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Mountain adaptation of caprine herding in the eastern Pyrenees during the Bronze Age: A stable oxygen and carbon isotope analysis of teeth

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ABSTRACT

Pastoral activities in the northeastern Pyrenees increased substantially during the Bronze Age, raising the question of the modalities of occupations in zones where the snow cover limited access to grasslands for a significant part of the year. The present study explores how stable isotope analysis may characterize the adaptation of husbandry to mountain environments through herding strategies, including the vertical mobility of livestock. It also addresses the broader issue of the occupation of territories by Bronze Age communities in the Western Mediterranean area, focusing on possible links between coastal plains and mountainous areas. For this purpose, sequential stable carbon and oxygen isotope analyses were conducted on caprines' teeth from the mountain site of Llo (Pyrénées-Orientales, 1630 m asl, Middle Bronze Age) and the permanent coastal site of Portal-Vielh (Hérault, 0 m asl, Late Bronze Age). An exploratory analysis was also conducted on modern sedentary and transhumant ewes to investigate the effect of altitudinal mobility on enamel oxygen isotope values. The range of $\delta^{18}\text{O}$ values measured in modern and archaeological caprines raised in mountain zones was lower than the one measured in the lowland caprines, while no significant difference could be observed in the range of $\delta^{13}\text{C}$ values. Co-variations between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences reveal the most information. The positive correlation observed in all instances at low elevation sites was not the leading pattern at Llo, where a variety of schemes could be observed, including opposite $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences. This opposition could not be explained by a reversal of the $\delta^{18}\text{O}$ cycle due to vertical mobility. Other causes could involve changes in the pattern of variation of $\delta^{13}\text{C}$ values, potentially linked to human responses to the local constraints, including vertical mobility and/or foddering. Portal-Vielh delivered a fully lowland signal. At Llo, although a full adaptation to a mountain environment seems clear, the question of the vertical mobility of the livestock cannot be resolved at the moment. Most importantly, Llo was characterized by a high inter-individual variability in the co-variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles, reflecting great plasticity of the husbandry practices on the inter-annual scale. This could have been a key to the adaptation to these marginal environments. The apparent disjunction between the coastal and mountain settlements, as far as herd trajectory is concerned, must be reaffirmed by further investigations in a larger number of sites.

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1. Introduction

As observed by Carozza et al. (2005, 2007), mountain zones have long been viewed as too harsh and inhospitable to be settled by Bronze Age societies. Recent research in the Pyrenees Mountains

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revealed a different reality. In the French northeastern Pyrenees, the earliest evidence of pastoral activities above 1500 m asl appears during the second half of the early Neolithic (around 4700 and 4500 cal BC) (Reille, 1990; Rendu, 2003; Guiter et al., 2005). Those intensified during the Middle Neolithic (around 4200 cal BC) at a time when pollen and archaeological data reflect an opening in forest cover, the emergence of plants associated with agropastoral activities and the presence of habitat structures in the sub-alpine and alpine zones (Rendu et al., 1996; Davasse et al., 1997; Galop, 1998, 2000; Vanni re et al., 2001; Rendu, 2003; Miras et al., 2007; Palet Martinez and Orengo Romeu, 2009; Ejarque et al., 2010).

The agropastoral pressure in the mountain to alpine zones increased substantially during the Bronze Age (Galop, 1998; Rendu, 2003; Carozza and Galop, 2008; Orengo Romeu, 2010; Rius et al., 2012). This phenomenon is well-documented in Cerdanya, where it is reflected by pollen indicators of pastoralism in the Enveitg Mountain subalpine zone (*Plantago lanceolata*, *Rumex* and *Artemisia*, Cichorioideae, Chenopodiaceae) (Galop, 1998; Galop et al., 2003) and by increasing fire frequency in the medium altitude forests (Vanni re et al., 2001). Landscape anthropization also included the building of cultivation terraces between 1600 and 2000 m in the Enveitg slope, as highlighted by pedo-anthracological and archaeological analysis (Rendu, 2003; Bal, 2006; Bal et al., 2010; Harfouche and Poupet, 2013). Furthermore, a large stone building ('site 88'), discovered at 2100 m on the Enveitg slope, was unusually large for a pastoral site. It could have been a type of *summer farm*, unless its use was perennial (Rendu et al., 2012).

The rhythmicity and period of occupation of the mountain slopes (mountain to alpine zones) is therefore a central focus of ongoing research on the management of mountain environments (Bal et al., 2010; Rendu et al., 2012). In particular, uncertainty remains about the modalities of exploitation of middle altitude landscapes for the dominantly caprine husbandry. Bearing in mind that the snow cover might have limited access to grasslands for a significant part of the year, a perennial occupation in middle altitude zones could have created the necessity of foddering during the shortage season. An alternative solution could have included herd mobility towards lower plain grasslands in the winter and/or higher elevation grasslands in the summer to find available grazing resources. Moreover, on a regional scale, another question is to determine whether agropastoral activities in this mountain area were connected to the occupation in the coastal plains as part of a unique cultural landscape in the Bronze Age. Explaining the pattern and rhythms of the seasonal livestock mobility along the altitudinal gradients would contribute to an improved understanding of the mountain territories' structuration and the modalities of their use.

To address these questions, we analysed intra-tooth variations in stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic ratios in Bronze Age caprines' tooth remains. These biogeochemical signatures are governed by environmental factors, some of which vary with altitude. They are integrated in vertebrates' skeletons through diet and drinking. In particular, isotopic signals are recorded in enamel bioapatite during tooth mineralization with no remodelling. Sequential analysis in tooth enamel gives access to the animal's isotopic history with an infra-annual resolution (Bryant et al., 1996a, b; Fricke and O'Neil, 1996), potentially revealing seasonal altitudinal mobility. This approach has been successfully applied to detect the vertical movements of wild and domestic small stock in East Africa (Balasse and Ambrose, 2005), North America (Fisher and Valentine, 2013), the Peruvian Andes (Goepfert et al., 2013) and Armenia (Tornerio et al., 2016). These works demonstrated that the isotopic 'mountain signature' varies from one place to another depending on the environmental and climatic contexts: in mixed C_3 – C_4 plants areas, a key parameter may be the decreasing relative

proportion of C_4 plants with altitude, whereas in places where C_3 plants dominate, the focus is on the altitudinal effect inducing increasing $\delta^{13}\text{C}$ values in plants and decreasing $\delta^{18}\text{O}$ values in precipitations. These parameters are exacerbated when the considered altitudinal gradient is very high. In the present study, we aim to characterize the mountain signature for the French Pyrenees. For this purpose, a combined analysis of stable carbon and oxygen isotope ratios could be more efficient than strontium isotope analyses, which are well-adapted for detecting mobility (e.g., Bentley and Knipper, 2005; Viner et al., 2010; Valenzuela-Lamas et al., 2015) but not adapted to a patchy and complicated geological substratum such as the one of the Pyrenean mountains and, generally speaking, complex orogenic areas.

First, we explored the signature of the mountain environment and vertical mobility on the oxygen isotopic ratios of modern transhumant and sedentary ewes raised in the Western Pyrenees, filling the absence of such modern dataset for European mountains context to date. Then, the approach combining the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequential analysis was applied to animal remains from the Bronze Age mountain settlement of Llo (1630 m asl) (Campmajo, 1983), on the one hand, to address the adaptation of husbandry to mountainous environments and to the Late Bronze Age site of Portal-Vielh (coastal plain of the Languedoc) (Carozza and Burens, 2000) on the other hand, to consider whether herding strategies may have created a link between coastal plains and mountainous areas. Additionally, we refer to the unique set of previously published sequential stable isotope analyses in caprines' teeth available to date for the Mediterranean margin of France at the late Neolithic sites of Collet-Redon and La Citadelle, respectively, coastal and hinterland settlements (Blaise et al., 2006; 2010; Blaise and Balasse, 2011) (Fig. 1 A).

2. Stable oxygen and carbon isotopes, altitudinal mobility and diet

2.1. Stable oxygen isotopes

In large mammals from temperate Europe, a direct relationship was established between $\delta^{18}\text{O}$ values in skeleton bioapatite and that of local surface water though the ingested water (Land et al., 1980; Luz and Kolodny, 1989; D'Angela and Longinelli, 1991). The $\delta^{18}\text{O}$ values in precipitation change spatially and temporally, according to climatic and geographical factors. Under intermediate and high latitudes, the rainfall $\delta^{18}\text{O}$ values are mainly controlled by the water vapour source and transport patterns, and ambient temperature is a key parameter to seasonal variations: ^{18}O -enriched rains occur in summer and ^{18}O -depleted rains in winter (Dansgaard, 1964; Gat, 1980; Rozanski et al., 1993). In the study area, seasonal variations in monthly isotopic data in modern rainfall support this global pattern (Avignon, Dax and Montpellier, Fig. 1A; IAEA/WMO, 2016; data reported in Supplementary Material 1). Presently, the study area is principally under Atlantic climatic influence. Paleoclimate proxies do not indicate any change in the atmospheric circulation and weather pattern within the mid-latitudes during the Holocene period (Magny et al., 2009b). The Bronze Age was marked by climatic instability. Two climatic deteriorations are observed across Europe. The first one, dated to 1650–1350 cal. BC, induced a temperature cooling (mean annual temperature decreased by c. 0.7 °C) and increasing humidity (annual precipitation increased by c. 70–100 mm, more particularly during summer) (Magny et al., 2009a, 2009b). The second pejo-ration occurred around 850 cal. BC (van Geel et al., 1996; Magny et al., 2007). On a global scale, a possible consequence when comparing modern and Bronze Age $\delta^{18}\text{O}$ values would be lower ratios for the latter.

