



Evidence for Marine Consumption During the Upper Palaeolithic at “El Pirulejo” Inland Rock-Shelter (Southern Iberia Peninsula, Spain)

RESEARCH PAPER

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ABSTRACT

During the Last Glacial Maximum and deglaciation, the Iberian Peninsula served as a faunal and human population refugium. Human foodways have always played a pivotal role in understanding social and cultural practices in prehistory. Nonetheless, the limited number of archaeological sites and human remains in this region hinders the complete understanding of these critical communities' diet.

To increase our knowledge about human consumption patterns, we selected three Magdalenian levels from the site of El Pirulejo (Southern Iberia Peninsula, Spain). These levels are characterized by a high abundance of rabbit (*Oryctolagus cuniculus*) remains (76–97% MNI), initially suggesting that rabbits were the primary source of protein for site inhabitants. Stable isotope analysis was conducted on two human teeth in tandem with stable isotope analysis of the rabbit teeth. Contrary to the expectations derived from the zooarchaeological analysis, rabbits were not a significant source of dietary protein. Carbon and nitrogen bulk isotopic values are the most enriched found in sampled human remains for this area and context.

Our data supports aquatic food resource inclusion and increased resource diversity among Iberian hunter-gatherers during the Magdalenian. This study is consistent with previous studies that suggested a socio-economic network among human groups between inland and coastal regions in the terminal Pleistocene Southern Iberia.

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1. INTRODUCTION

The Iberian Peninsula served as a faunal and human refugium during the Last Glacial Maximum when vast areas of the European continent were covered by ice (Bhagwat & Willis 2008; Finlayson & Carrión 2007; Holt 2003; Stewart & Stringer 2012). The transition between the extreme cold Heinrich stadial 1 (H1) (17.9 to 15.7 cal kyr BP) to the abrupt warming during the Bølling-Allerød interstadial (B-A) (~15.7 cal kyr BP) (Camuera et al. 2021), with an estimated increase in sea surface temperatures of ~10°C (Morcillo-Montalbá et al. 2021), witnessed the last significant genetic population bottleneck in Eurasian prehistory until the Neolithic (Morin 2008; Pardiñas et al. 2012; Fu et al. 2016). Despite the impact of this transition on human populations, little is known about these communities' diets due to the low number of archaeological sites.

The consistent and methodological exploitation of marine resources by hominins is usually attributed to the appearance of anatomically modern humans in Africa's coastal environments (Manne & Bicho 2011; Manne et al. 2012). However, a rapid increase in the exploitation of marine resources occurs from the Final

Upper Palaeolithic and in context of hunter-gatherers of the Holocene (Gutiérrez 2008, Cortés-Sánchez et al. 2020) evinced by the increase in the number of sites with considerable marine consumption evidence. While populations in coastal sites along North Iberia during the Upper Palaeolithic exploited freshwater fish (Adan et al. 2009), there is a dearth of records for the Upper Palaeolithic in South Iberia along the Mediterranean coast, especially inland (Cortés-Sánchez et al. 2020; Román et al. 2022). Present data indicate that the exploitation of freshwater and marine aquatic food resources across the southwestern coastal Mediterranean region intensified prominently between the Solutrean (c. 21–16 kyr) and the Magdalenian periods (c. 16–10 kyr) and even more so in later periods (Cortés-Sánchez et al. 2008). However, despite a substantial increase in archaeological studies and increased use of novel analytical methods, direct evidence of human food-ways in Southern Iberia Upper Palaeolithic (UP) are still sporadic.

To increase our knowledge about Upper Palaeolithic communities during the H1 to B-A transition, we selected the rock-shelter site of El Pirulejo (southern Iberia, Spain; [Figure 1](#)). This site sequence has been dated from the last deglaciation to Bronze Age (Cortés-Sánchez et al.

