern France (SW France; Szmjdt et al., 2009; Drucker et al., 2011c), while the lowest amounts were observed in northern Germany (N Germany; Drucker et al., 2011b), western Germany (W Germany; Stevens et al., 2009), southwestern Germany (SW Germany; Drucker et al., 2011b), and the Jura Mountains and Alps in France (Jura and NW Alps; Drucker et al., 2009 and this work). Thus, the highest reindeer $\delta^{15}\text{N}_{\text{coll}}$ values were detected in the southern part of the study area (SW France) where a discontinuous permafrost at best was present during the LGM, and the lowest reindeer $\delta^{15}\text{N}_{\text{coll}}$ values were found in regions where continuous permafrost and ice caps (N, W and SW Germany, Jura and NW Alps) were present (Figs. 4 and 5). Intermediate $\delta^{15}\text{N}_{\text{coll}}$ values were measured in northern France, which was farther away from the glacier front. This result is consistent with soil maturity being the control factor of $\delta^{15}\text{N}_{\text{coll}}$ values in Jura reindeer. Whereas a change in diet composition seems to better explain variation in $\delta^{13}\text{C}_{\text{coll}}$ values, environmental parameters, such as soil activity, appear to be the predominant

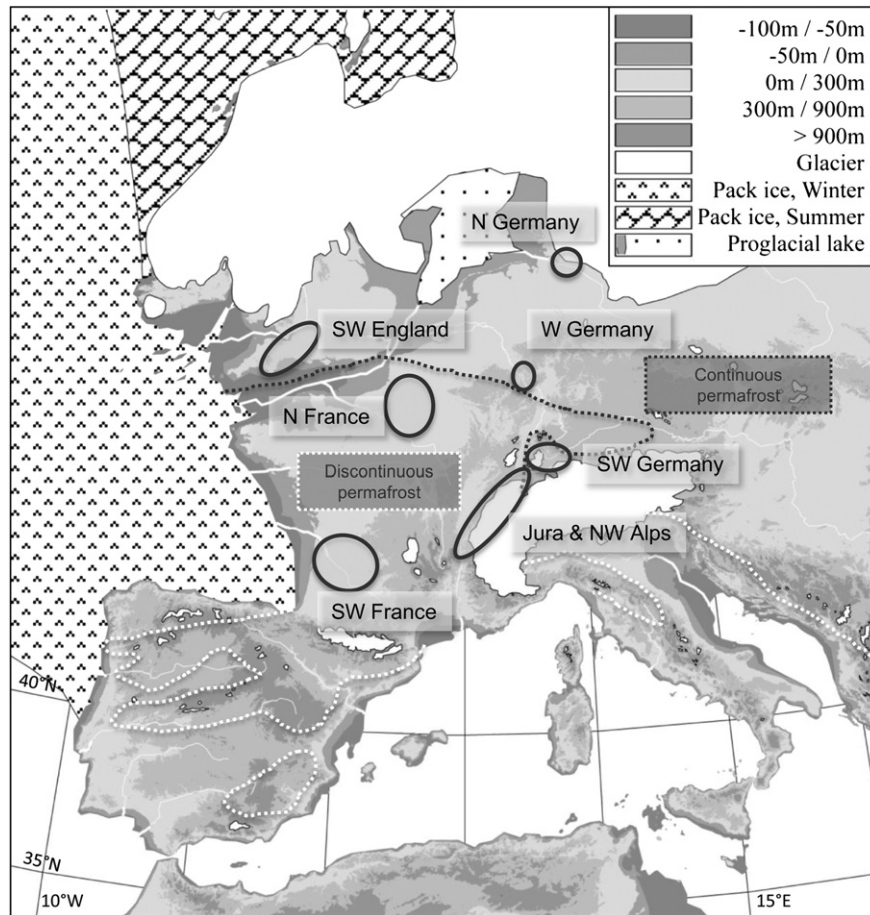


Fig. 4. Distribution of the glaciers (ice sheets and ice caps) and the permafrost (continuous in dark dotted line and discontinuous in white dotted line; from Renssen and Vandenberghe, 2003 and Bertran et al., 2009) in northwestern Europe during the Last Glacial Maximum (map modified from Fig. 4 in Serangeli, 2004). Study regions considered in Figs. 5–7 are given.

driving force for variation in $\delta^{15}\text{N}_{\text{coll}}$ values of reindeer in the Lateglacial.