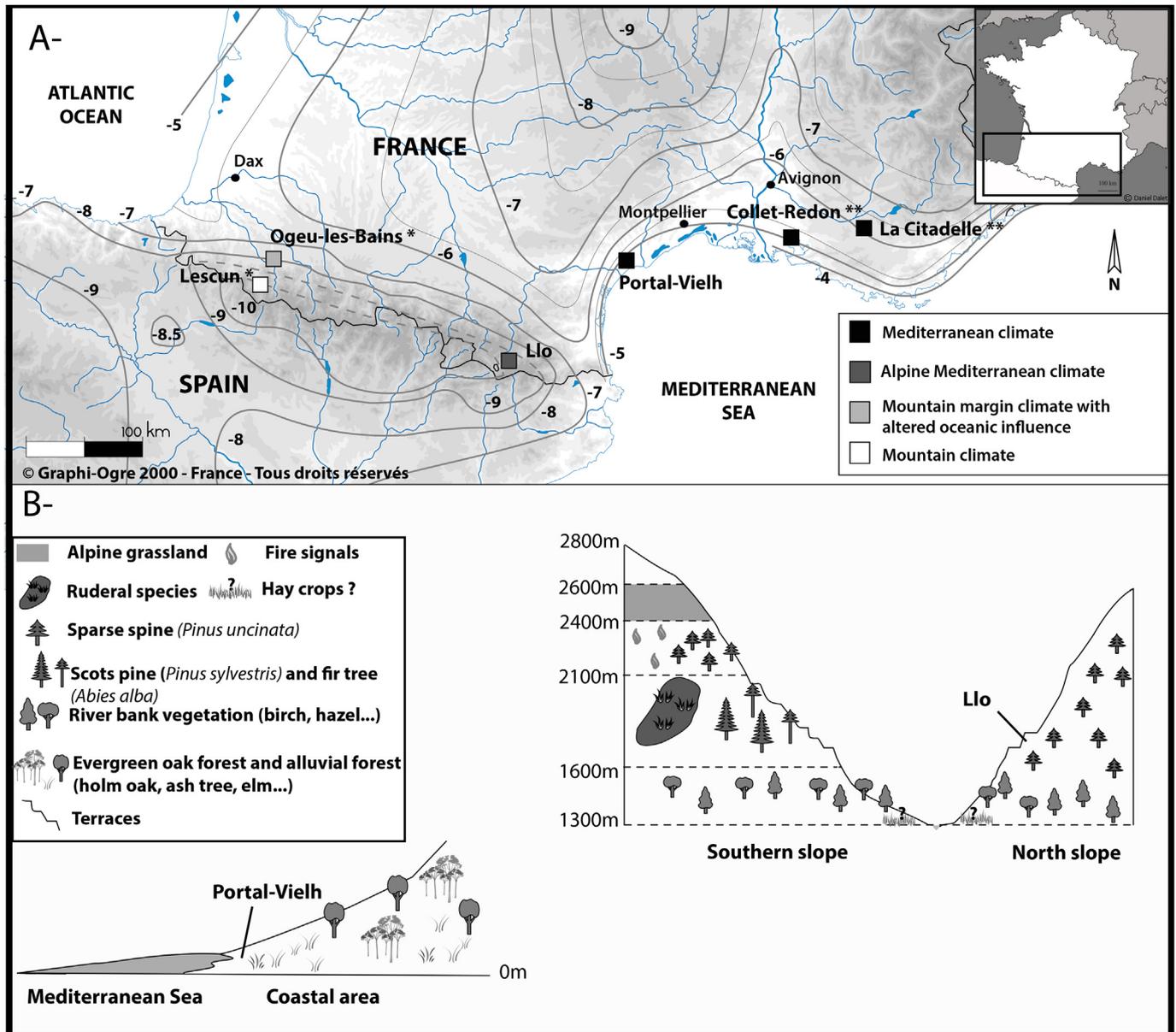


Fig. 1. a. Location of the modern and archaeological sites. One asterisk indicates the modern dataset and two refers to the published data (Blaise et al., 2006; 2010 and Blaise and Balasse, 2011). The curves correspond to the mean annual $\delta^{18}\text{O}$ composition of rainwaters (V-SMOW) according to Millot et al. (2010) and Plata-Bedmar, 1994 for Spain. The dotted curves indicate that few dataset were available and the relief was too uneven to draw reliable curves. The IAEA stations mentioned in the text are plotted on the map by black circles. Climate conditions are defined according Dupias, 1985 and Joly et al., 2010; b. Vegetation zonation in the surrounding landscape of Llo and Portal-Vielh during the Bronze Age. After Bal (2006), Bouby et al. (1999), Ruas and Bouby (2009), Harfouche and Poupet (2013).

At the regional scale, two other factors may influence rainfall $\delta^{18}\text{O}$ values: the continental effect inducing higher rainfall $\delta^{18}\text{O}$ values in the coastal plains, decreasing with distance from the sea; and the altitude effect inducing decreasing $\delta^{18}\text{O}$ values with increasing altitude, due to a gradual removal of moisture from uplifted air masses with a preferential removal of ^{18}O during condensation (Rozanski et al., 1993). Isovalues contour lines of the modern mean annual oxygen isotopic composition of rainwater are shown in Fig. 1A (Millot et al., 2010). Although a complex topography in the Pyrenean chain did not allow to define precisely the isotopic composition of rainwater in this area (dashed lines in Fig. 1A), globally the estimated $\delta^{18}\text{O}$ values from coastal plains are approximately 4–5‰ higher than those expected in the Pyrenees. The altitude effect on rainfall $\delta^{18}\text{O}$ values is not quantified in the

French Pyrenees, however gradients reported for the Alps vary from 0.1 to 0.4‰/100 m according to local conditions (Swiss Alps: Siegenthaler and Oeschger, 1980; Kern et al., 2014; Italian Alps: Longinelli and Selmo, 2003). Additionally, high elevation water sources may also be seasonally supplied with snowmelt or ice-melt, generating a release in the spring/early summer of water accumulated through cold-condition precipitation with lower $\delta^{18}\text{O}$ (Bhatia et al., 2011).

To summarize, (1) the coastal plains and mountain areas are marked by radically different rainfall $\delta^{18}\text{O}$ signatures. This difference should be inherited in the $\delta^{18}\text{O}$ values of animals herded in these respective territories if these referred to different entities with no interactions at the regional scale; (2) settling in a mountainous location and/or summer grazing in the high elevation

alpine grasslands could lead to globally and/or seasonally (in summer time) lower $\delta^{18}\text{O}$ values. Furthermore, summer mobility in highland areas could induce reduced $\delta^{18}\text{O}$ amplitude of intra-tooth variation.

2.2. Stable carbon isotopes

Tooth enamel bioapatite $\delta^{13}\text{C}$ provides information about grazing on vegetation (Lee-Thorp and van der Merwe, 1987; Cerling et al., 2003). A predominance of C_3 plants is expected in this region, as well as on a global scale in present day southwestern Europe (Pyankov et al., 2010). Wild C_4 plants would not occur in altitude sites and some C_4 plants, may have occurred only in salt-marsh vegetation from coastal areas, as in Iron Age Catalonia (Valenzuela-Lamas et al., 2015). Among Bronze Age C_4 domestic plants, broomcorn millet and foxtail millet (*Panicum milliaceum*, *Setaria italica*), are not mentioned in the archaeobotanical record of Portal-Vielh (Bouby et al., 1999). Only one grain, identified as 'Panicum type', is suspected at Llo (Ruas and Bouby, 2009).

C_3 plants $\delta^{13}\text{C}$ values have been shown to vary moderately (1–2‰) on a seasonal scale, the highest values occurring in the dry/warm season and the lowest in wet/cold season (Smedley et al., 1991; Diefendorf et al., 2010; Hartman and Danin, 2010). Adaptation to mountainous zones, where seasonal scarcity of vegetation may have required alternative solutions including foddering and vertical mobility, could interfere with this cycle. In humid areas, plants $\delta^{13}\text{C}$ values have been shown to increase along altitudinal gradients due to decreasing temperature and atmospheric partial pressure (Körner et al., 1988, 1991; Friend et al., 1989; Morecroft and Woodward, 1990). However, the observed correlations are in some instances rather weak (Kohn, 2010), and the effect is of modest amplitude: a 1.5‰ increase from 400 m to 2500 m was observed by Körner et al. (1988) in the Alps. Furthermore, increasing plants $\delta^{13}\text{C}$ values have been reported with decreasing mean annual precipitation. The effect seems to be noticeable under very dry (<500 mm/y) or very humid conditions (>1000 mm/y) (Kohn, 2010). In our study area, the lowest annual precipitation reaches approximately 650 mm/y in coastal environments (Béziers <http://fr.climate-data.org>) while the highest are measured in the intermediate mountain zone, reaching 1040 mm/y at the Llo station (<http://fr.climate-data.org>). No data is available for the highlands. Considering this, it is likely that the precipitation amount effect on plants $\delta^{13}\text{C}$ values should be insignificant. Last, different elevation zones are also characterized by a succession of landscapes whose degree of opening may also affect plants $\delta^{13}\text{C}$ values due to the canopy effect, leading to lower values in plants from dense forests' understories (Van der Merwe and Medina, 1991) and on animals feeding on them (Drucker et al., 2008).