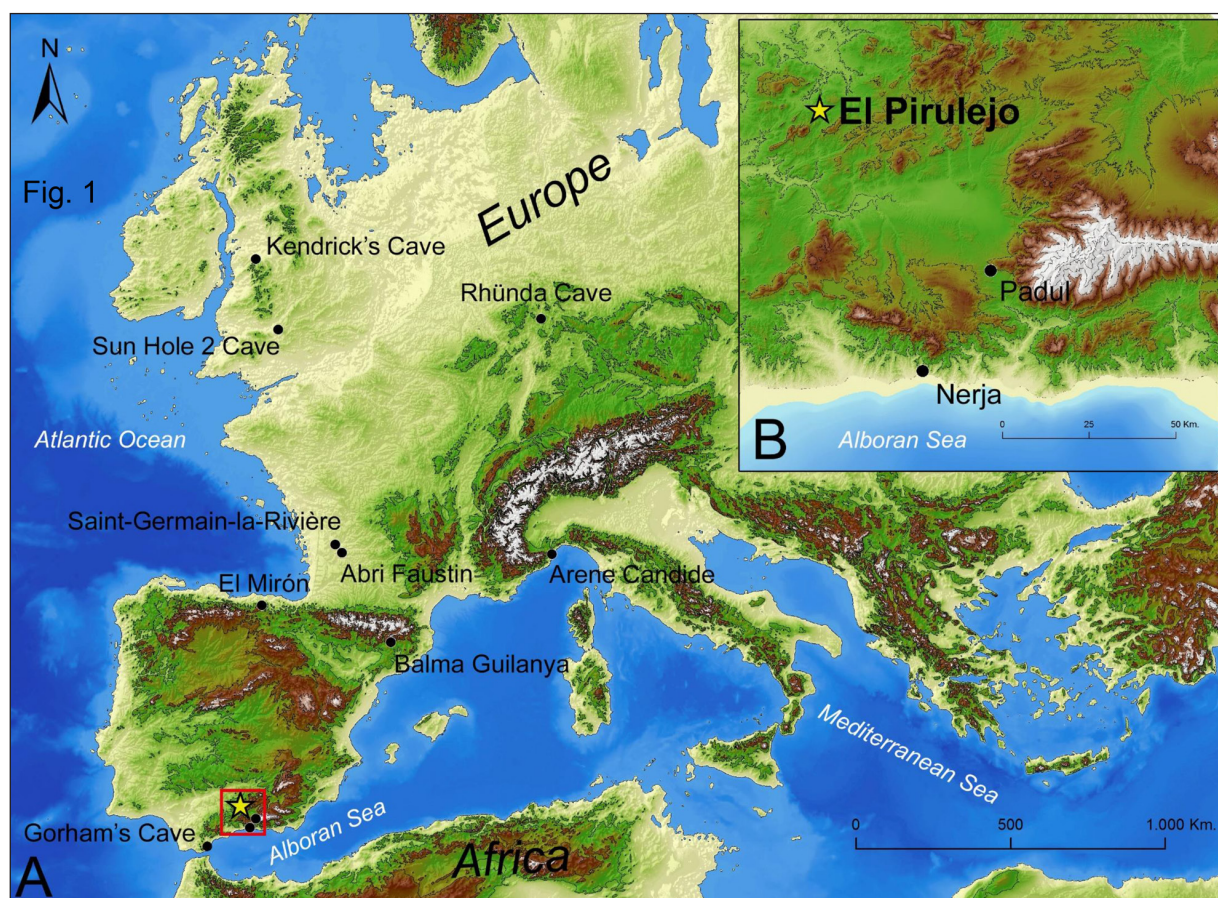


Figure 1 A) Selected archaeological and paleoclimatic records discussed in this study in Western Europe and Africa; **B)** the insert includes the study location around El Pirulejo rock-shelter. Map reconstruction with the coastline at -75 m below sea level, including elevations (contours every 500 m) consistent with the conditions of the B-A period although European permafrost and ice sheets are not shown. Base map from NOAA National Geophysical Data Center. 2009: ETOPO1 1 Arc-Minute Global Relief Model, NOAA National Centers for Environmental Information. Data obtained from reproduced from Ehlers et al. 2011.

2014; Monge et al. 2015). A ^{14}C on charcoal (Poz-22164) yielded dates of $14,250 \pm 90$ uncal yr BP or 17,130–17,414 cal yr BP (Cortés-Sánchez et al. 2014). The deposits of El Pirulejo contain abundant faunal remains (e.g. Cortés-Sánchez et al. 2017), lithic assemblages, and human remains, providing an exceptional opportunity for investigating human subsistence and behavior in westernmost Europe during the terminal Pleistocene. Two human teeth, identified as *Homo sapiens*, found at the site (archaeological level P/2) were analyzed using stable isotope methods to study human subsistence during the Magdalenian period. Rabbits (*Oryctolagus cuniculus*), the most abundant faunal taxa throughout Upper Palaeolithic at El Pirulejo (76 to 97% MNI; Cortés-Sánchez et al. 2014), were sampled in comparison with the human teeth to test whether they constituted the largest source of protein and to explore their use as an indicator of past vegetation (Wicks et al. 2015).