3.3. Soil maturity and territory occupation by the Jura reindeer

To confirm the influence of soil maturity on $\delta^{15}\text{N}$ values of Jura reindeer, isotopic data obtained from other species were considered, such as horse (*Equus* sp.) and red deer (*C. elaphus*) from Lateglacial archaeological sites (ca. 16,600–14,000 cal BP and ca. 14,800–14,000 cal BP, respectively) in southwestern England (SW England; Jacobi and Higham, 2009), W Germany (Stevens et al., 2009), SW France (Drucker and Henry-Gambier, 2005; Drucker et al., 2005, 2011c), N France (Bocherens et al., 2011a), Jura and the NW Alps (Drucker et al., 2009, 2011a; Bocherens et al., 2011a). The distribution of the averaged $\delta^{15}\text{N}_{\text{coll}}$ values is strikingly similar to what was observed for Lateglacial reindeer (Figs. 6 and 7). For each species, the highest $^{15}\text{N}_{\text{coll}}$ amounts were found in SW France, the lowest in the Jura/northwestern Alps and southwestern England. This geographical contrast in $\delta^{15}\text{N}_{\text{coll}}$ values of reindeer, horse and red deer fits the expected pattern based on the soil maturity contrast inherited from the LGM conditions. It also confirms the key role played by the environment on the $\delta^{15}\text{N}_{\text{coll}}$ variation in Lateglacial reindeer of the Jura Mountains, even if a change in the diet better explains the variation in $\delta^{13}\text{C}_{\text{coll}}$ values.

The influence of LGM conditions in term of soil development seemed to be observable in the $\delta^{15}\text{N}_{\text{coll}}$ values of large mammals from the first part of the Lateglacial, at the end of GS-2a to GI-1e

transition. This imprint of the LGM after a period of several thousand years is quite remarkable. Moreover, the chronological survey demonstrates that the relatively low values of $\delta^{15}\text{N}_{\text{coll}}$ values in Lateglacial reindeer appeared only after ca. 15,600 cal BP in the Jura Mountains after some previous variations. Higher $\delta^{15}\text{N}_{\text{coll}}$ values ($>2.5\text{‰}$) were found between ca. 18,300 and 15,600 cal BP in the Jura reindeer. As a result, the decline in reindeer $\delta^{15}\text{N}_{\text{coll}}$ values took place during the GS-2a, at the same time as the pollen studies documented a global development of vegetation associated with increasing maturity of soils (e.g. Argant et al., 2009), which should have conducted to higher ^{15}N abundance in the ecosystem. Thus, the decreasing $\delta^{15}\text{N}_{\text{coll}}$ values of reindeer can only be explained by the colonization of areas recently deglaciated, where the slow rate of soil activity yielded low ^{15}N amounts to plants. Interestingly enough, such low $\delta^{15}\text{N}_{\text{coll}}$, around 2‰ , were also observed in reindeer dated at ca. 18,600 and 19,900 cal BP shortly after the end of the estimated time of retreat of the Jura ice sheet (Buoncristiani and Campy, 2004). In this last case, the availability of new areas formerly glaciated is attested and associated with low reindeer $\delta^{15}\text{N}_{\text{coll}}$ values in accordance with this hypothesis.

