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Evolution of habitat and environment of red deer (*Cervus elaphus*) during the Late-glacial and early Holocene in eastern France (French Jura and the western Alps) using multi-isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, $\delta^{34}\text{S}$) of archaeological remains

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ABSTRACT

Red deer (*Cervus elaphus*) is a flexible species that survived the significant climatic and environmental change toward warming temperature and forested landscape of the Late-glacial to early Holocene transition (ca. 17–6 ka cal BP). To investigate the conditions of ethological adaptation of red deer at that time, isotopic analysis of carbon, nitrogen, sulfur in collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and of oxygen in phosphate ($\delta^{18}\text{O}_\text{p}$) were performed on red deer from archaeological sites of the French Jura and the western Alps. Fifty out of eighty two samples benefited from direct AMS radiocarbon dating, which confirmed the few number of red deer record during the cold Younger Dryas oscillation (ca. 12.8–11.6 ka cal BP) in Western Europe. The French Jura red deer showed a significant decrease in their $\delta^{13}\text{C}_{\text{coll}}$ values and increase in their $\delta^{15}\text{N}_{\text{coll}}$ values in the early Holocene compared to the Late-glacial, which is most likely due to the change in environment from open areas with low pedogenic activity to warm dense forests with increasing soil maturity. In contrast, the stable $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values over time in the western Alps were thought to indicate a change to higher altitude for the red deer habitat in this mountainous region. A decrease of the $\delta^{18}\text{O}_\text{p}$ values between the Late-glacial and the early Holocene was observed in the western Alps red deer, in contrast to the expected increase with rising temperature which was indeed confirmed for the French Jura red deer. The multi-isotope results pointed to open areas home range at higher altitude for the Alps red deer in the Holocene compared to the previous period. The similarity of the $\delta^{34}\text{S}_{\text{coll}}$ patterns with those of the $\delta^{15}\text{N}_{\text{coll}}$ suggested the primarily influence of soil activity on the ^{34}S abundances recorded by red deer in a purely terrestrial context. Red deer of the French Jura on one hand and of the western Alps on the other hand showed different adaptive response to the global warming of the early Holocene, with an ethological change in the first case and a change in home range in the second case.

1. Introduction

The Late-glacial to early Holocene transition, from ca. 17 to 6 ka cal BP, was marked by significant climatic change leading to a global warming, and the development of temperate landscape and faunal recomposition in western Europe. The succession of

rapid oscillations between warm (interstadial) and cold (stadial) events before the final global warming of the early Holocene is now extensively documented through oxygen-isotope investigation on ice-cores from Greenland (Björck et al., 1998; Lowe et al., 2008). As a result, the vegetation composition changed from steppe-tundra during the Oldest Dryas (ca. 17.0–14.7 ka cal BP) to temperate dense deciduous forest that developed by the end of the Preboreal (ca. 11.6–10.0 ka cal BP). Stadial episodes were reflected by the development of herbaceous vegetation during the Younger Dryas (ca. 12.8–11.6 ka cal BP), and interstadial episodes corresponded to

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the development of pine-birch forest during the Bölling/Alleröd (ca. 14.7–12.8 ka cal BP) and Preboreal (e.g. Amman and Lotter, 1989; De Beaulieu et al., 1994). A major change also occurred in the faunal composition with the extinction of megafaunal species inherited from the Pleniglacial, such as woolly rhinoceros (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*) and mammoth (*Mammuthus primigenius*) in Western Europe (e.g. Stuart et al., 2004). Other glacial species such as reindeer (*Rangifer tarandus*) were extirpated from most regions of northwestern Europe including eastern France (Bridault et al., 2000), while temperate species such as red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) increased in abundance (e.g. Sommer et al., 2008a, 2008b).

Species that survived the climatic changes and the vegetation modifications of this period offer the opportunity to track potential habitat change using phenotypic indicators. Stable isotopic composition of carbon, nitrogen, sulphur and oxygen in fossil bones are some of these ecological tracers. Among these species, red deer (*C. elaphus*) is an opportunistic mixed feeder and is able to live in variable habitat from open steppe to closed temperate forest (Heptner et al., 1989; Geist, 1999). The question that this paper will attempt to answer is, which strategy did red deer use to survive the global warming of the early Holocene? Eastern France offers a favorable context to document ecological changes in this large ungulate in different topographical contexts. French Jura and the western Alps exhibit contrasted altitudinal ranges that could have triggered different ecological responses of red deer facing warming. Isotopic tracers offer the opportunity to investigate several aspects of mammal, and especially red deer, ecology as reviewed in the following paragraphs.

2. Habitat and environmental tracking using carbon-13

The carbon-13 abundances ($\delta^{13}\text{C}$) of herbivore tissues reflect those of plants, which depend on the source of atmospheric carbon and the photosynthetic process (review in Tieszen, 1991; Heaton, 1999). In Western Europe, ancient and modern indigenous plants exhibit a C_3 photosynthesis pattern, and their $\delta^{13}\text{C}$ values vary according to environmental conditions, especially water availability. Recent studies confirmed a positive correlation between the discrimination against ^{13}C in plants and mean annual precipitation (MAP) leading to the decrease of plant $\delta^{13}\text{C}$ values when the MAP increases (Diefendorf et al., 2010; Kohn, 2010). Light intensity, temperature, salinity and short term change in the atmospheric CO_2 pressure (pCO_2) can also induce variation in plant $\delta^{13}\text{C}$ values through stomatal conductance, water use efficiency (WUE) and photosynthetic intensity control (review in Tieszen, 1991; Heaton, 1999; Dawson et al., 2002). Plant $\delta^{13}\text{C}$ values increase with altitude as the result of increasing WUE with lower temperature and partial atmospheric pCO_2 (e.g. Farquhar et al., 1989; Morecroft and Woodward, 1990; Körner et al., 1991; Hultine and Marshall, 2000). Landscape closure is another important source of variation in plant $\delta^{13}\text{C}$ values since plants that develop under close canopies present depleted $\delta^{13}\text{C}$ values compared to the same plant form growing in more open conditions (review in Tieszen, 1991; Heaton, 1999; Dawson et al., 2002). Concentration of recycled CO_2 due to poorly ventilated air, light attenuation and relative high water availability in closed canopy forest are evoked to explain the so-called “canopy effect”. (e.g. Gebauer and Schultze, 1991; van der Merwe and Medina, 1991; Broadmeadow et al., 1992). Altitude and canopy effect leading to change in $\delta^{13}\text{C}$ values of plants are passed on to collagen values of herbivores, as it was confirmed by data from modern ecosystems (e.g. Männel et al., 2007; Drucker et al., 2008, 2010). Thus, herbivores dwelling and foraging in at low altitude and/or in dense forest are expected to have $\delta^{13}\text{C}_{\text{coll}}$ values relative

lower than those of their counterparts living at higher altitude and/or in more open habitat.