In summary, (1) a mobility pattern involving summer stays in highland pastures could result in higher summer $\delta^{13}\text{C}$ values and higher amplitude of seasonal variation compared to a sedentary pattern at lower altitude; and (2) herding at middle altitude on an annual scale with grazing on surrounding pastures would result to globally higher $\delta^{13}\text{C}$ values than herding at a lower altitude. For both (1) and (2), the expected impact due to the altitude effect is moderate. (3) Winter foddering with leafy hay from dense forests would lower winter $\delta^{13}\text{C}$ values and increase seasonal amplitude of variation. (4) Winter foddering with late season forage should maintain winter $\delta^{13}\text{C}$ values to a summer/early fall value and therefore moderate the seasonal amplitude of variation. A multiplicity of schemes may also be envisaged, depending on the altitude where grass fodder may have been grown/collected.

3. Material

3.1. Archaeological and environmental contexts

The material comprises six modern ewes and 14 archaeological complete or sub-complete sheep (*Ovis aries*), goat (*Capra hircus*) and Iberian ibex (*Capra pyrenaica*) tooth rows belonging to different individuals. Those were identified to species from morphological criteria (defined by Couturier, 1962; Prat, 1966; Payne, 1985; Crégut-Bonnoure, 1992; Guérin and Patou-Mathis, 1996; Helmer, 2000; Halstead et al., 2002; Balasse and Ambrose, 2005; Gillis et al., 2011). The stable isotope analyses targeted lower second molars (M_2) with full crown development and lower third molars (M_3) with crown preserved at least over 17.5 mm following recommendation by Balasse et al. (2012) to prevent a major loss in the measured time sequence due to tooth wear. The archaeological contexts for previously published datasets from the late Neolithic sites of La Citadelle (Vauvenargues), Bouches-du-Rhône, 723 m; (Fig. 1A) and Collet-Redon (Martigues, Bouches-du-Rhône, coastal location; Fig. 1A) are described in Supplementary Material 2.

The open site of Llo is located on a rocky spur (1630 m asl) overlooking the high plateau of Cerdanya (Eastern Pyrenees) (Fig. 1). Today, the Alpine Mediterranean climate brings high sunlight, intermediate annual rainfall concentrated during spring and snowfall up to six months (from October to March). In the Bronze Age, riverbank vegetation and deciduous forests dominated on the Cerdanian plateau (1300 m). The Northern slopes supported sparse spine forests between 1600 and 2400 m (Bal, 2006). On the Southern slopes, the zonation of vegetation was a mixed pine and fir tree forest in the intermediate zone (1600–2100 m), changing to a sparse spine forest (2100–2400 m), and an asylvatic alpine grassland zone above 2400–2500 m (Galop, 1998; Vannièrè et al., 2001; Bal, 2006; Ruas and Bouby, 2009; Harfouche and Poupet, 2013). Hay crops were possibly grown in the intermediate zone (Bal, 2006), while high frequencies of ruderal plants (Galop, 1998) and a high occurrence of fire signals (Vannièrè et al., 2001; Bal, 2006) attest to agropastoral activities in the higher altitude zones.

Household refuse areas dated to the Middle and Late Bronze Age yielded a rich assemblage of faunal and botanical remains. The volume of these finds and a possible stonewall enclosing the habitat may indicate a permanent occupation, at least for some phases (Campmajo, 1983). The archaeobotanical analysis suggests local cultivation of legumes and cereals on the limestone outcrops or terraces in a possibly permanent system involving rotation of crops and forage plants for grazing (Ruas and Bouby, 2009). Animal subsistence economy relied mainly on caprines (sheep, *Ovis aries*, and goat, *Capra hircus*) and cattle (*Bos taurus*) husbandry (Vigne, 1983; Berlic, 1995a,b; Bréhard and Campmajo, 2005; Knockaert, 2012). Hunting is represented in low proportions. At Llo, ten caprine M_3 were selected, including seven sheep, one goat, one Iberian ibex and one indeterminate caprine. All came from a single archaeological level corresponding to a household refuse area dated to the Middle Bronze Age (C4N31a: [1430–1261] cal BC; C4N31b: [1419–1231] cal BC) (Campmajo et al., 2014; Supplementary Material 3), contemporaneous to the 1650–1350 cal. BC pejoration phase (Magny et al., 2009a, 2009b).

Portal-Vielh (Vendres, Hérault) is a coastal site located on a small promontory on the northern shore of the Vendres lagoon (Fig. 1). The settlement, occupied during Late Bronze Age II-III (1211–1020 cal BC and 820–594 cal BC) (Supplementary Material 3) by Mailhac culture communities, expanded substantially during the latest phase of occupation and an enclosure system was built. This defensive system, as well as clay pits, pottery kilns and structures probably intended to food storage, strongly suggests a permanent settlement (Carozza and Burens, 2000). The occupation

pattern at Portal-Vielh differs from the model of semi-settled communities for the Late Bronze Age in eastern Languedoc, describing main habitations in the hinterland and coastal settlements used as summer camps (Py, 1990, 1993). Today, the Mediterranean climate brings cool winters, hot and dry summers and maximum rainfall during autumn. The mean annual precipitation are globally low. The latest occupation phase at Portal-Vielh coincides with the peoration resulting in wetter and cooler conditions than today (ca. 850 cal. BC) (van Geel et al., 1996; Magny et al., 2007). The surrounding landscape was characterized by evergreen oak forest and dry meadows (Dupuis et al., 1968; Rameau et al., 1989). Animal husbandry focused primarily on caprines, while fishing and shellfish also played a significant role in the subsistence. Barley, wheat and beans were recovered at the site, which could have been cultivated in the basins, slopes and alluvial plains, while the plateau may have supported cattle grazing (Bouby et al., 1999). At Portal-Vielh, four teeth were selected, including the M₂s of two sheep, and the M₃s of one sheep and one goat. All came from a pit dated to the Late Bronze Age III (PVV St 31: [850–594] cal. BC; dates in Supplementary Material 3) first used as a clay pit then converted back a rubbish pit. All the teeth come from the single homogeneous fill.

3.2. Modern reference set

3.2.1. The transhumant ewes

The five transhumant ewes are from a Basco-Bearnaise dairy herd raised in the Western Pyrenees (Lescun, Aspes valley, Pyrénées Atlantiques, Fig. 1A). This region is under the influence of a mountain climate, subject to high precipitation (Joly et al., 2010). Four transhumant ewes were born in late autumn and one in March (Table 1). The farm, settled in the valley (800 m asl), is supplied with water from a local source. Every year, the ewes move to summer subalpine pastures (Cabanes d'Ansabère; 1500 and 2000 m asl) from the end of June to the end of September. Drinking water comes from the 'Gave d'Ansabère' river. One ewe (Oss 36 T) moved to 1300 m asl (Plateau du Bénou, Lasbordes) (Table 1), where the main water sources are seasonal ponds directly filled by precipitation. All individuals were slaughtered in June 2015 at the age of five to nine years.

3.2.2. The sedentary ewe

The sedentary ewe (Oss S10) came from a Manech-à-tête-rousse dairy herd raised in the Western Pyrenees, in a valley located further north (Ogeu-les-Bains, Ossau valley, Pyrénées Atlantiques) under a mountain margin climate with altered oceanic influence (Joly et al., 2010). It was born in November 2010 and was kept at 320 m asl before being slaughtered in June 2015. Its drinking water came from a local source in the village. All modern specimens only contribute their $\delta^{18}\text{O}$ values; their $\delta^{13}\text{C}$ values may not be considered here as reference values because of the moderate contribution of maize (C₄) to their diet.

Table 1

Information data of modern transhumant and sedentary ewes.

Specimen	Year of birth	Birth period	Breed	Husbandry system	Principal location		Location of summer pastures	
					Place	Altitude (m Asl.)	Place	Altitude (m Asl.)
Oss T 19	2006	March	Basco-Béarnaise	Transhumant	Lescun	800	Cabanes d'Ansabère	1500–2000
Oss T 24	2010	Late autumn	Basco-Béarnaise	Transhumant	Lescun	800	Cabanes d'Ansabère	1500–2000
Oss T 17	2007	Late autumn	Basco-Béarnaise	Transhumant	Lescun	800	Cabanes d'Ansabère	1500–2000
Oss T 14	2007	Late autumn	Basco-Béarnaise	Transhumant	Lescun	800	Cabanes d'Ansabère	1500–2000
Oss T 36	2009	Late autumn	Basco-Béarnaise	Transhumant	Lescun	800	Cabane de Lasbordes	1300
Oss S 10	2010	November	Manech-à-tête-rousse	Sedentary	Ogeu-les-Bains	320	Ogeu-les-Bains	320

4. Methods

4.1. Sequential sampling and chemical pre-treatment

Enamel sampling was performed on the buccal side of the molar, preferentially on the second lobe or on the first lobe when the second one was broken ('Llo O 58' and 'PVV O 3'). Sampling is perpendicular to the tooth growth axis and spans crown height from the apex to the enamel-root junction (ERJ). Enamel powders weighing 4.5–8 mg were pre-treated with 0.1 M of acetic acid [CH₃COOH] (0.1 ml solution/0.1 mg of sample) during 4 h rinsed five times with distilled water and freeze-dried. This protocol is recommended for archaeological samples to eliminate contamination from exogenous carbonates. Because it known to induce a shift in $\delta^{18}\text{O}$ values (Koch et al., 1997; Balasse et al., 2012), it was also applied to the modern samples. The previously published dataset from Collet-Redon and La Citadelle used for comparison had been additionally treated with sodium hypochlorite 2–3% (Blaise and Balasse, 2011). Approximately 600 μg of pre-treated bioapatite were reacted with 100% phosphoric acid [H₃PO₄] at 70 °C in individual vessels in an automated cryogenic distillation system (Kiel IV device) interfaced to a Delta V Advantage isotope ratio mass spectrometer. An internal laboratory calcium carbonate standard (Marbre LM normalized to NBS 19) allows checking the accuracy of the data. Over the period of analysis of these bioapatite samples (from April to October 2015), 162 analyses of Marbre LM gave a mean $\delta^{13}\text{C}$ value of $2.12 \pm 0.02\text{‰}$ (1 σ ; expected value = 2.13 ‰) and a mean $\delta^{18}\text{O}$ value of $-1.68 \pm 0.04\text{‰}$ (1 σ , expected value = -1.83‰). The analytical precision for each run varies from 0.01 to 0.03 ‰ for $\delta^{13}\text{C}$ values and from 0.02 to 0.07 ‰ for $\delta^{18}\text{O}$ values.