2. MATERIALS AND METHODS

2.1. MATERIALS

The site of El Pirulejo (Priego de Córdoba, Spain), was discovered in 1988 and excavated by MD Asquerino. It is located within the municipality of Priego de Córdoba (Córdoba, Spain) in the Andalusian Subbaetic mountains 580m a.s.l. ($37^{\circ}26'32''\text{N}$, $4^{\circ}11'15''\text{W}$). The site is located >80 km from the nearest Mediterranean seashore. An isolated human tooth and skull were found in level P/4 corresponding to the middle Magdalenian period. A radiocarbon date on charcoal from the same level suggested a date of $17,458 \pm 257$ cal yr BP (Cortés-Sánchez et al. 2014). This level also yielded symbolic objects, ochre, personal ornaments, and Palaeolithic

mobile art such as semi-cylindrical rods with an incised motif. A high Pb level, the presence of galena mineral possibly used as a pigment in the cave sediment, and fossil elephant molars tainted with a composite pigment suggest the symbolic activity of humans living in this cave (Monge et al. 2015; Cortés-Sánchez et al. 2017).

For this study, we selected two human teeth identified as a right upper lateral incisor and a deciduous canine from level P/2 (Figure 2). Rabbit teeth were obtained from levels P/6, P/5, P/4, and P/2 corresponding to the indeterminate Upper Palaeolithic (P/6–P/5) and the Magdalenian (P/4–P/2) periods. The rabbit teeth positions are shown in Table 1.

Taxonomy

Faunal taxonomic and anatomical identifications were conducted using morphological and metric comparison with specimens from collections of modern fauna held at the University of Córdoba (Spain) and The University of Tulsa (USA).

2.2. COLLAGEN EXTRACTION

Collagen was extracted from the dentine of two human teeth and five mandible bones of rabbits from the same level (P/2) according to Sealy et al. (2014) with the addition of an ultrafiltration step (Bocherens et al. 1997). Around 0.1 g of the human tooth roots were cut and surface-cleaned with a handheld drill to remove surface contamination. The chunk was washed with distilled water (DW) for 5 min in an ultrasonic bath, rinsed, washed with acetone for 5 min, rinsed, and washed again with distilled water for 5 min. The dried chunk was weighed and placed in a glass vial with 0.2 M HCl at room temperature. The acid was repeatedly replaced



Figure 2 Permanent right upper lateral incisor (left) and a lower deciduous canine (right) from El Pirulejo, Spain (Layer P/2). For the upper incisor the left photo is the distal view and the right side in the mesial view. For the lower canine, the left photo is the mesial view and the left side is the distal view.

Table 1 Carbon and nitrogen isotopic composition and ^{14}C date of the human tooth and rabbit bones from El Pirulejo and list of AMS ^{14}C dates obtained in this site.

[†]Weight percent of > 3k Da fraction of the extracted organic matter from whole bone samples. ^{††}AMS dates have been calibrated using Oxcal v4.4.3 (Bronk Ramsey, 2009). Atmospheric calibration data from Reimer et al. (2020).

SPECIES	LEVEL	%C COLLAGEN	%N COLLAGEN	C:N ATOM	YIELD (%) [†]	$\delta^{13}\text{C}$ VPDB (‰)	$\delta^{15}\text{N}$ AIR (‰)	^{14}C AGE (UNCAL YR BP $\pm 1\sigma$)	^{14}C AGE (CAL YR BP $\pm 1\sigma$) ^{††}	LAB. ID
Homo	P/2	35.0	11.6	3.5	3.1	-18.4	13.2	12,615 \pm 45	14,965-15,115	PLD-36293
Homo	P/2	43.4	15.5	3.3	5.6	-18.7	12.4	13,800 \pm 40	16,641-16,856	Beta-580894
<i>Oryctolagus cuniculus</i>	P/2	41.6	14.7	3.3	3.6	-21.3	3.4	13,498 \pm 41	16,201-16,345	PLD-39291
<i>Oryctolagus cuniculus</i>	P/2	41.8	14.8	3.3	2.8	-20.6	4.3	13,568 \pm 43	16,290-16,455	PLD-39292
<i>Oryctolagus cuniculus</i>	P/2	42.7	14.9	3.3	1.2	-20.4	4.8	-	-	-
<i>Oryctolagus cuniculus</i>	P/2	43.6	15.4	3.3	2.1	-20.6	6.3	-	-	-
<i>Oryctolagus cuniculus</i>	P/2	43.0	15.3	3.3	4.5	-20.6	3.4	-	-	-
<i>Oryctolagus cuniculus</i>	P/4A	42.8	15.2	3.3	0.4	-20.7	2.9	-	-	-
<i>Oryctolagus cuniculus</i>	P/4D	43.3	15.3	3.3	0.9	-20.9	3.6	-	-	-
<i>Oryctolagus cuniculus</i>	P/4	41.1	14.0	3.4	0.6	-21.0	4.5	-	-	-
<i>Oryctolagus cuniculus</i>	P/6	42.5	15.0	3.3	1.0	-20.9	3.1	-	-	-