3. Habitat and environmental tracking using nitrogen-15

The nitrogen isotopic composition of bone collagen ($\delta^{15}\text{N}$) from herbivores depends on dietary, physiological and climatic parameters. The enrichment in ^{15}N during the first months of life due to the consumption of animal protein through maternal milk was convincingly documented in herbivores (e.g. Jenkins et al., 2001). For adults, seasonal change in diet composition, nutritional quality of the forage and physiological status (pregnancy, lactation) can significantly impact the $\delta^{15}\text{N}$ values of tissues (e.g. Barnett, 1994; Sponheimer et al., 2003a, 2003b; Barboza and Parker, 2006). The effect of such punctual changes on isotopic signature can be retained in dentine collagen coming from tooth roots, which grow on short period of time and are not remodeled once completely formed (e.g. Balasse et al., 2001; Britton, 2009; Drucker et al. in press). In contrast, bone collagen is reflecting long-term isotopic trend as bone is continuously remodeled with a turnover of several years over life (review in Koch, 2007). Thus, bone $\delta^{15}\text{N}_{\text{coll}}$ values of mature individuals of a given species are more sensitive to environmental change through long time periods. Temperature and aridity are mostly quoted as climatic parameters driving significant changes in $\delta^{15}\text{N}_{\text{coll}}$ values of herbivores as a result of change in $\delta^{15}\text{N}$ values of foraged plants in modern and ancient ecosystems (e.g. Iacumin et al., 2000; Drucker et al., 2003a; Murphy and Bowman, 2006; Stevens et al., 2006). In Western Europe during the last 40,000 years, the chronological and geographical variation in $\delta^{15}\text{N}_{\text{coll}}$ values of large herbivore seemed to follow the intensity of soil activity driven by temperature and glacier occurrence (Drucker et al., 2003a, 2003b; Stevens et al., 2008). A previous study focused on the Late-glacial and early Holocene red deer from the Rochedane site in Jura has confirmed the relation between increasing $\delta^{15}\text{N}_{\text{coll}}$ values and rising temperature over time (Drucker et al., 2009). Implied mechanism most probably involved increasing nitrogen cycling process in soils since a positive relation was found between ^{15}N abundances in plants and pedogenic activity (e.g. Hobbie et al., 1998, 2005). The same mechanism can also explain the lower $\delta^{15}\text{N}$ values of herbivores, plants and soils observed with higher altitude in modern ecosystems (e.g. Mariotti et al., 1980; Männel et al., 2007). Hence, the $\delta^{15}\text{N}$ values of the red deer considered in this study should reflect change in global temperature over time and local altitude at a given period of time.

4. Habitat and environmental tracking using oxygen-18

Oxygen isotopic ($\delta^{18}\text{O}$) values in the phosphate fraction of bone relate to those of ingested water for large mammals (e.g. Longinelli, 1984; Iacumin et al., 1996; Kohn et al., 1996). In the case of red deer, the $\delta^{18}\text{O}$ values of bone phosphate reflect those of the local precipitation (D'Angela and Longinelli, 1990; Iacumin et al., 1996). This results points to the main contribution of drinking water and the negligible influence of relative humidity in the oxygen isotopic signature of red deer. The $\delta^{18}\text{O}$ value of meteoric water reflects essentially the temperature in boreal and temperate contexts (Fricke and O'Neil, 1999). A consistent pattern was found in modern red deer between intra-tooth variations in phosphate $\delta^{18}\text{O}$ values and seasonal change in temperature (Fricke et al., 1998). In the context of eastern France during the Late-glacial and early Holocene, $\delta^{18}\text{O}$ values of meteoric water are predicted to decrease with lower temperatures and higher altitudes. In areas with important altitudinal gradients, it would be possible to track the altitude at which the studied animals obtained their drinking water at a given period of time.

5. Habitat and environmental tracking using sulphur-34

The sulfur isotopic values ($\delta^{34}\text{S}$) of the diet are passed on to a consumer's tissues, such as bone, with almost no fractionation effect (Richards et al., 2001). The measurement of $\delta^{34}\text{S}$ of bone and tooth collagen has recently been developed and its application on archaeological material was first devoted to the distinction between aquatic and terrestrial sources in diet (e.g. Richards et al., 2001; Craig et al., 2006; Privat et al., 2007). While marine ecosystems are characterized by rather uniform high $\delta^{34}\text{S}$ values (ca. +20‰), freshwater and terrestrial ecosystems display more variable $\delta^{34}\text{S}$ values as the result of the environmental parameters, such as bedrock weathering, atmospheric deposition and microbial processes (Peterson and Fry, 1987). The possible discrimination in $\delta^{34}\text{S}_{\text{coll}}$ values among geographical origins of diet sources was also mentioned (Vika, 2009; Craig et al., 2010). Studies on modern herbivores have confirmed that the natural abundance in ^{34}S in unpolluted plants is essentially a function of distance from the sea and geology of the local area (e.g. Rossmann et al., 2000; Camin et al., 2007). A recent work from Britton (2009) has shown contrasted collagen $\delta^{34}\text{S}$ values in modern reindeer and bison, which are correlated with strontium isotope ratios, a direct indicator of geological context. The potential of sulphur isotope analyses as a tracker of geographical origin was suggested in studies of human remains from archaeological sites as a result of local geology contrast and proximity of the sea (Vika, 2009; Craig et al., 2010). So far, there was no sulfur isotope investigation based on herbivores from continental ecosystems, where marine influence through sea spray effect is insignificant and pollution by industrial activity inexistent. It is hypothesized that in such conditions, the $\delta^{34}\text{S}$ values passed to herbivore through plants should reflect contrast in local geology and soil microbial activity.

The present study aims to (1) evaluate the change in habitat and pedogenic activities through time reflected by the collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of red deer from French Jura in contrast to French Alps, (2) to consider the temporal trends in $\delta^{18}\text{O}$ values in phosphate fraction of skeletal remains for red deer in French Jura and Alps (3) to explore the collagen $\delta^{34}\text{S}$ values as a potential marker of mobility of red deer in both regions.

6. Material and methods

Sixty-two skeletal parts of red deer (*C. elaphus*) were selected from nine archaeological sites of French Jura ($n = 62$, Table 1, Fig. 1; Pétrequin, 1970; Thévenin and Sainty, 1980; Thévenin, 1982; Vuallat et al., 1984; Campy et al., 1989; Pion et al., 1990; Aimé, 1993; Cupillard and David, 1995; Cupillard et al., 2000; Pion, 2004; Voruz et al., 2004; Cupillard, 2008). In addition, twenty red

deer remains from five stratified sites located in the neighboring region of the western Alps were considered (Table 1, Fig. 1; Chaffenet and Cordier, 1999; Bintz and Pelletier, 2000; Nicod and Picavet, 2003; Pion and Mével, 2005). In both cases, identified anatomical parts were sampled and bones were favored to teeth in order to access to a time-life record. Tooth root was analyzed in only two cases, for which the nitrogen-15 abundances were not retained because of the possible interference caused by the suckling effect, as previously mentioned. For the same reason, bones of mature individuals were systematically chosen. In some cases, different individuals from the same site were sampled by selecting the same anatomical part.

New direct AMS radiocarbon (^{14}C) dating were performed on fifteen red deer samples from French Jura in addition to those already available on other red deer bones included in this study (Table S1). The results were calibrated at 2 sigma based on the intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009). Corresponding chronological phases were indicated using pollen chronozone succession based on studies in Jura (Table S1 and S2; Richard and Bégeot, 2000; Magny et al., 2006) and NGRIP isotopic record stratigraphy (Table S1; Lowe et al., 2008). Chronological attribution were assigned to undated samples based on the AMS ^{14}C dates obtained on the red deer remains from the same levels for the sites of French Jura and on published ^{14}C dating of the archaeological deposits for the sites of the western Alps (Table S2).

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 a 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), was $\pm 0.1\text{‰}$ 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 its chemical composition, 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 with atomic C/ S_{coll} and N/ S_{coll} ratios in the

Table 1

List of the studied archaeological sites from the French Jura and the western Alps with their geographical location and altitude.

Site	Locality	District	Region (district)	Altitude (m)	Lab code	N° in Fig. 1
Mannlefelden I	Oberlarg	Haut-Rhin	French Jura	550	OB-	1
La Baume	Gonvillars	Haute-Saône	French Jura	388	GNV-	2
Sous la Roche	Bavans	Doubs	French Jura	275	BVN-	3
Rochedane	Villars-sous-Dampjoux	Doubs	French Jura	355	RCD-	4
La Baume de Montandon	Saint-Hippolyte	Doubs	French Jura	590	STH-	5
Gigot 1 and 2	Bretonvillers	Doubs	French Jura	457	BRT-	6
Les Cabônes	Ranchot	Jura	French Jura	216	RAN-	7
La Baume	Gigny-sur-Suran	Jura	French Jura	485	GIS-	8
Le Gardon	Ambérieu-en-Bugey	Ain	French Jura	373	GAR-	9
Les Douattes	Musièges	Haute-Savoie	western Alps	370	LDT-	10
La Fru	St-Christophe-la-Grotte	Savoie	western Alps	570	FRU-	11
Aulp du Seuil	St-Bernard-du-Touvet	Isère	western Alps	1700	APS-	12
La Grande Rivoire	Sassenage	Isère	western Alps	580	GRV-	13
Les Corréardes	Lus-la-Croix-Haute	Drôme	western Alps	1070	LUS-	14

range of 300–900 and 100–300, respectively (Nehlich and Richards, 2009) were retained.