4.2. Data treatment and statistical methods

Inter-individual variability was explored using the amplitude of variation and the mid-point value ((min + max)/2) of the sequence. Only sequences spanning at least half an annual cycle, for which both a minimum and a maximum value could be clearly identified, were included. Statistical analyses used non-parametric statistical tests (Kruskal-Wallis and the Turkey's pairwise post hoc tests). They considered for each specimen the series of data measured in the sequence delimited by the minimum and maximum values. The correlation between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences was estimated using Pearson's correlation coefficient. All statistical analyses were conducted using Past version 3.10 (Hammer et al., 2001) with a threshold of significance at p-value < 0.05.

5. Results

5.1. Oxygen stable isotope values

5.1.1. The modern dataset

Results from stable isotope analyses are presented in Table 2 and

Table 2
 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (VPDB ‰) of enamel bioapatite from the caprines' second and third lower molars (M2 and M3) from Portal-Vielh (Pvv) and Llo (Llo). Oss T: modern transhumant ewes; Oss S: modern sedentary ewes. Amplitude of intra-tooth variation. Max: highest value. Min: lowest value. The mid-point value of the annual cycle is calculated from $(\text{Min} + \text{Max})/2$. *: incomplete cycle.

Samples	Tooth	N	$\delta^{18}\text{O}$ VPDB				$\delta^{13}\text{C}$ VPDB			
			Mid-point	Max	Min	Amplitude	Mid-point	Max	Min	Amplitude
Pvv O 6	M2	19	-0.7	0.0	-2.3	2.3	-12.2	-11.0	-13.4	2.4
Pvv O 2	M2	17	1.6	0.3	-2.1	2.4	-12.0	-10.9	-13.0	2.2
Pvv O 3	M3	15	-1.6	0.0	-3.3	3.3	-11.5	-10.1	-12.9	2.8
Pvv C 1 *	M3	13	-	0.1	-	-	-	-11.2	-	-
Llo O 5	M3	18	-2.5	-0.6	-4.3	3.7	-10.8	-9.8	-11.8	2.0
Llo O 9	M3	18	-4.2	-2.0	-6.4	4.4	-11.8	-11.5	-12.1	0.6
Llo O 11	M3	13	-3.1	-1.7	-4.4	2.7	-11.9	-11.3	-12.4	1.1
Llo O 15	M3	19	-4.3	-2.7	-5.9	3.2	-11.7	-11.1	-12.3	1.2
Llo O 58	M3	20	-5.1	-3.5	-6.7	3.2	-12.4	-12.0	-12.7	0.7
Llo O 159	M3	18	-4.6	-2.5	-6.7	4.2	-11.6	-10.9	-12.3	1.4
Llo O 161	M3	21	-4.7	-2.6	-6.7	4.1	-10.8	-10.2	-11.4	1.2
Llo C pyr. 156	M3	18	-4.0	-1.8	-6.1	4.3	-11.1	-10.7	-11.4	0.7
Llo C 250	M3	15	-0.7	1.3	-2.6	3.9	-10.9	-10.3	-11.5	1.1
Llo Capr 160 *	M3	13	-	-1.1	-4.8	3.7	-	-10.8	-	-
Oss T 19	M3	13	-4.7	-2.0	-7.3	5.3	-	-	-	-
Oss T 24	M3	17	-4.6	-2.1	-7.0	4.9	-	-	-	-
Oss T 17	M3	18	-4.9	-2.4	-7.4	5.0	-	-	-	-
Oss T 14	M3	19	-4.4	-2.0	-6.8	4.7	-	-	-	-
Oss T 36	M3	20	-5.1	-3.5	-6.7	3.1	-	-	-	-
Oss S 10	M2-M3	25	-3.3	-1.6	-5.0	3.4	-	-	-	-

in Figs. 2–4 (see also Supplementary Materials 4, 5 and 6). The sequences measured in the four transhumant ewes born in autumn are compared to the one measured in the transhumant ewe born in March (Oss T19) in Fig. 2. Because the timing of tooth formation is fixed, the observed shift in the sequence of the seasonal cycle measured in Oss T19 M3 reflects the difference in the birth season. In contrast, the series of $\delta^{18}\text{O}$ values measured in the sedentary and transhumant ewes born in the same season (autumn births) vary according to the same pattern, suggesting that despite their vertical mobility in summer, the expected scheme of seasonal variation of $\delta^{18}\text{O}$ values was maintained.

The four modern transhumant ewes from Lescun, grazing at 1500–2000 m in summer, yielded $\delta^{18}\text{O}$ values between -7.4 and -2‰ (and mid-point values from -4.9 to -4.4‰) with intra-tooth amplitudes varying from 4.7‰ to 5.3‰ (Fig. 3). This group yielded highly homogenous values. The ewes Oss T 14 and Oss T 17, born in the same year, show a moderate inter-individual variability on the mid-point value (0.5‰) and on the amplitude of intra-tooth variation (0.3‰). Inter-individual variability in the mid-point value

between individuals born in different years does not exceed 0.5‰, while the highest inter-individual difference in the intra-tooth amplitude of variation reaches 0.6‰. Oss T 36, which spent the summer in another grazing area at a lower altitude (1300 m asl), exhibits reduced amplitude of variation (3.1‰) due to a lower maximum $\delta^{18}\text{O}$ value (-3.5‰; Fig. 3a&b). Compared to the transhumant ewes, the sedentary ewe from the valley (Oss S 10 from Ogeu-les-Bains) exhibits a higher mid-point value (-3.3‰) than the ewes from Lescun—as expected based on the isovalues contour lines (Fig. 1A)—and a lower amplitude of intra-tooth variation (3.4‰) albeit one that is comparable to that measured in Oss T 36 (Fig. 3a&b).

5.1.2. Comparison of modern and archaeological $\delta^{18}\text{O}$ datasets

Globally, the range of $\delta^{18}\text{O}$ values measured in caprines from Llo, varying between -6.7 and 1.3‰, are closed to those measured in the modern mountain ewes and differs from those measured in the late Neolithic hinterland site of La Citadelle (-2.6 to -0.9‰) and the coastal site of Collet-Redon (-1.8–1.8‰; Fig. 3a&b). Conversely,

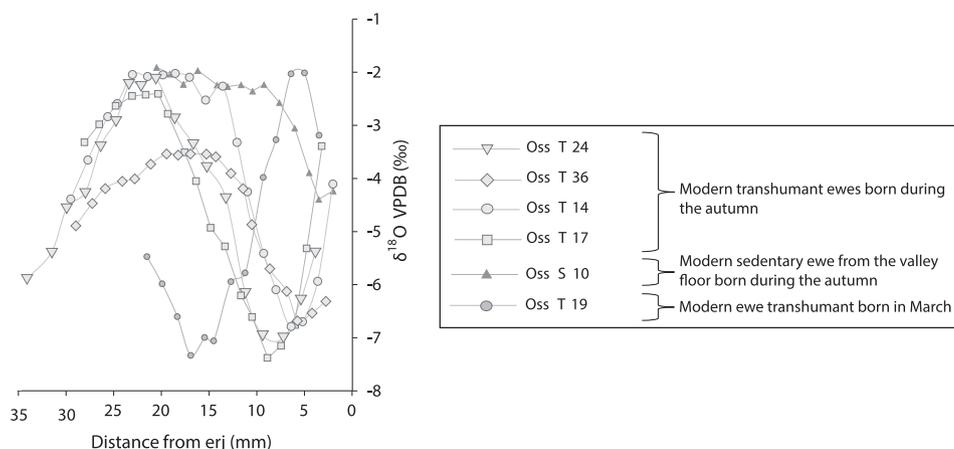


Fig. 2. Location of the highest and lowest $\delta^{18}\text{O}$ values in the M₃ crown of the modern ewe from the valley floor ('Oss 10') and the transhumant ewes born in autumn ('Oss T 14', 'Oss T 17', 'Oss T 24', 'Oss T 36') and in March ('Oss T 19'). Each sample is located in the tooth crown relative to its distance from the enamel root junction (ERJ) in mm.