After the LGM, the cooling Heinrich event 1 (ca. 18,000–15,000 cal BP; Elliot et al., 2002) has been shown to have slowed and even reversed the warming process of the post-LGM. For that time, a re-advance of mountain glacier in the Alps (Ivy-Ochs et al., 2006) and ice sheets in the British Islands and southern Scandinavia has been documented (McCabe et al., 1998; Nygård et al., 2004). The end of this intense cold episode, dated to

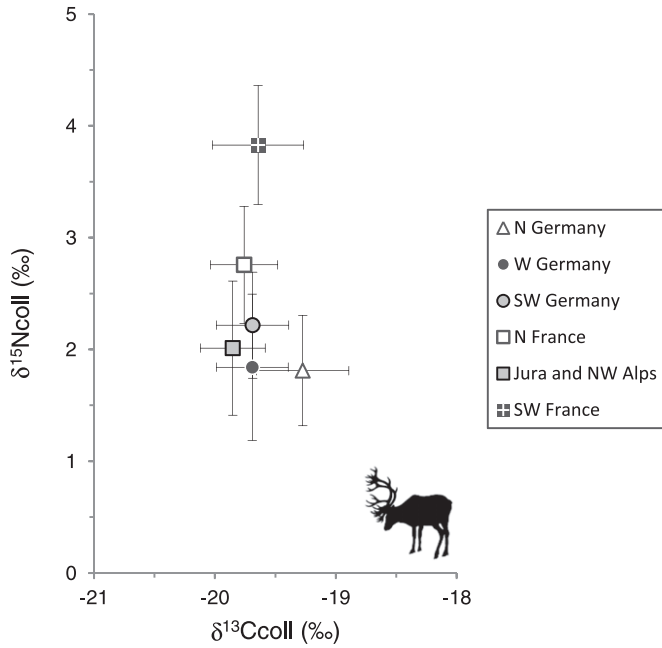


Fig. 5. Mean $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values measured on reindeer (*Rangifer tarandus*) for 15,600–14,000 cal BP time range from archaeological sites in northern Germany (N Germany; Drucker et al., 2011b), western Germany (W Germany; Stevens et al., 2009), southwestern Germany (SW Germany; Drucker et al., 2011b), northern France (N France; Bocherens et al., 2011a), eastern France (Jura and NW Alps; Drucker et al., 2009 and this work), southwestern France (SW France; Szmidt et al., 2009; Drucker et al., 2011c). Vertical and horizontal bars represent standard deviations.

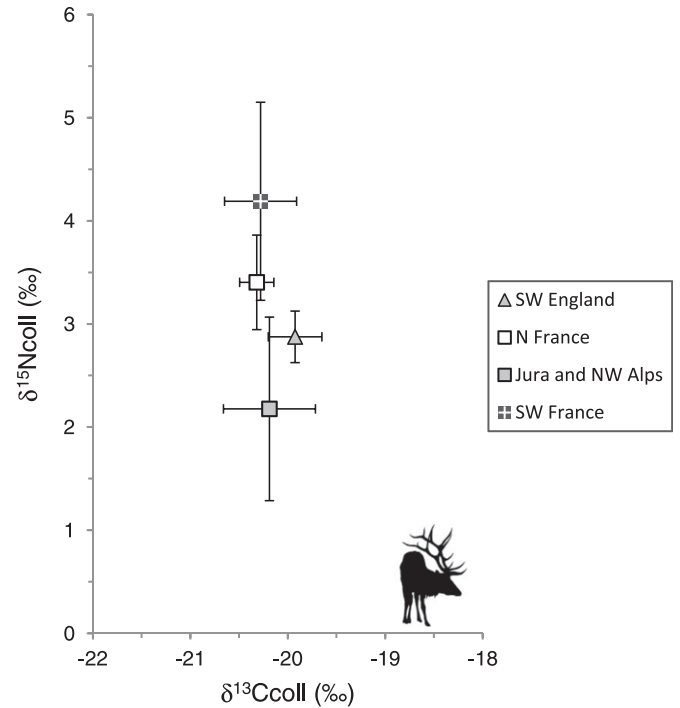


Fig. 7. Mean $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values measured on red deer (*Cervus elaphus*) for 14,800–14,000 cal BP time range from archaeological sites in southwestern England (SW England; Jacobi and Higham, 2009), northern France (N France; Bocherens et al., 2011a), eastern France (Jura and NW Alps; Drucker et al., 2011a), southwestern France (SW France; Drucker et al., 2005 and 2011c). Vertical and horizontal bars represent standard deviations.