The $\delta^{18}\text{O}$ analyses of phosphate were performed at the Department of Geosciences (University Tübingen, Germany). Prior to these analyses of the bone phosphate fraction, bone powders were chemically pre-treated with 2% NaOCl solution, followed by a 1 M Ca-acetate from acetic acid buffer solution (Bocherens et al., 1996). Oxygen isotope composition of phosphate ($\delta^{18}\text{O}_\text{p}$) was measured on silver phosphate (Ag_3PO_4). About 4 mg of pre-treated powder were dissolved in 2 M HF, neutralized with NH_4OH and the PO_4 in solution was rapidly precipitated as Ag_3PO_4 by adding 2 M AgNO_3 according to the method described in Tütken et al. (2006). Ag_3PO_4 of each sample and standard was analysed in triplicate ($\sim 500\text{ }\mu\text{g}$ for a single measurement) for $\delta^{18}\text{O}_\text{p}$. The $\delta^{18}\text{O}_\text{p}$ measurements were performed using a Finnigan TC-EA at $1450\text{ }^\circ\text{C}$ linked via a Finnigan Conflow III to a ThermoFinnigan Delta Plus XL CFIRMS at the University of Tübingen with a reproducibility of $\pm 0.3\text{‰}$. Samples are calibrated to $\delta^{18}\text{O}$ values of TU-1 ($\delta^{18}\text{O} = 21.11\text{‰}$, relatively to VSMOW); TU-2 ($\delta^{18}\text{O} = 5.35\text{‰}$, relatively to VSMOW); 130–0.5–1 ($\delta^{18}\text{O} = -1.13\text{‰}$, relatively to VSMOW) and 130–0.5–9 ($\delta^{18}\text{O} = 8.42\text{‰}$, relatively to VSMOW).

7. Results and discussion

7.1. Chronological distribution of red deer

When considering the fifty direct radiocarbon AMS dates obtained so far (Table S1), a gap was observed for red deer from French Jura and northern Alps for the most part of the Younger Dryas (Fig. 2). The absence of data could be due either to the scarcity of this species during this period or to the lack of preservation of archaeological deposits as the result of the harsh climatic conditions during the Younger Dryas in Jura. Since the development of systematic radiocarbon dating of a given species, some temporal gaps have been documented especially around the Last Glacial Maximum (ca. 29.0–18.5 ka cal BP) for carnivores, such as the cave lion (*Panthera spelaea*), and for large herbivores such as giant deer and mammoth (Stuart et al., 2004; Stuart and Lister, 2010). These gaps have been interpreted as the reflection of local extirpation and possible bottleneck events. Sommer et al. (2008b) noted the small number of direct evidence of red deer during the Younger Dryas (GS-1) in northwestern Europe. This decrease in red deer record was considered to be the result of the harsh climatic conditions and

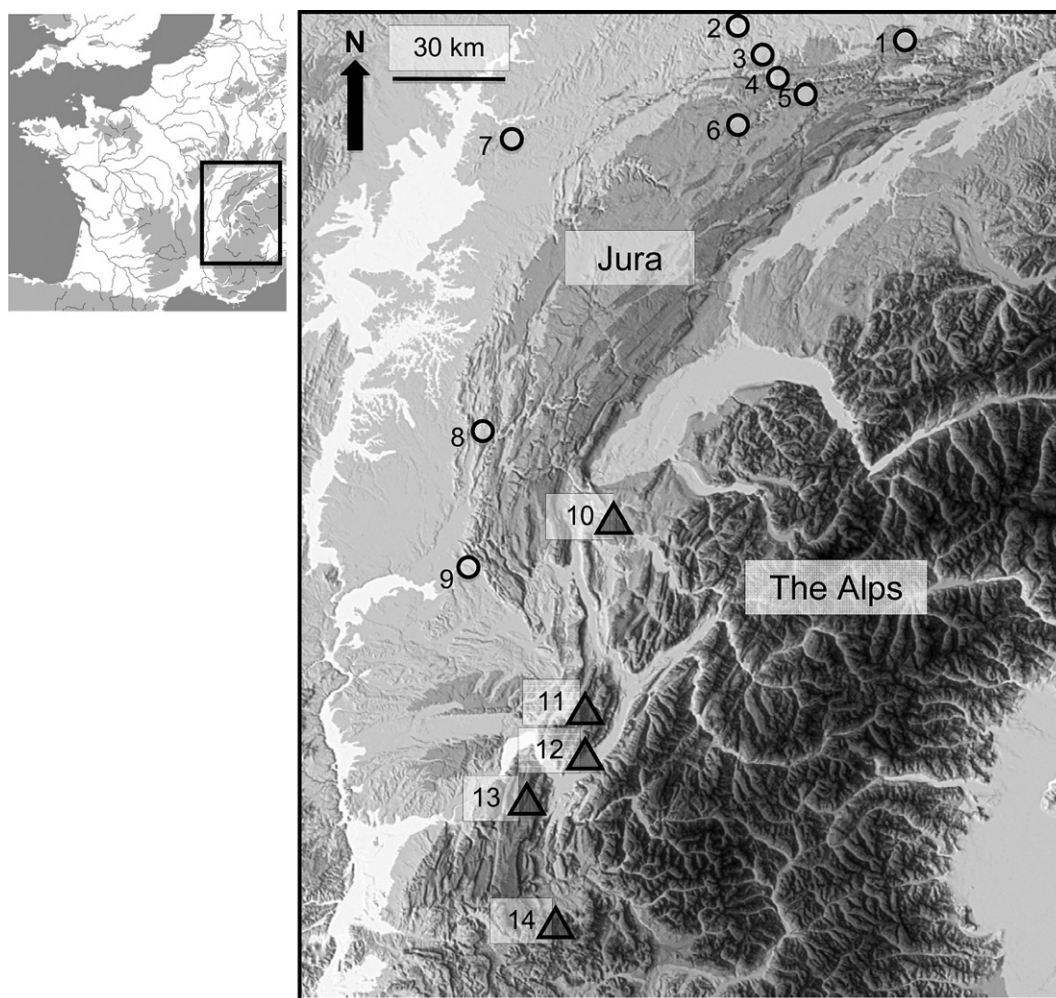


Fig. 1. Geographical location of the archaeological sites in eastern France that provided Late-Glacial and early Holocene red deer samples selected for isotopic analysis. In French Jura: 1 = Oberlarg – Mannlefelden 1 (Haut-Rhin), 2 = Gonvillars – La Baume (Haute-Saône), 3 = Bavans – Sous la Roche (Doubs), 4 = Villars-sous-Dampjoux – Rochedane (Doubs), 5 = Saint-Hippolyte – Montandon (Doubs), 6 = Bretonvillers – Gigot 1 et 2 (Doubs), 7 = Ranchot – Les Cabônes (Jura), 8 = Gigny-sur-Suran – La Baume (Jura), 9 = Ambérieu-en-Bugey – Le Gardon (Ain); in the Alps: 10 = Musièges – Les Douattes (Haute-Savoie), 11 = Saint-Christophe-la-Grotte – La Fru (Savoie), 12 = Saint-Bernard-du-Touvet – Aulp du Seuil (Isère), 13 = Sassenage – La Grande Rivoire (Isère), 14 = Lus-la-Croix-Haute – Les Corréardes (Drôme).