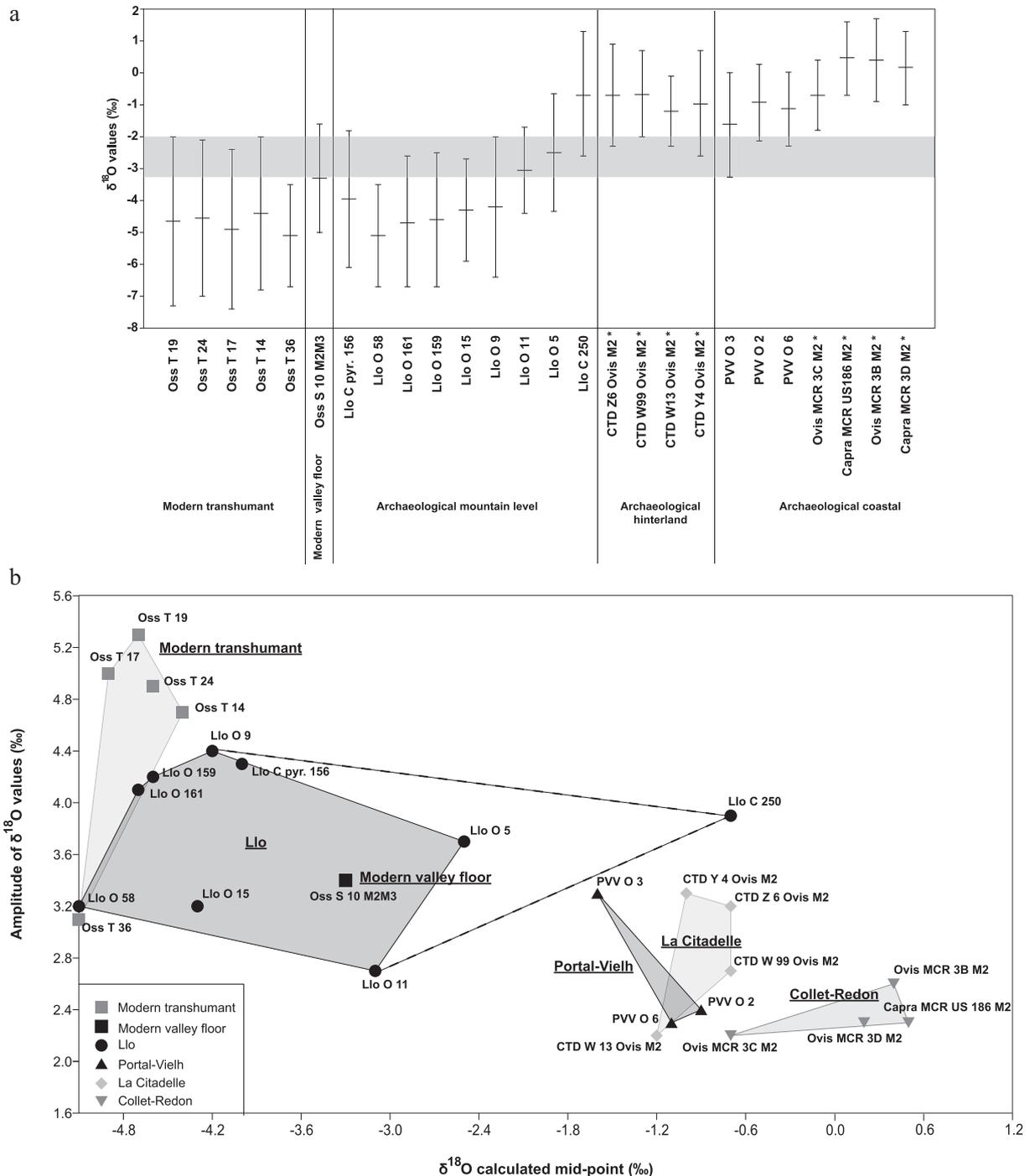


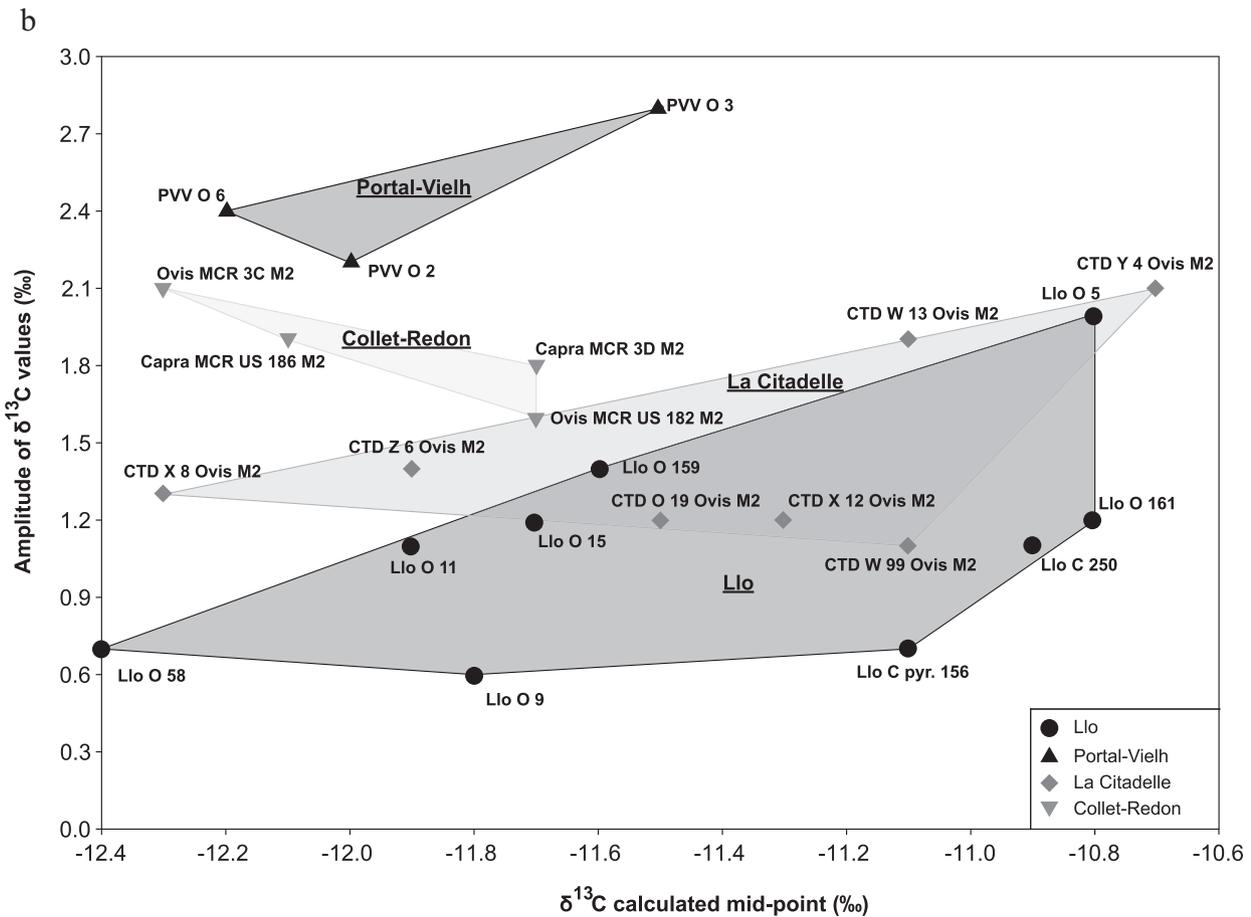
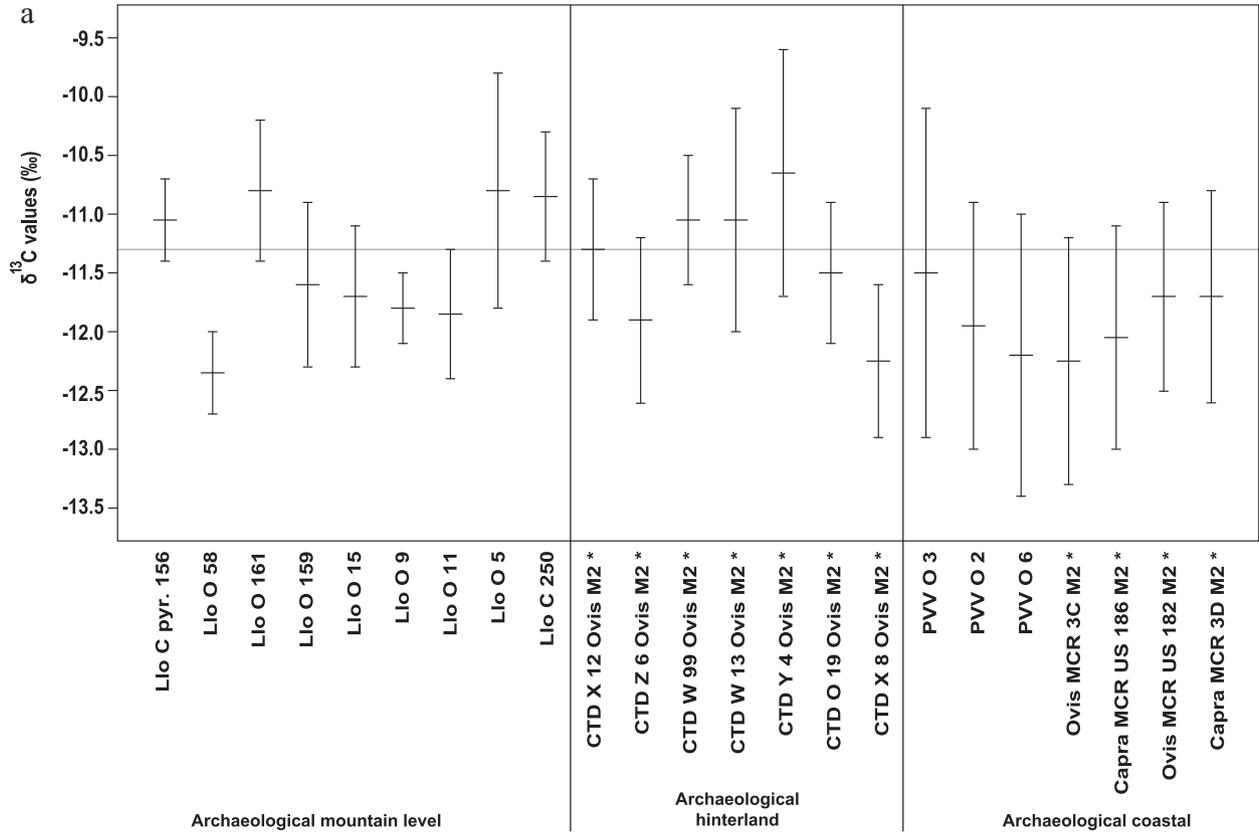
Fig. 3. a. Lowest and highest $\delta^{18}\text{O}$ values and mid-point value ($(\min + \max)/2$) of the annual cycle for individuals from Llo (Llo), Portal-Vielh (PVV) and the modern transhumant and sedentary ewes (Oss), compared to data from the late Neolithic sites of La Citadelle (CTD) and Martigues-Collet Redon (MCR) (* Blaise, 2010; Blaise and Balasse, 2011). The grey zone corresponds to overlapping values of modern transhumant and archaeological coastal. 3. b. Amplitude of intra-tooth variation in $\delta^{18}\text{O}$ values and mid-point values of the annual cycle in the modern and archaeological assemblages. Data for Collet-Redon and La Citadelle are from Blaise (2010), Blaise and Balasse (2011).