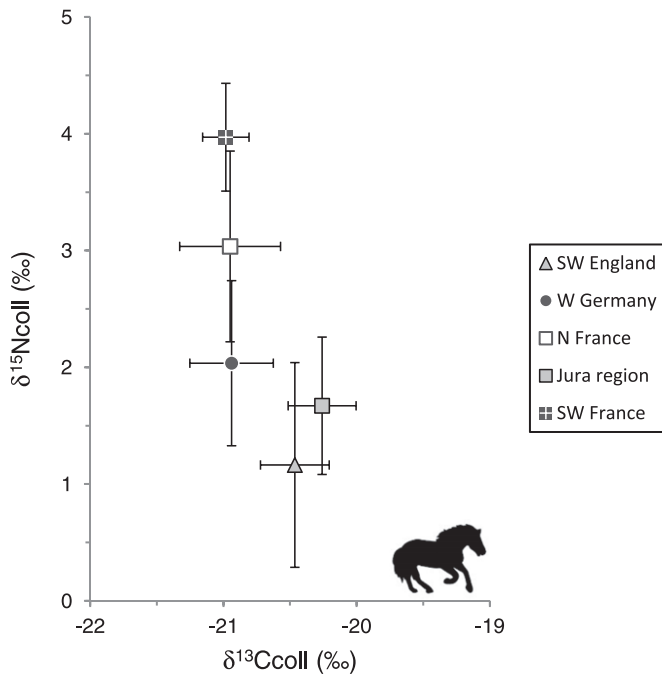


Fig. 6. Mean $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values measured on horse (*Equus* sp.) for 16,600–14,000 cal BP time range from archaeological sites in southwestern England (SW England; Jacobi and Higham, 2009), western Germany (W Germany; Stevens et al., 2009), northern France (N France; Bocherens et al., 2011a), Jura region (Drucker et al., 2009; Bocherens et al., 2011a), southwestern France (SW France; Drucker and Henry-Gambier, 2005; Drucker et al., 2005). Vertical and horizontal bars represent standard deviations.

15,400 ± 1400 cal BP in the Alps (Ivy-Ochs et al., 2006), could have released areas from the glacial influence in the Jura mountains, reproducing the processes that occurred during the Jura ice sheet retreat around 19,000–21,000 cal BP. The decrease in $\delta^{15}\text{N}_{\text{coll}}$ values of reindeer during these two key periods is interpreted as the reflection of the colonization of formerly glaciated areas. In contrast, values of $\delta^{15}\text{N}_{\text{coll}}$ higher than 5‰ would reflect the occupation of territories with high soil activity, which could have acted as refugium areas.

A study on the Jura red deer (*C. elaphus*) at the Lateglacial to early Holocene transition showed a coeval increase in $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{34}\text{S}_{\text{coll}}$ values, which suggested that ^{34}S could also be used as an

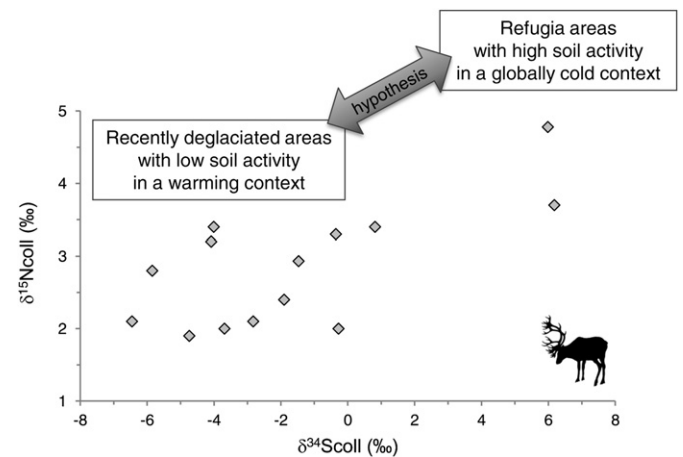


Fig. 8. The $\delta^{34}\text{S}_{\text{coll}}$ values against the $\delta^{15}\text{N}_{\text{coll}}$ values of AMS dated reindeer (*Rangifer tarandus*) from the Jura Mountains with the hypothesized interpretation of the two groups of $\delta^{34}\text{S}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values.