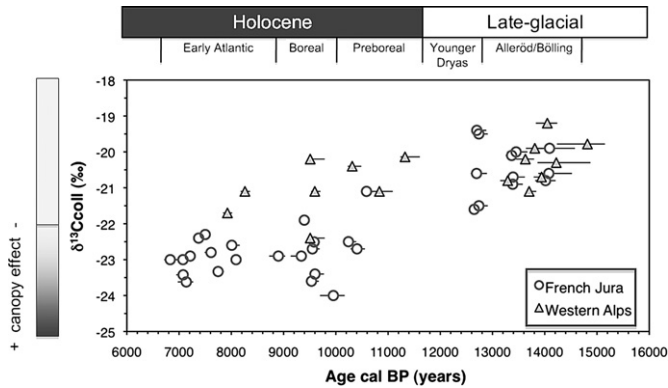


Fig. 2. The $\delta^{13}\text{C}_{\text{coll}}$ values of AMS dated red deer (*Cervus elaphus*) from the French Jura (white circles) and the western Alps (gray triangles) against time through the Late-glacial to early Holocene transition. Values below ca. -22‰ are interpreted as the result of the canopy effect. The AMS results were calibrated at based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009).

the disappearance of the interstadial forest, which would have favored the cold-adapted reindeer. A larger dataset of dates on red deer as well as on archaeological contexts in the French Jura and the western Alps would be necessary to confirm the observed temporal gap and to interpret it in terms of prey distribution.

7.2. Carbon-13 and canopy development in French Jura and western Alps

The red deer $\delta^{13}\text{C}_{\text{coll}}$ values varied from -24.0 to -19.4‰ in Jura (Table 2) and from -22.4 to -18.7‰ in the Alps (Table 3) during the Late-glacial and early Holocene. Directly dated red deer from Jura showed a clear decrease in $\delta^{13}\text{C}_{\text{coll}}$ values over time, as previously observed in Drucker et al. (2008) on a more limited number of specimens (Fig. 2). Before the onset of the early Holocene (ca. 11.6 ka cal BP), Jura red deer yielded relatively high $\delta^{13}\text{C}$ values (from -21.6 to -19.4‰), which were comparable to those of red deer from the Alps (-21.1 to -19.2‰). In the beginning of the Holocene, the Preboreal period (ca. 11.6–10.0 ka cal BP) exhibited an initial decrease in $\delta^{13}\text{C}_{\text{coll}}$ values of red deer in Jura with a range of -22.7 to -21.1‰ . Later, Jura red deer had $\delta^{13}\text{C}_{\text{coll}}$ values ranging from -24.0 to -21.9‰ , which are lower than the values of those observed during the Late-glacial as well as those measured on the early Holocene red deer from the Alps (from -22.4 to -20.1‰). The decrease of $\delta^{13}\text{C}_{\text{coll}}$ values of red deer from Jura was previously described and interpreted as the result of habitat change from open to closed habitat (Drucker et al., 2003b, 2008). Some authors insisted on the effect of increase in atmospheric $p\text{CO}_2$ between the Late-glacial and the Holocene to explain a comparable decrease in $\delta^{13}\text{C}_{\text{coll}}$ values of horse in northern Europe (Richards and Hedges, 2003; Stevens and Hedges, 2004). However, plants were found to maintain a stable $\delta^{13}\text{C}$ values while they were facing long-term change in atmospheric CO_2 thanks to their capacity to adapt their stomatal conductance (see Arens et al., 2000). Therefore, $\delta^{13}\text{C}$ value of atmospheric CO_2 has a more significant impact on plant $\delta^{13}\text{C}$ values over time (Arens et al., 2000). Between the post Last Glacial Maximum and the Holocene, a decrease of up to 0.5‰ in the atmospheric CO_2 $\delta^{13}\text{C}$ value was reconstructed from fossil plant remains (Marino et al., 1992) and thus cannot entirely explain the mean $\delta^{13}\text{C}_{\text{coll}}$ decrease of 2.3‰ observed for the Jura red deer. Temperature was another quoted factor that could influence the $\delta^{13}\text{C}$ amounts of red deer as a negative correlation was observed between the $\delta^{13}\text{C}_{\text{coll}}$ values of modern deer and the mean annual maximum temperatures (Stevens et al., 2006). However, different

pattern of $\delta^{13}\text{C}$ decrease was found among ungulate species in the Paris Basin at the Late-Glacial/early Holocene transition, which could hardly be explained by the sole impact of a global environmental parameter such as temperature (Drucker et al., 2008). Moreover, the effect of temperature change on carbon isotope fractionation in plants can be considered as minor (Diefendorf et al., 2010; Kohn, 2010). Altitudinal effect in Jura could not either account alone for the decrease in red deer $\delta^{13}\text{C}_{\text{coll}}$ value, since it would imply a difference of at least 2,000 m between the dwelling areas of red deer over time, a value that exceeds the whole altitudinal range found in the Jura mountains. Finally, the canopy effect appears to be the most likely explanation of the significant depletion in red deer $\delta^{13}\text{C}$ values at the Late-glacial/early Holocene transition in Jura.

The review of the $\delta^{13}\text{C}_{\text{coll}}$ values from directly and indirectly dated red deer samples from Jura (Fig. 3) confirmed the trend of significant decrease between the Late-glacial and the early Holocene periods, with a possible intermediate step during the Preboreal (Fig. 3). The change of red deer habitat toward dense forested areas in Jura, reflected by $\delta^{13}\text{C}_{\text{coll}}$ values lower than -22‰ (Drucker et al., 2008), seemed to take place by the end of the Preboreal. In contrast, the red deer $\delta^{13}\text{C}_{\text{coll}}$ values in the Alps were rather stable over time (Fig. 3). Most of the values are comprised between -21.1 and -19.2‰ . As a result the red deer exhibited significantly less negative values in the Alps than in Jura during the early Holocene (Mann–Whitney–Wilcoxon test, $p < 0.0001$). Thus, the habitat of red deer in the Alps did not reflect a significant canopy effect. This absence of canopy effect could be a consequence of higher altitude and/or lower degree of canopy density in the Alps than in Jura. Interestingly, one specimen from a high altitude site in the Alps (LUS-2 from Les Corréardes) yielded a $\delta^{13}\text{C}_{\text{coll}}$ value of -18.7‰ during the early Atlantic, which is 2.5‰ higher than the mean values of the coeval red deer of the same region. For a raise of 1000 m in altitude, an increase in $\delta^{13}\text{C}$ value of about 1.1‰ was measured in plants as the result of increasing water use efficiency along altitudinal gradient (e.g. Körner et al., 1991; Männel et al., 2007). Such a rate of $\delta^{13}\text{C}$ increase with altitude would imply a difference of about 2300 m of altitude between the dwelling area of LUS-2 specimen and those of the red deer from the other Alpine sites. Such an altitudinal contrast is larger than the actual difference of altitude among the considered sites and their surroundings, which corresponds to the Prealps range. Therefore, a slight influence of understory vegetation from dense forest could be suspected in the Alps, especially as a significant decrease in the early Holocene was detected when the LUS-2 specimen, most likely from high altitude territory, was excluded (Mann–Whitney–Wilcoxon test, $p < 0.05$). Either the forest stands of the Alps were less dense than in Jura and/or the red deer hunted in the Alps were consuming only occasionally understory vegetation from closed woodland.