until the chunk yielded a ‘pseudomorph’ translucent and flexible appearance. Samples were rinsed three times in distilled water, then treated for 24 h in 0.1 M NaOH to remove base-soluble contaminants, such as humic acids and some lipids. The sample was then soaked in distilled water for several days (changed regularly) until the liquid’s pH reached a neutral value. The chunk was gelatinized at 100°C for 17h, and the liquid part was filtrated with a glass filter and ultrafiltration filter (Vivaspin® Turbo 15 or Vivaspin® 20; Sartorius AG) with a cut-off molecular size of 3k Da.

All samples were frozen at –20°C for the final freeze-drying step. A yield (%) of organic matter (≈collagen) was calculated as the weight of the organic matter as a percentage of the weight of the original bone/dentine tissues.

2.3. RADIOCARBON DATING

About 2 mg of collagen, containing ~0.9 mg of carbon, were oxidized to CO₂ inside evacuated tubes with copper dioxide, and CO₂ was cryogenically purified in a vacuum system. The CO₂ was reduced to graphite using hydrogen with iron powder catalysis. The mixture of graphite and iron powder was measured for radiocarbon content by AMS at the BETA laboratories (Florida, USA), and Paleolab Co, Ltd. (Japan). AMS dates have been calibrated using Oxcal v4.4.3 software (Bronk Ramsey 2009) and atmospheric calibration data from Reimer et al. (2020).

2.4. COLLAGEN CARBON AND NITROGEN ISOTOPE ANALYSIS

The dentine collagen was combusted to CO₂ and N₂ gases, and δ¹³C and δ¹⁵N values were measured in a Flash EA1112 automated elemental analyzer coupled with a ThermoScientific™ DELTA V™ Isotope Ratio Mass Spectrometer at Nagoya University. Isotopic compositions are conventionally expressed as follows (Coplen, 2011): δ(‰) ≡ 10³ [R_{sample}/R_{standard} – 1], where the R denotes the ¹³C/¹²C ratio for carbon, the ¹⁵N/¹⁴N ratio for nitrogen, with the international reference (standards) being VPDB for δ¹³C and atmospheric nitrogen (AIR) for δ¹⁵N values. We estimated the uncertainty of each measurement using the standard deviations of the standard internal materials (L-Alanine, L-Histidine and L-Glycine with –19.6, –10.7 and –33.8‰ for δ¹³C vs. VPDB, respectively and three types of L-Alanine with 1.6, 9.97, and –20.6‰ for δ¹⁵N vs. AIR, respectively) for three replicates analyzed together with the unknown samples. Results suggest that our uncertainty level is lower than ±0.15‰ for δ¹³C and ±0.40‰ for δ¹⁵N.

It may be argued that δ¹⁵N values from sampled dentin may be affected by breastfeeding because they are formed during the early stage of life and not remodeled after formation (Fogel, Tuross, & Owsley 1989). Breastfeeding is believed to have a trophic level effect; namely, breastmilk is a higher trophic level than

food consumed as an adult, leading to a more enriched δ¹⁵N value of collagen in infants. However, we sampled the dentine below the tooth crown. According to Alqahtani, Hextor & Liversidge (2010), this part of the permanent incisor is only formed between 3.5 to 6.5 years of age. The average weaning age in hunter-gatherer human societies is 3.5 years after birth (Sellen & Smay, 2001). Thus, although the estimation of breastfeeding duration for any Palaeolithic population is speculative, we argue that the observed δ¹⁵N value of the permanent tooth in our study was not significantly affected by this practice. However, this is not the case for the deciduous canine. The root of this tooth is formed between 1.5 and 2.5 years old; thus, its δ¹⁵N value may have been affected by the trophic level effect.