individuals from Portal-Vielh delivered a range of $\delta^{18}\text{O}$ values (-3.3 to 0.3‰) closer to the coastal and highlands specimens (Fig. 3a&b).

Llo O 161, Llo O 159, Llo O 9 and Llo C pyr. 156, yielded similar $\delta^{18}\text{O}$ mid-point values ranging from -4.7 and -4‰ and intra-tooth $\delta^{18}\text{O}$ amplitude of variation varying from 4.4 to 4.1‰ (Fig. 3b). No significant difference appears between the range of $\delta^{18}\text{O}$ values of all individuals except between Llo O 5 and Llo O 58 (Tukey's pairwise test: $p = 0.03$). The goat Llo C 250 is significantly different from

all other specimens from Llo (Tukey's pairwise test $p < 0.05$), except from Llo O 5 (Tukey's pairwise test: $p = 0.3$). Llo C 250 yielded the highest mid-point $\delta^{18}\text{O}$ value (-0.7‰).

When excluding Llo C 250, the range of $\delta^{18}\text{O}$ values measured at Llo is not significantly different (Kruskal-Wallis test: $p = 0.1$) from those measured in the modern transhumant ewes from Lescun, located on the same isovalue contour line (Fig. 1A). Both datasets differ significantly from the archaeological specimens from the



hinterland (La Citadelle; Kruskal-Wallis test: $p < 0.0001$) and from the coastal sites (Collet-Redon; Kruskal-Wallis test: $p < 0.0001$ and Portal-Vielh; Kruskal-Wallis test: $p < 0.0001$) located on lower-isovalue contour lines (Fig. 1A). Globally, the lowest intra-tooth amplitudes of variations are observed on the coastal and hinterland sites while the highest are measured in the modern transhumant ewes and Llo specimens (Fig. 3b), although both groups overlap on his criterion. The inter-individual variability in the amplitude of variation of $\delta^{18}\text{O}$ values is higher at Llo (1.7‰) than in the hinterland and coastal sites (Citadelle = 1.1‰, Portal-Vielh = 1.1‰, and Collet-Redon = 0.4‰).

In summary, despite the cooler climate during the 1550–1150 cal. BC and 800–400 cal. BC peoration phases at the time of occupation of Llo and Portal-Vielh respectively—which could have interfered in a comparison involving sites from different time periods—the caprines from both sites delivered $\delta^{18}\text{O}$ values setting them clearly in distinct systems, the first being fully settled in the mountain while the second fully adapted to coastal/lowlands, although a larger variability of patterns may be observed in the former.

5.2. Range and amplitude of stable carbon isotope values

The $\delta^{13}\text{C}$ values vary from -12.7 to -9.8 ‰ at Llo and from -13.4 to -10.1 ‰ at Portal-Vielh, compared to 12.9 to -9.6 ‰ at la Citadelle and -13.3 to -10.8 ‰ at Collet Redon (Fig. 4 a&b). Using the $\delta^{13}\text{C}$ mid-point values, no distinction can be made between caprines herded in lowland and highland sites (Fig. 4 a&b). The caprines from Llo delivered the lowest amplitude of intra-tooth variation of $\delta^{13}\text{C}$ values (0.6–2‰), while those from Portal-Vielh delivered the highest (2.2–2.8‰, Fig. 4 a&b). Statistical analysis of the range of $\delta^{13}\text{C}$ values distinguishes caprines from Llo from those from the coastal sites (Portal-Vielh vs Llo: Kruskal-Wallis test, $p < 0.001$; Collet-Redon vs Llo: Kruskal-Wallis test, $p < 0.001$), but no significant difference appears between datasets from Llo and La Citadelle (La Citadelle vs Llo; Kruskal-Wallis test, $p = 0.1$).

Considering the threshold value of -31.5 ‰ for understory vegetation in modern times (Kohn, 2010), a 1.5‰ correction for the fossil-fuel effect (Freyer and Belacy, 1983; Leavitt and Long, 1982) and an enamel-diet 14.1‰ enrichment factor (ϵ^*) (Cerling and Harris, 1999), all $\delta^{13}\text{C}$ values (≥ -12.4 ‰) indicate the consumption of C_3 plants from open areas and no significant contribution of resources gathered in a closed forest environment on a seasonal scale (Fig. 4a).

5.3. Sequential $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ series

At Llo and Portal Viehl, the sequences of $\delta^{18}\text{O}$ values vary along tooth crown following a sinusoidal pattern, reflecting the seasonal cycle (Fig. 5). At Portal-Vielh, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values co-vary with a positive correlation (Fig. 6 and Table 3). In contrast, the sequential isotope profiles from Llo present a variety of patterns with shifted to opposite $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences (Figs. 5b and 6). Significant positive correlations between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are only observed in the Iberian ibex (Llo C pyr. 156) and in sheep Llo O 58 (Table 3 and Supplementary Material 7).

6. Discussion

6.1. The transhumance $\delta^{18}\text{O}$ signature in modern ewes

On this limited dataset of modern transhumant and sedentary ewes, the pattern of variation of $\delta^{18}\text{O}$ values on a seasonal scale does not seem to conform to the expected model. First, mobility up to 1500–2000 m in four ewes did not lead to lower summer $\delta^{18}\text{O}$ values compared to those measured in the ewe moving to 1300 m. This could be explained by differences in the types of water sources available for drinking (river vs seasonal ponds). This would suggest that, on a local scale, the pattern of decreasing $\delta^{18}\text{O}$ values with increasing altitude described in meteoric water is not always directly reflected in the $\delta^{18}\text{O}$ values of surface water and consequently does not always lead to a straightforward signature in tooth enamel. Furthermore, a transhumant pattern did not lead to reduction of the annual amplitude of variation, although the sedentary ewe used for comparison was raised in another valley, located further north. Further research involving more specimens from both transhumant and sedentary herds are needed to refine these points.

6.2. Interpretation of the archaeological datasets

The archaeological dataset from Llo is globally characterized by the following:

- (1) a lower range of $\delta^{18}\text{O}$ values compared to the lowlands dataset and great similarity regarding this criterion with the values measured in the modern mountain ewes located further west;
 - (2) similar $\delta^{13}\text{C}$ mid-point values compared to those measured at the lowlands sites but globally lower intra-tooth variation compared to the coastal sites;
 - (3) dissimilar patterns of co-variation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences to those observed in the lowlands areas, sometimes leading to opposed variations of the two signals;
 - (4) a higher inter-individual variability in the patterns of variations at the seasonal scale, possibly referring to higher inter-annual instability in environmental/climatic constraints.
- (1) Lower $\delta^{18}\text{O}$ values set the sheep herds from Llo in the mountain zone. From this criterion alone, a sedentary pattern at the site elevation may not be distinguished from vertical mobility within the mountain zone, for example, towards higher elevation pastures in the summer and/or lower elevations to escape the snow cover in winter.
 - (2) The inter-sites comparison shows overlapping $\delta^{13}\text{C}$ mid-point values with no gradient between coastal and high elevation sites. This suggests no significant altitude effect on plants $\delta^{13}\text{C}$ values in the study area, casting doubt on the usefulness of $\delta^{13}\text{C}$ values *per se* to highlight vertical mobility in this particular area. However, herding strategies could mask this effect. The significantly reduced amplitude of intra-tooth variation at Llo compared to the coastal sites may reflect adaptation to a high elevation zone and could be due to local vegetation dynamics, herding practices including mobility, or foddering (see below). Furthermore, the high inter-individual variability in this last criterion could suggest a great diversity of dietary patterns.