7.3. Nitrogen-15, soil development and altitude of habitat

Dated collagen of the red deer from Jura exhibited a dramatic increase in $\delta^{15}\text{N}$ values in the early Holocene (3.4 – 7.8‰) compared to the Late-glacial (0.8 – 3.8‰) (Table 2, Fig. 4). As for the $\delta^{13}\text{C}_{\text{coll}}$ values, the Preboreal red deer provided intermediate $\delta^{15}\text{N}_{\text{coll}}$ values compared to those of the Late-Glacial on one hand and those of the Boreal and early Atlantic on the other hand. The trend in increasing $\delta^{15}\text{N}_{\text{coll}}$ values of Jura red deer followed the trend in increasing temperature due to the global warming witnessed during the Late-glacial to early Holocene transition. Enhanced biological activity linked to soil development leads to ^{15}N enrichment in soils and plants through the intensification of nitrogen turnover (e.g. Nadelhoffer and Fry, 1994; Hobbie et al., 2005). The increase in pedogenic activities during the early Holocene is evidenced by the increase in plant biomass linked to the development of temperate

Table 2

Results of the isotopic analysis of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and of phosphate ($\delta^{18}\text{O}_{\text{p}}$) for the French Jura red deer. The carbon, nitrogen and sulfur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). Chronological attributions, based on radiocarbon dating, are indicated using pollen chronozone.

Lab n°	C_{coll} (%)	N_{coll} (%)	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$ (‰)	$\delta^{15}\text{N}_{\text{coll}}$ (‰)	S_{coll} (%)	$\text{C}/\text{S}_{\text{coll}}$ (%)	$\text{N}/\text{S}_{\text{coll}}$ (%)	$\delta^{34}\text{S}_{\text{coll}}$ (‰)	$\delta^{18}\text{O}_{\text{p}}$ (‰)	Pollen chronozone
BVN-2	37.9	13.3	3.3	-23.0	7.1	0.15	656	197	8.6	15.8	Early Atlantic
BVN-1	31.5	12.3	3.0	-23.5	7.5	—	—	—	—	16.2	Early Atlantic
GNV 3	40.4	14.1	3.3	-23.0	6.5	—	—	—	—	—	Early Atlantic
GNV-6	39.7	15.2	3.0	-23.4	7.1	0.16	676	222	8.5	—	Early Atlantic
RCD-10500	42.2	16.5	3.0	-23.6	4.8	0.19	599	201	8.4	16.6	Early Atlantic
RCD-10600	40.7	15.1	3.1	-22.3	6.0	0.16	688	219	8.8	16.8	Early Atlantic
RCD-10700	40.6	14.9	3.2	-23.7	5.5	—	—	—	—	16.5	Early Atlantic
GIS-1	41.9	16.6	2.9	-22.9	6.4	0.16	711	242	8.1	—	Early Atlantic
STH-1	43.7	16.4	3.1	-22.4	5.9	0.15	753	242	10.3	—	Early Atlantic
GAR-1	39.7	14.6	3.2	-21.7	4.7	—	—	—	—	—	Early Atlantic
OB-15	42.5	14.9	3.3	-22.3	5.6	0.18	617.2	185.5	10.0	—	Early Atlantic
RCD-10100	37.4	13.5	3.2	-22.8	5.8	—	—	—	—	15.6	Early Atlantic
RCD-10200	38.2	14.2	3.1	-22.7	4.3	—	—	—	—	15.7	Early Atlantic
RCD-10300	38.1	14.0	3.2	-22.9	6.4	—	—	—	—	17.2	Early Atlantic
RCD-10400	37.7	13.7	3.2	-22.6	4.2	—	—	—	—	17.1	Early Atlantic
BVN-7(2)	40.6	15.2	3.1	-23.3	7.2	—	—	—	—	16.1	Early Atlantic
OB-14	23.3	8.3	3.3	-22.6	6.4	—	—	—	—	—	Early Atlantic
RCD-6500	40.5	14.6	3.2	-23.0	5.2	0.15	719	222	9.7	15.9	Early Atlantic
OB-11	24.7	9.6	3.0	-22.9	7.3	—	—	—	—	—	Boreal/E. Atlantic
RAN-9(2)	36.8	13.6	3.1	-22.9	7.8	—	—	—	—	—	Boreal
RAN-8(2)	37.3	13.9	3.1	-21.9	6.6	—	—	—	—	—	Boreal
BVN-4(2)	34.9	11.7	3.5	-22.7	4.9	0.15	602	173	6.4	16.4	Boreal
BVN-5(2)	39.2	13.9	3.3	-22.4	4.7	—	—	—	—	16.0	Boreal
BVN-3(2)	41.4	15.2	3.2	-23.2	5.8	0.15	716	226	5.6	—	Boreal
RCD-6300	39.1	14.3	3.2	-23.4	4.7	—	—	—	—	16.8	Boreal
BRT-4	40.3	14.4	3.3	-22.5	4.0	0.18	603	185	10.3	—	Boreal
RAN-2	44.7	15.8	3.3	-23.6	7.4	0.15	818	248	1.1	—	Boreal
RAN-3	41.6	15.3	3.2	-23.5	8.1	—	—	—	—	—	Preboreal/Boreal
RAN-4	43.3	14.9	3.4	-23.4	7.0	—	—	—	—	—	Preboreal/Boreal
RAN-5	42.7	15.2	3.3	-24.0	7.8	—	—	—	—	—	Preboreal/Boreal
RAN-6	44.0	14.8	3.5	-22.4	6.4	0.17	681	196	5.6	—	Preboreal/Boreal
RCD-6200	38.8	14.2	3.2	-22.5	3.5	0.19	559	175	7.2	16.9	Preboreal
STH-2	41.5	15	3.2	-22.7	3.4	0.17	667	207	7.9	—	Preboreal
OB-5	42.8	15.9	3.1	-21.1	4.4	0.19	601	191	5.8	—	Preboreal
OB-3	20.6	7.9	3.0	-21.6	2.7	—	—	—	—	—	Alleröd/Y.Dryas
BRT-2	40.7	15.1	3.2	-19.4	3.1	—	—	—	—	—	Alleröd/Y.Dryas
RCD-6400	36.8	13.4	3.2	-21.5	3.8	—	—	—	—	15.1	Alleröd/Y.Dryas
RCD-4700	39.7	14.8	3.1	-19.5	1.4	—	—	—	—	14.5	Alleröd/Y.Dryas
RCD-4800	40.7	14.7	3.2	-20.6	1.3	—	—	—	—	14.9	Alleröd/Y.Dryas
RCD-4900	39.9	14.8	3.2	-20.0	1.3	0.14	747	237	3.1	14.0	Alleröd/Y.Dryas
RCD-5000	39.5	14.3	3.2	-20.3	0.4	0.17	629	195	2.7	14.4	Alleröd/Y.Dryas
RCD-5100	39.8	14.7	3.2	-20.0	0.2	0.18	593	187	8.5	14.1	Alleröd/Y.Dryas
OB-1	39.3	13.7	3.4	-20.1	2.7	—	—	—	—	—	Alleröd
BRT-1	42.1	14.5	3.4	-20.9	1.4	—	—	—	—	—	Alleröd
BRT-3	38.6	14.1	3.2	-20.6	1.0	0.13	763	239	0.4	—	Alleröd
RCD-2300	38.5	14.2	3.2	-20.8	1.6	0.15	673	212	4.0	14.9	Alleröd
RCD-2400	38.9	13.3	3.2	-20.6	3.1	0.18	575	169	1.7	14.8	Alleröd
RCD-2500	40.0	14.6	3.2	-21.2	2.6	—	—	—	—	14.6	Alleröd
RCD-2600	38.8	14.0	3.2	-20.0	2.3	0.16	656	204	3.3	15.1	Alleröd
RCD-2700	38.2	14.2	3.2	-20.9	1.6	0.16	653	207	1.4	15.4	Alleröd
RCD-2800	40.3	14.7	3.2	-20.5	1.3	0.14	771	241	-0.1	14.8	Alleröd
RCD-900	40.3	14.6	3.2	-20.1	1.8	—	—	—	—	15.0	Alleröd
RCD-1000	42.5	15.4	3.2	-20.7	2.5	—	—	—	—	15.1	Alleröd
RCD-1100	42.0	15.3	3.2	-21.9	3.0	0.15	728	228	4.2	15.3	Alleröd
RCD-1200	38.9	14.4	3.1	-19.9	1.3	—	—	—	—	14.8	Alleröd
RCD-1300	37.8	13.9	3.2	-20.6	2.0	—	—	—	—	14.8	Alleröd
RCD-1400	41.0	15.0	3.2	-20.7	0.4	—	—	—	—	14.9	Alleröd
BVN-9(2)	28.1	10.3	3.2	-20.8	2.1	—	—	—	—	15.3	Bölling/Alleröd
RCD-500	42.3	15.5	3.2	-19.9	0.8	—	—	—	—	15.0	Bölling/Alleröd
RCD-600	41.2	14.8	3.2	-20.1	—	0.15	744	229	1.8	14.9	Bölling/Alleröd
RCD-10900	41.7	16.0	3.0	-20.4	2.0	—	—	—	—	—	Bölling/Alleröd
RCD-11000	44.0	16.1	3.2	-20.6	2.4	—	—	—	—	—	Bölling/Alleröd