indicator of soil activity (Drucker et al., 2011a). The $\delta^{34}\text{S}_{\text{coll}}$ values measured on Jura reindeer varied from -6.5‰ to 6.2‰ (Table 3, Fig. 8). The $\delta^{34}\text{S}_{\text{coll}}$ values were not higher than $+0.8\text{‰}$ for reindeer that exhibited $\delta^{15}\text{N}_{\text{coll}}$ values from 1.9 to 3.4‰ and no clear pattern of co-variation is apparent. In contrast, $\delta^{34}\text{S}_{\text{coll}}$ values higher than 5‰ were measured on reindeer with $\delta^{15}\text{N}_{\text{coll}}$ values higher than 3.5‰ . Interestingly, this last group was composed of reindeer from the site of Baume Noire at Frétagne, which had delivered dates at ca. 21,500 and 23,000 cal BP. The proximity of refugium areas, characterized by soil maturity delivering high ^{15}N and ^{34}S amounts to herbivores, could have been favorable to the human occupation at Frétagne. The occurrence of cryptic refugia far north to the 49°N limit classically given for the Pleniglacial refugium area in western Europe (e.g. Verpoorte, 2009) has been evoked for animal and plant communities (e.g. Svenning et al., 2008; Stewart et al., 2010). Such cryptic refugia could have existed in the surroundings of the Jura Mountains, from where reindeer groups could rapidly colonized newly available territories.

4. Conclusion and perspectives

The new AMS dating of reindeer samples resulting from human activity in sites that yielded Magdalenian artefacts confirmed that the Jura region was not completely deserted during the post-LGM period, before the intense phase of Lateglacial settlement. The relatively continuous record from ca. 24,000 to 14,000 cal BP provided by the dated reindeer allow to observe a slight decrease of their $\delta^{13}\text{C}_{\text{coll}}$ values, most probably linked to a change in their dietary composition, in particular a decrease in lichen consumption compared to the pre-LGM period. Two episodes of decreasing reindeer $\delta^{15}\text{N}_{\text{coll}}$ values over time are thought to correspond to two separate phases of colonization of areas that were recently freed from glacier ice, one time after the LGM around 21,000 to 20,000 cal BP and the other by the end of the Heinrich event 1 around 15,500 cal BP. The re-extension of the ice sheet in north Europe and of ice caps in the mountains could explain the maintenance of the geographical contrast in ecosystem ^{15}N abundance from the LGM reflected in reindeer, horse and red deer at the onset of the Lateglacial.

The highest $\delta^{15}\text{N}_{\text{coll}}$ values of Jura reindeer are associated with higher $\delta^{34}\text{S}_{\text{coll}}$ values, interpreted as the signature of refugium areas where soil maturity was high enough to allow the maintenance of ecosystems during the cold post-LGM period of the Upper Pleniglacial. The occurrence of such refugia could explain the rapid response of the ecosystems, including animal and human populations, to climate change until the definitive occupation of the Jura Mountains during the Lateglacial. Local refugia would have maintained ecosystems that were sporadically exploited by human populations, as confirmed by the dating evidence from Kastelhöhle and Grotte Grappin. The same refugia could have acted as a reservoir from which large mammals could rapidly expand to colonize new territories released from glacial conditions. In such a scenario, the intensification of human settlement would have responded to this sudden increase of foraging territories.

The use of the multi-element stable isotope analysis of hunted large herbivores to track processes of change in territory occupation during the late Quaternary is encouraged. Coupled with other markers, such as ancient DNA, isotopic tracking could allow deciphering local scenarios of post-LGM colonization.

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