Fig. 4. a. Lowest and highest $\delta^{13}\text{C}$ values and mid-point values ((min + max)/2) of the annual cycle from individuals from Llo (Llo) and Portal-Vielh (PVV), compared to data from the late Neolithic sites of La Citadelle (CTD) and Martigues-Collet Redon (MCR) (* Blaise et al., 2006; 2010). The horizontal line represents the average expected $\delta^{13}\text{C}$ value for consumption of C_3 plants from open areas (Kohn, 2010). 4. b. Amplitude of intra-tooth variation in $\delta^{13}\text{C}$ values and mid-point values of the annual cycle in the archaeological assemblages. Data for Collet-Redon and La Citadelle from Blaise et al. (2006, 2010).

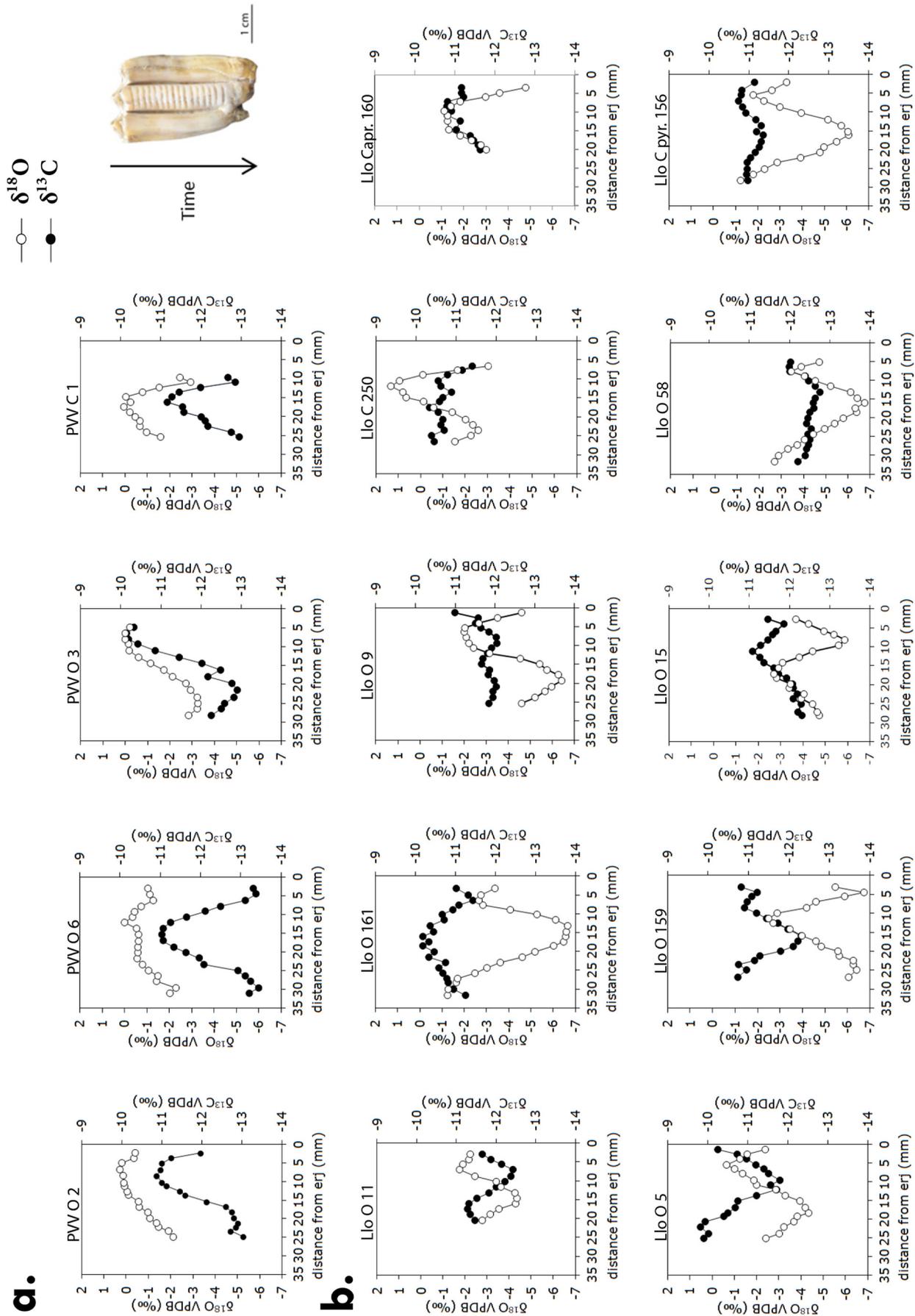


Fig. 5. Results from sequential $\delta^{18}\text{O}$ (white symbols) and $\delta^{13}\text{C}$ (black symbols) analysis in enamel bioapatite of the caprines molars (M_2 and M_3) from Portal-Vielh (a) and Llo (b). Samples are located in tooth crown using the distance from the enamel-root junction (ERJ) in mm.

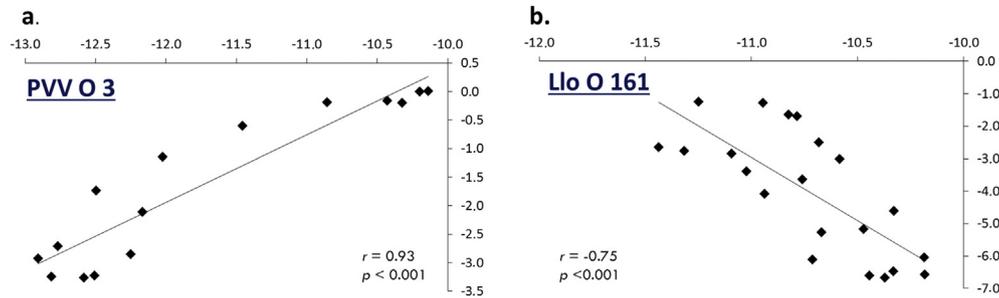


Fig. 6. Relationship between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values within intra-tooth sequential series a. Positive correlations are observed at Portal-Vielh: example for 'Pv O 3' (M_3). b. Negative correlations may be observed at Llo: example for 'Llo O 161' (M_3). Plots for all individuals are shown in supplementary data (Supp. Data 7).

Table 3

Statistical data of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ cycle: correlation coefficient (Pearson's r), degree of freedom (df), significance level (p). The significant results are in bold.

Sample	Pearson's r	df	p
Pvv O 2	0.91	15	<0.001
Pvv O 3	0.93	13	<0.001
Pvv O 6	0.79	17	<0.001
Pvv C 1	0.77	11	<0.01
Llo C pyr. 156	0.83	16	<0.001
Llo O 161	-0.75	19	<0.001
Llo O 58	0.56	18	<0.01
Llo O 5	-0.47	16	<0.05
Llo O 11	-0.54	11	>0.05
Llo O 159	-0.44	16	>0.05
Llo O 15	-0.12	17	>0.05
Llo O 9	0.08	16	>0.05
Llo C 250	0.22	13	>0.05

- (3) A positive correlation in the variations of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values on a seasonal scale is ordinarily observed in sequential datasets from caprines raised in middle latitude lowland areas of Europe (e.g., Balasse, et al., 2012, 2013, *in press*) and under Mediterranean climates in particular (e.g., Kasteelberg: Balasse et al., 2002; Collet-Redon and La Citadelle: Blaise et al., 2006, 2010; Blaise and Balasse, 2011; and Portal-Vielh, this study). This is explained by the natural trends of seasonal variation in C_3 plants $\delta^{13}\text{C}$ values, with higher values occurring during summer and lower values during winter (Smedley et al., 1991; Hartman and Danin, 2010). In mixed C_3/C_4 grassland, this seasonal trend may sometimes compound with a higher relative proportion of C_4 plants in summer. In some cases, the sequence of $\delta^{13}\text{C}$ values may be slightly shifted to reach maximum values later than $\delta^{18}\text{O}$ values. Foddering practices have been suggested as the cause when the co-variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values do not follow this global trend (Balasse et al., 2013).

At Llo, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences are not positively correlated, showing from a significant shift (Llo O 5; Llo O 15; Fig. 5) to opposition of the sequences in some individuals (Llo O 11, Llo O 161; Figs. 4 and 6). This could refer either to different growth dynamics for vegetation in the highlands compared to the lowlands, or it could result from interference due to herd management, possibly including altitudinal mobility or a seasonal contribution of fodder.

Opposite patterns of variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values have been observed in wild sheep (*Ovis orientalis gmelini*) remains from the Epigravetian site of Kalavan 1 in Armenia (Tornerio et al., 2016). Those were interpreted as reflecting vertical mobility towards high elevation alpine meadows in the summer and midlands to lowlands in the winter. The reason for this opposition could not be

ascertained, and two hypotheses were considered: (i) a higher relative proportion of C_4 plants in the lowlands would have created higher $\delta^{13}\text{C}$ values in winter, or (ii) a contribution of low $\delta^{18}\text{O}$ ice-melt water in high elevation sites would have lowered the $\delta^{18}\text{O}$ values in summer. The first explanation may not apply to this study, given the insignificant occurrence of C_4 plants in the area (as reflected in the $\delta^{13}\text{C}$ values measured even at the coastal sites). A reversal of the $\delta^{18}\text{O}$ cycle, *i.e.*, with lowest values occurring in summer and the highest in the winter, was also described in historic mountain sheep (*Ovis canadensis*) from central Utah (Fisher and Valentine, 2013). Although this hypothesis deserves careful consideration, it does not seem to apply to our study area. Indeed, the modern transhumant ewes born in late autumn do not show a reversed $\delta^{18}\text{O}$ cycle when compared to the sedentary ewe from the valley floor, born in the same season (Fig. 2).