forest (De Beaulieu et al., 1994). Moreover, increase in temperature favors plant biomass decomposition, organic nitrogen mineralization and loss of soil nitrate by volatilization (Sprent, 1987; Garten, 1993), all those processes driving to higher $\delta^{15}\text{N}$ values in plants from boreal and peri-arctic ecosystems (Nadelhoffer and Fry, 1994; Amundson et al., 2003). During the Late-glacial, soils in Jura and the

Alps were recently released from the influence of the local glaciers. The persistence of low temperature, low biomass and low soil N content could explain the relatively low $\delta^{15}\text{N}_{\text{coll}}$ of red deer with no distinction between the two regions (0.2–3.8‰ in Jura, 1.3–3.6‰ in the Alps; Tables 2 and 3, Fig. 5). Based on the same mechanisms, the gradient of decreasing $\delta^{15}\text{N}$ values of soils and plants and their

Table 3
Results of the isotopic analysis of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and of phosphate ($\delta^{18}\text{O}_\text{p}$) from the western Alps red deer. The carbon, nitrogen and sulfur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). Chronological attributions, based on radiocarbon dating, are indicated using pollen chronozone.

Lab n°	C_{coll} (%)	N_{coll} (%)	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$ (‰)	$\delta^{15}\text{N}_{\text{coll}}$ (‰)	S_{coll} (%)	$\text{C}/\text{S}_{\text{coll}}$ (%)	$\text{N}/\text{S}_{\text{coll}}$ (%)	$\delta^{34}\text{S}_{\text{coll}}$ (‰)	$\delta^{18}\text{O}_\text{p}$ (‰)	Pollen chronozone
LUS-2	41.7	15.2	3.2	-18.7	2.2	0.12	908	283	6.4	—	Early Atlantic
APS-2	42.9	15.9	3.2	-21.7	4.2	—	—	—	—	—	Early Atlantic
GRV-12	39.9	14.7	3.2	-20.9	4.0	—	—	—	—	12.7	Early Atlantic
GRV-9	41.8	15.6	3.1	-21.1	3.6	0.16	692	221	3.9	15.1	Early Atlantic
GRV-5	41.4	15.1	3.2	-21.1	3.2	0.12	935	292	6.4	14.7	Boreal
FRU-2	35.2	13.7	3.0	-22.4	4.2	0.15	620	207	6.0	15.7	Boreal
FRU-9	39.4	14.8	3.1	-20.2	1.6	0.15	693	223	2.3	—	Boreal
GRV-1	42.1	15.3	3.2	-20.4	2.2	0.15	749	234	6.4	—	Preboreal
FRU-3	32.7	12.4	3.1	-21.1	2.7	—	—	—	—	—	Preboreal
FRU-1	38.1	13.7	3.2	-20.1	2.4	—	—	—	—	—	Preboreal
FRU-6	36.8	13.9	3.1	-20.2	1.8	0.15	635	206	3.0	—	Y. Dryas
FRU-7	34.5	13.2	3.1	-20.3	1.6	0.17	530	174	3.5	—	Y. Dryas
FRU-4	29.5	11.6	3.0	-20.8	3.1	0.12	676	228	5.5	16.7	Alleröd
FRU-13	43.3	16.0	3.2	-20.2	3.0	0.15	772	245	6.6	15.9	Alleröd
FRU-15	42.7	15.9	3.1	-21.1	3.3	0.17	689	219	5.9	—	Alleröd
FRU-10	43.7	16.0	3.2	-19.9	2.2	0.15	765	239	3.4	—	Alleröd
LDT-200	41.7	15.3	3.2	-20.7	—	—	—	—	—	—	Bölling/Alleröd
FRU-11	41.5	15.7	3.1	-19.2	1.3	0.16	698	227	2.6	—	Bölling/Alleröd
FRU-5	36.3	14.1	3.0	-20.3	3.6	0.16	614	205	-0.2	18.3	Bölling
LDT-600	41.8	15.4	3.2	-19.8	2.0	0.14	786	249	-3.1	—	O. Dryas/Bölling

consumers is found with increasing altitude (e.g. Männel et al., 2007). It could explain the lower red deer $\delta^{15}\text{N}_{\text{coll}}$ found in the Alps than in Jura during the early Holocene (Mann–Whitney–Wilcoxon test, $p < 0.0001$). However, the lack of significant $\delta^{15}\text{N}_{\text{coll}}$ increase in the Alps red deer over the Late-glacial to early Holocene transition was rather unexpected. Occurrence of oak mixed forest was documented as high as 1500 m asl during the Boreal in the Alps. Thus, the development of soil maturity in the Alps should be reflected by an increase in the $\delta^{15}\text{N}$ values of soils and thus on plants consumed by red deer. The stability of the red deer $\delta^{15}\text{N}_{\text{coll}}$ values in the Alps through the considered period as well as the lack of significant canopy effect could be linked to a change in home range toward higher altitude areas in the early Holocene.

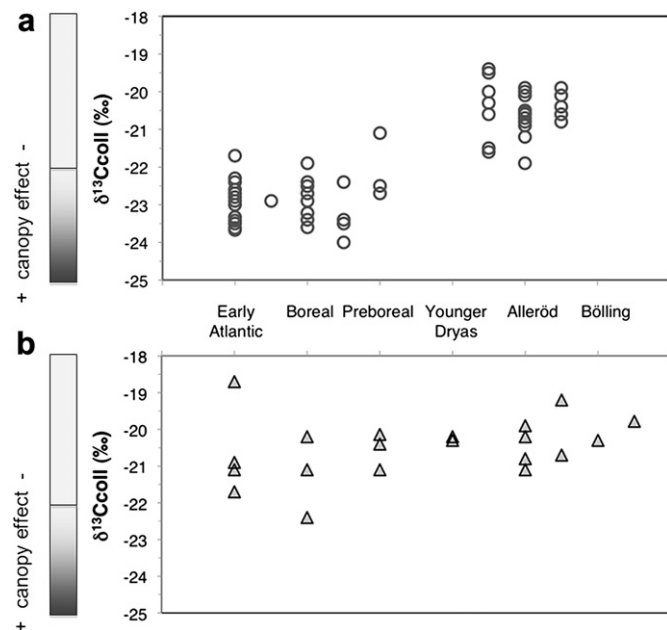


Fig. 3. The $\delta^{13}\text{C}_{\text{coll}}$ values of directly and un-directly red deer (*Cervus elaphus*) from the French Jura in a) and the western Alps in b). Values below ca. -22‰ are interpreted as the result of the canopy effect. Chronological attributions are given in Table S1 and S2.

7.4. Oxygen-18 and altitude

The increase in red deer $\delta^{18}\text{O}_\text{p}$ values observed in the French Jura site of Rochedane at the Late-glacial/early Holocene transition (Drucker et al., 2009) was confirmed by the new data obtained in the nearby site of Bavans (Table 2). The linear relationship between the $\delta^{15}\text{N}_{\text{coll}}$ values and $\delta^{18}\text{O}_\text{p}$ values measured on the same specimens was also confirmed but with a coefficient of correlation slightly lower ($r^2 = 0.60$) than the one calculated for the sole site of Rochedane ($r^2 = 0.67$) (Fig. 6). Local effect in terms of hydrogeology could influence the general pattern of global warming resulting in global increase in $\delta^{18}\text{O}$ values of available drinking water.

The isotopic contrast between Jura and Alps red deer was also reflected in $\delta^{18}\text{O}_\text{p}$ values of red deer despite more limited number of data (Tables 2 and 3, Fig. 7). While higher $\delta^{18}\text{O}_\text{p}$ values were measured in the Alps (La Grande Rivoire and La Fru sites) than in Jura during the Late-glacial, a reverse pattern was observed during the early Holocene. Difference in Late-glacial $\delta^{18}\text{O}_\text{p}$ values between both regions may be explained by higher aridity rather than higher temperature in the Alps compared to French Jura. In the early

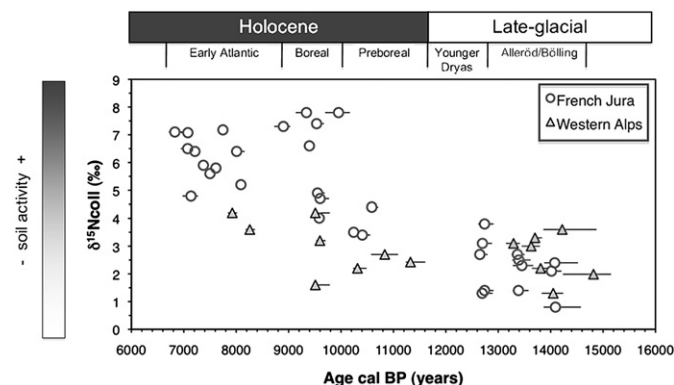


Fig. 4. The $\delta^{15}\text{N}_{\text{coll}}$ values of AMS dated red deer (*Cervus elaphus*) from the French Jura (white circles) and the western Alps (grey triangles) against time through the Late-glacial to early Holocene transition. Increasing collagen $\delta^{15}\text{N}$ values are interpreted as the result of increasing soil activity. The AMS results were calibrated at based on intcal09.14C calibration dataset and calculated by CALIB REV6.0.0 program (Reimer et al., 2009).

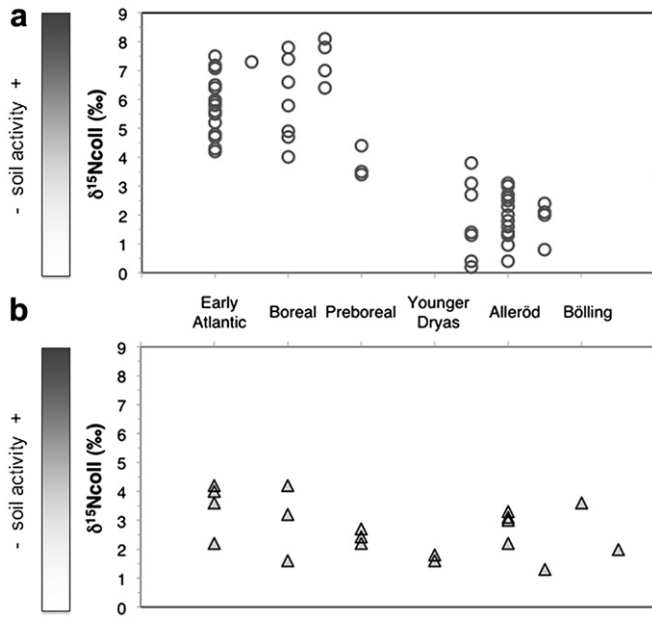


Fig. 5. The $\delta^{15}\text{N}_{\text{coll}}$ values of directly and un-directly red deer (*Cervus elaphus*) from the French Jura in a) and the western Alps in b). Increasing collagen $\delta^{15}\text{N}$ values are interpreted as the result of increasing soil activity. Chronological attributions are given in Table S1 and S2.

Holocene, the low $\delta^{18}\text{O}_p$ values of the Alps red deer could correspond to local temperatures lower than in Jura. However, the $\delta^{18}\text{O}_p$ values of red deer from the Alps were not only lower to those of the red deer from Jura, but also from those of the red deer of the same sites in the previous period of the Late-Glacial. A decrease of $\delta^{18}\text{O}_p$ values at the Late-glacial to early Holocene transition could be attributed to the driving effect of increasing humidity instead of the impact of increasing temperature observed in Jura. However, the combined action of lower aridity and higher temperature should have led to higher $\delta^{15}\text{N}$ values of plants and their consumers over time, while no change in ^{15}N abundances of red deer collagen was observed in the Alps. Similarly, the increase in water availability

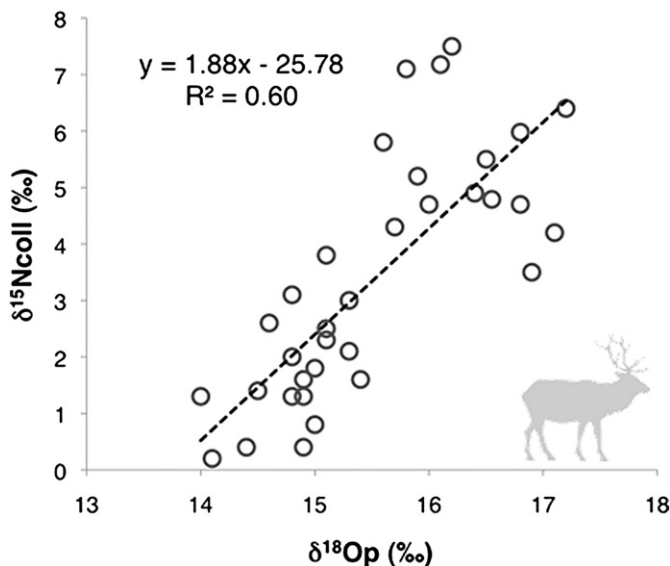


Fig. 6. Relationship between the $\delta^{15}\text{N}_{\text{coll}}$ values and the $\delta^{18}\text{O}_p$ values measured on the same bone of red deer (*Cervus elaphus*) from Rochedane and Bavans in French Jura. A positive linear correlation is found that confirms the indirect influence of climate on the ^{15}N amounts in red deer collagen at the Late-glacial to early Holocene transition.

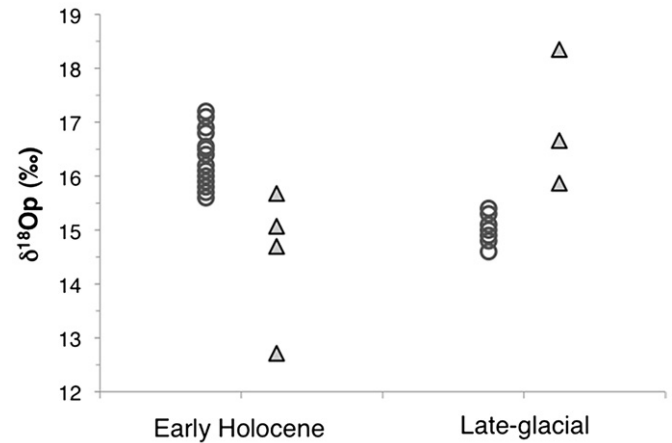


Fig. 7. The $\delta^{18}\text{O}_p$ values of red deer (*Cervus elaphus*) from the French Jura (white circles, sites of Rochedane and Bavans) and the western Alps (grey triangles, sites of La Grande Rivoire and La Fru) at the Late-glacial and early Holocene periods. The increase in red deer $\delta^{18}\text{O}_p$ values in the French Jura over time is considered to be the result of the global rise of temperature. In contrast, the decreasing in red deer $\delta^{18}\text{O}_p$ values in western Alps is interpreted as a change in habitat toward areas higher in altitude in the early Holocene compared to the Late-glacial.

was expected to enhance the decrease in $\delta^{13}\text{C}$ of forage linked to the canopy effect, whereas only a slight decrease in $\delta^{13}\text{C}_{\text{coll}}$ values of red deer could be suspected in the western Alps. Thus, higher altitude in the home range of the Alps red deer, due to an altitudinal movement of the animals and/or a change in human hunting territories, could explain the trends provided together by the $\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{18}\text{O}_p$ values in the early Holocene compared to the Late-glacial.