Interestingly, the archaeological Iberian ibex Llo C pyr. 156 exhibited a positive correlation between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences (Pearson's r : 0.83, $p < 0.001$; Table 3 and Supplementary Material 7). Currently, this wild species is known to move seasonally over a large altitudinal range, between high altitudinal zones in summer and lower mountain range in winter due both to the snow cover and human pressure (Couturier, 1962). This would suggest that a pattern of vertical mobility in this area is not necessarily reflected in opposite variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values, although using one annual trajectory of one individual precludes formulating definite conclusions. The closest pattern observed in the domestic caprines from Llo is the one measured the sheep Llo O 58, with positive correlation between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences (Pearson's r : 0.58, $p < 0.01$; Table 3 and Supplementary Material 7) but significantly lower $\delta^{13}\text{C}$ values compared to the wild ibex (Llo O 58 vs Llo C pyr. 156 Tukey's pairwise test: $p < 0.0001$). Although the wild caprines are only represented by one individual in this sample, none of the domestic caprines from Llo delivered stable isotope patterns resembling this specimen, suggesting that seasonal pathways followed by the domestic herds may have been to some extent different from the wild ones. It is difficult to make any conclusions about the altitudinal mobility of the livestock at Llo.

Considering the possibility that the inhabitants lived in the settlement all year, feeding the livestock over the winter would probably have required specific efforts on diet management. Forest grazing and tree leaf foddering are both reported in recent history from Norway to the Mediterranean area (Brockmann-Jerosch, 1936; Hédin, 1967; Salvi, 1982; Austad, 1988; Magnier, 1991). Archaeobotanical analysis (phytoliths, pollen, charcoal and vegetal macroremains) in rock shelters from the circum alpine, alpine and Mediterranean areas highlighted leafy foddering from the middle Neolithic (Rasmussen, 1989, 1993; Haas and Rasmussen, 1993; Brochier and Claustre, 1994; Halstead and Tierney, 1998; Thiébaud, 2005; Delhon et al., 2008; Martin et al., 2011). At Llo, the use of tree leaves or understory plants (less exposed to the

snow cover) to feed the small stock in winter/springtime could have been an alternative to grazing at this elevation where snowfall may currently occur over six months. However, the $\delta^{13}\text{C}$ values do not indicate any significant consumption of plants from closed forests. The degree of opening of the forest cover in the surroundings of the site during Bronze Age (Bal, 2006) could also make it more difficult to evidence this practice from $\delta^{13}\text{C}$ values.

Alternatively, the constitution of hay preserves during summer could also have facilitated winter foddering. Fodder could have been harvested in summer from the terraces adjoining the settlement (Ruas and Bouby, 2009) or even from slopes—terraced or not—at higher altitudes in the neighbouring mountain (Rendu, 2003; Bal, 2006). Furthermore, hay crops located in the valley may also have provided fodder reserves during Bronze Age (Bal, 2006). If livestock were supplied with this fodder in late autumn and throughout winter, it would create a rupture in the expected seasonal trend in the $\delta^{13}\text{C}$ sequential series. This scenario might explain the pattern observed in Llo O 9 and Llo O 58, where $\delta^{13}\text{C}$ values have moderate annual amplitudes of variation.

At Llo, the diversity of the profiles could reflect high adaptability of husbandry strategies in a mountainous context characterized by important inter-annual variation in climate with direct consequences for the availability of pastures on a seasonal scale. Different strategies could have been adopted to cope with this instability at the inter-annual scale, including changes in mobility patterns. Some archaeological artefacts from the Middle Bronze Age occupation of Llo reflect exogenous influence, notably from the Italic sphere (thumb handles), suggesting that the settlement was integrated in a large Mediterranean cultural dynamic (Campmajo and Cabrol, 1990; 1991; Carozza et al., 2005; Galop et al., 2007). Moreover, the cultivated plant remains and pottery findings suggest some affinity with cultural aspects of the Catalan hinterlands (Segre and Cinca valleys) (Campmajo, 1983; Gasco et al., 1996; Alonso i Martinez, 1999; 2008; Ruas and Bouby, 2009). Livestock exchanges between those communities could have occurred, driven by social and economic causes including strategies aiming at diversifying and/or renewing the livestock. Despite this, none of the specimens analysed at Llo had profiles resembling those measured in lowlands plains, characterized by higher $\delta^{18}\text{O}$ values and a positively correlated variation in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences. The goat Llo C 250 yielded significantly higher $\delta^{18}\text{O}$ values compared to all other individuals (Fig. 3a&b). *A priori*, no physiological reason could explain such differences between sheep and goat; for example, the $\delta^{18}\text{O}$ values of sheep and goats from Le Collet-Redon are very similar to each other (Blaise et al., 2006; 2010; Blaise and Balasse, 2011). Goats are also known to be much more mobile than sheep because of their rustic and adaptable nature (Fernández et al., 2006). However, the absence of a positive correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences (Fig. 5) precludes a firm identification of a lowland origin for this goat.

At Portal-Vielh, the range of variation of $\delta^{18}\text{O}$ values and a positive correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences similar to those previously observed at Collet-Redon and La Citadelle (Blaise et al., 2006; 2010; Blaise and Balasse, 2011 and Fig. 3a) set this site in the lowland group with no incursion in the mountain zone. This supports the hypothesis that herding strategies did not include vertical mobility at Portal-Vielh. Still, the semi-sedentary model proposed by Py (1990, 1993) cannot be totally ruled out. Stable oxygen isotope values measured in the caprines from La Citadelle, located at 50 km from the sea, further east in the hinterland of Marseille, do not significantly differ from those measured at Portal-Vielh. At the moment, no $\delta^{18}\text{O}$ data is available to characterize the hinterland Languedoc. Therefore, the livestock may have moved seasonally, even to a long distance but would not have gone higher up in the mountain area.

7. Conclusion

The results from this study clearly set the caprines from Llo apart from the lowlands archaeological caprines herds based on the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures, while a great similarity is observed with modern ewes raised in the mountain. Adaptation to mountain zones was reflected in lower enamel bioapatite $\delta^{18}\text{O}$ values compared to lowlands locations, confirming an expected pattern. It did not induce higher $\delta^{13}\text{C}$ values, suggesting that the global pattern of increasing $\delta^{13}\text{C}$ values in C_3 plants with increasing altitude does not apply significantly in this area of the French Eastern Pyrenees or is not directly reflected in caprines' tooth profiles due to animal behaviour and human intervention in feeding practices.

On the infra-annual scale, the intra-tooth $\delta^{13}\text{C}$ sequences reveal very informative when combined with $\delta^{18}\text{O}$ sequences. At Llo, where the positive correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences measured in all instances at low elevation sites was not the leading pattern, shifts to opposite $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences could be observed instead. This opposition could not be explained by a reversal of the $\delta^{18}\text{O}$ cycle due to vertical mobility towards higher elevation in summertime: indeed, transhumant ewes did not show reversed $\delta^{18}\text{O}$ cycles compared to a sedentary ewe born in the same season. If the $\delta^{18}\text{O}$ cycle varied seasonally with similar trends to those in lowland locations, then the observed reversal might have rather occurred in the pattern of variation of $\delta^{13}\text{C}$ values. Ruptures or differences in the expected natural seasonal variation in plants $\delta^{13}\text{C}$ could be caused by different vegetation growth dynamics in higher elevation zones, vertical mobility and/or bad season foddering with plants collected at the growing season. Human intervention in the feeding strategies was also evoked to explain the significantly reduced amplitude of intra-tooth variation in $\delta^{13}\text{C}$ values observed at Llo compared to lowlands sites. In this regard, the Llo dataset was also characterized by a high inter-individual variability in the co-variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles, potentially reflecting greater plasticity of the husbandry practices in mountain zones. Mountainous zones are traditionally considered marginal and risky; this study helps to define human adaptability to these constraining environments. A key element to this adaptability could be a great plasticity in herding practices involving different feeding and mobility strategies on the inter-annual scale.

This study addresses the broader issue of the occupation of territories by Bronze Age communities in the western Mediterranean area (France-Spain) (Carozza et al., 2005). No exogenous origin for domestic caprines could be clearly revealed at Llo, as far as the Mediterranean lowlands are concerned. While caprine herding at Llo seems fully settled in the mountain whereas Portal-Vielh delivered a fully lowland signal, the apparent disjunction between the coastal and mountain settlements, as far as herds' trajectories are concerned, must be reaffirmed by further investigations in a larger number of sites.

At Llo, full adaptation to a mountain environment seems clear, but the question of the vertical mobility of the livestock cannot be resolved at the moment. In particular, the opposed variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles still needs to be investigated to understand more precisely whether it specifically indicates herding practices including vertical mobility *per se* or a specificity of the mountain environment signal. It is striking to note that the only representative of wild caprines at Llo did not deliver this pattern of opposition of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals. Further research is needed, including studies of a larger number of wild herbivores with known vertical trajectories and sedentary caprines in mountain environments, focusing both on the amplitude of variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values and their co-variation.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2017.05.029>.

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