7.5. Sulphur-34, soil warming and mobility

The $\delta^{34}\text{S}_{\text{coll}}$ values measured on the red deer from Jura ranged between -0.1 and 8.5‰ for the Late-Glacial period and 1.1 and 10.3‰ for the early Holocene period (Table 2, Fig. 8). The collagen ^{34}S abundances of Jura red deer were thus significantly more positive in the Holocene than in the Late-glacial (Mann–Whitney–Wilcoxon test, $p < 0.001$). In the western Alps (Table 3, Fig. 8), the red deer $\delta^{34}\text{S}_{\text{coll}}$ values varied from -3.1 – 6.6‰ with no significant contrast between the Late-glacial (-3.1 – 6.6‰) and the early Holocene (2.3 – 6.4‰). There was also no significant difference in ^{34}S abundances between French Jura and the western Alps during the Late-glacial despite the rather low $\delta^{34}\text{S}_{\text{coll}}$ value exhibited by LDT-600 specimen (-3.1‰) from the Alps. In the early Holocene, the red deer from Jura had significantly higher $\delta^{34}\text{S}_{\text{coll}}$ values than those of red deer from the Alps (Mann–Whitney–Wilcoxon test, $p < 0.05$). Thus, the pattern of $\delta^{34}\text{S}_{\text{coll}}$ variation over time in a given region or between regions in a given period was comparable to the pattern of $\delta^{15}\text{N}_{\text{coll}}$ variation. A part of the sulphur assimilated by plants derives from soil sources (Peterson and Fry, 1987). Interestingly, both $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values in soil profiles show increase with depth, and similar behavior of N and S stable isotopes are found in soils like the preferential assimilation of lighter isotopes (^{14}N , ^{32}S) and the enrichment in heavier isotopes ^{15}N and ^{34}S of the *in situ* residues of mineralization (Novák et al., 2003). Moreover, volatilization processes favor the lighter isotopes and result in the enrichment of heavier isotopes in the remaining soil residues (Fry et al., 1986; Högborg, 1997).

The impact of the Late-glacial to early Holocene global warming through soil processes could be suspected for the evolution of red deer $\delta^{34}\text{S}_{\text{coll}}$ values over time in Jura as it was hypothesized for the

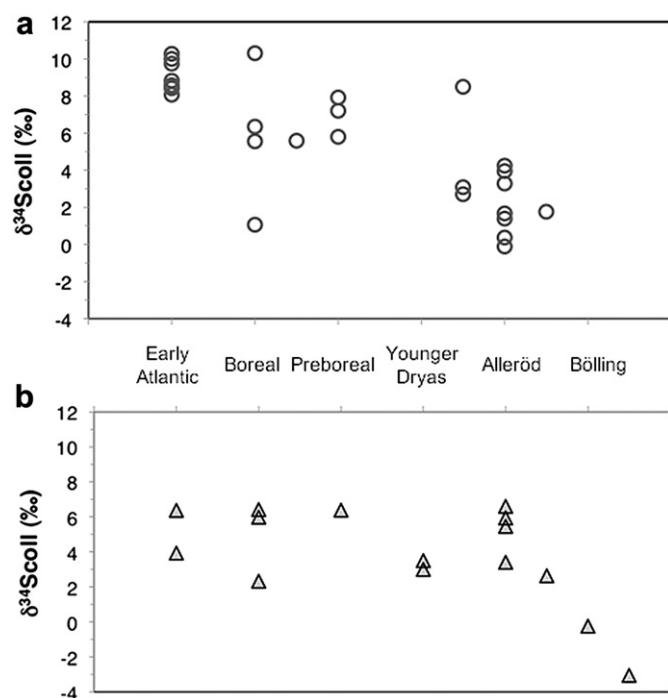


Fig. 8. The $\delta^{34}\text{S}_{\text{coll}}$ values of directly and un-directly red deer (*Cervus elaphus*) from the French Jura in a) and the western Alps in b). Difference in collagen $\delta^{34}\text{S}$ values for a given chronozone is thought to result from contrast in nature of geological bedrock. Chronological attributions are given in Table S1 and S2.

coeval $\delta^{15}\text{N}_{\text{coll}}$ values. Increasing temperatures could lead to an increase in the $\delta^{34}\text{S}$ values of soils by increasing the rate of mineralization and volatilization of sulphur (Fry et al., 1986; Novák et al., 2003). Moreover, higher temperatures lead to higher rate of bacterial reduction (Kaplan and Rittenberg, 1964), which results in less ^{34}S depletion in the reduced products (Krouse and Mayer, 2000). It would thus be possible that the $\delta^{34}\text{S}_{\text{coll}}$ values of red deer reflected the increasing soil activity linked to increasing temperature at the Late-glacial/early Holocene transition in Jura. Local effect could be hypothesized for RAN-2 specimens that had a relatively low $\delta^{34}\text{S}$ value (1.1‰) compared to the other Holocene red deer from Jura (5.6–10.3‰) as well as for the RCD-5100 specimen that gave a rather high $\delta^{34}\text{S}_{\text{coll}}$ value (8.5‰) compared to the other Late-Glacial red deer from Jura (−0.1–4.2‰). RAN-2 provided one of the highest $\delta^{15}\text{N}_{\text{coll}}$ values of the Boreal chronozone while RCD-5100 had the lowest $\delta^{15}\text{N}_{\text{coll}}$ value of the Late-glacial period. This is not consistent with the observed rough correlation between $\delta^{34}\text{S}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values over time. The studied sites of Jura are situated on soils dominated by limestones with some areas of detrital deposit and some granitic massifs such as the massif of La Serre close to Ranchot and the Vosges close to Oberlarg. Thus, some differences in the nature of the geological bedrock could explain the cause of local soil $\delta^{34}\text{S}$ values contrast reflected by some red deer specimens. A more systematic survey of $\delta^{34}\text{S}$ values of different bedrocks found in Jura could provide the baseline to investigate mobility during the Late-glacial and the Holocene in this region.

8. Conclusions

The analysis of different stable isotopes on red deer collagen offered the possibility to track combined local conditions of habitat using ^{13}C , climate using ^{18}O , and soil using ^{15}N . Results in ^{34}S confirmed the potential of this isotope to reflect the mobility of

mammals in purely terrestrial contexts. The multi-element stable isotope analysis of red deer from eastern France at the Late-glacial/early Holocene transition evidenced temporal and geographical contrasts linked to differences in the response of red deer populations facing a significant change in their environment. A drastic modification in ethology was reflected by the red deer of French Jura with the change of habitat to dense forest in warmer and more productive conditions. In contrast, the red deer of the western Alps persisted in open landscape and rather cool conditions with low soil productivity by dwelling at higher altitudes than before. This difference in adaptation to the global warming of the early Holocene was probably favored by the difference in topography between the two regions. It is also interesting to note that a species such as red deer, traditionally associated with forested environments, even if it is sufficiently flexible to cope with more open landscapes, continued to favor open environments, even when closed-canopy environments were available in the surrounding areas.

As the studied specimens come from archaeological sites, selection by prehistoric human hunters should also be considered. For example, the occurrence of red deer groups in dense forest at low altitude in the Alps cannot be excluded, as human populations may have preferred to hunt red deer in open areas for technical and/or cultural reasons. If it were the case, the isotopic results obtained on red deer would also give an insight on human foraging of their environment. In any case, the multi-element stable isotope tracking of red deer is a valuable tool to decipher the ecological response of a terrestrial ungulate to changing environment.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quaint.2011.07.015.

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