2.5. CARBON AND OXYGEN ISOTOPE ANALYSIS ON TOOTH ENAMEL CARBONATES

Enamel sampling was performed by drilling 2.7–6.7 mg of powder for rabbit teeth, 10.7 mg for the permanent human tooth and 2.4 mg for the deciduous human teeth using a handheld drill. Human teeth were sampled from the labial side of the upper lateral incisor and the buccal side of the deciduous canine. Due to the small amount of enamel available on each rabbit tooth, enamel of one to three teeth for each rabbit were aggregated. The collected powder was treated with minor modifications from Koch, Tuross & Fogel (1997). The powder was soaked in 2.5% sodium hypochlorite (NaOCl) for 24 h to remove organics. The NaOCl was then decanted, and the enamel powder was rinsed with distilled water and soaked in 0.1 M acetic acid for another 24 h to remove diagenetic carbonates. The acetic acid was then decanted, and the powder was rinsed with distilled water and oven-dried at 35°C for three days.

The carbon and oxygen isotopic compositions were measured with a ThermoScientific™ DELTA V™ Isotope Ratio Mass Spectrometer with an attached Gasbench. The measurement uncertainty was calculated using the standard deviation of the standard three replicate values (IAEA-CO-1 was +2.49‰ for δ¹³C vs. VPDB and –2.4‰ for δ¹⁸O vs. VPDB). Results suggest that the uncertainty of our samples are lower than ±0.2‰ for δ¹³C and ±0.3‰ for δ¹⁸O.

A one-way analysis of variance (ANOVA) followed by a Tukey’s HSD post hoc analysis was carried out on rabbit teeth isotope values to investigate significant differences among archaeological levels.

3. RESULTS

The human teeth dentine collagen had a C:N atomic ratio of 3.5, %C of 35.0%, and %N values of 11.6% for the permanent tooth, while the C:N atomic ratio was 3.3, %C of 43.3%, and %N values of 15.5% for the deciduous

tooth (**Table 1**). These isotope values are within the range obtained from fresh bone collagen (Ambrose 1990).

Four new radiocarbon dates have been obtained for this study (**Table 1**). The AMS dating on the human dentine collagen yielded ^{14}C ages of $12,615 \pm 45$ yr uncal BP for the permanent tooth ($14,965\text{--}15,115$ cal yr BP) and $13,000 \pm 40$ yr uncal BP for the deciduous tooth corresponding to the Middle Magdalenian period dated to $16,641\text{--}16,856$ cal yr BP (**Table 1**). The bone collagen of two rabbits from level P/2 yielded similar ^{14}C dates, albeit slightly older (>0.3 ka) than the date of the permanent tooth ($13,498 \pm 41$ and $13,568 \pm 43$ uncal yr BP, calibrated to 16.2 cal kyr BP (**Table 1**).

Human dentine collagen yielded $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of -18.4 and 13.2‰ for the permanent, and -18.7 and 12.4‰ for the deciduous tooth, respectively. Nine rabbit bone samples yielded bone collagen $\delta^{13}\text{C}$ values ranging from -20.4 to -21.3‰ and $\delta^{15}\text{N}$ values from 2.9 to 6.3‰ .

Tooth enamel carbonate samples for the human teeth had $\delta^{13}\text{C}$ values of -13.6 and -13.1‰ (**Table 2**). The rabbit teeth from the same level (P/2) showed $\delta^{13}\text{C}$ values of $-12.9 \pm 0.6\text{‰}$ ($n = 5$) while those from level P/4, P/5 and P/6 had $\delta^{13}\text{C}$ values of $-13.5 \pm 0.6\text{‰}$ ($n = 4$), $-12.2 \pm 0.4\text{‰}$ ($n = 4$), and $-12.8 \pm 0.6\text{‰}$ ($n = 5$), respectively. These $\delta^{13}\text{C}$ values differed significantly among the stratigraphic levels (one-way ANOVA $df = 3$, $F = 3.58$, $P < 0.05$), and particularly between levels P/4 and P/5 ($P < 0.05$).

The $\delta^{18}\text{O}$ values of the human teeth (-4.1 and -2.5‰) were lower than the rabbit values ($0.2 \pm 2.5\text{‰}$ to $2.5 \pm 4.0\text{‰}$). The $\delta^{13}\text{C}$ rabbit tooth values differ among levels, but the $\delta^{18}\text{O}$ values do not.

4. DISCUSSION

4.1. CARBON AND NITROGEN ISOTOPE ANALYSIS ON COLLAGEN

The zooarchaeological record suggests that rabbits were the most abundant prey fauna throughout levels P/5 to P/2 (76 to 97% as MNI; Cortés-Sánchez et al. 2014). The cut marks, fractures, and burning of rabbit bones are like those described in other Iberian Peninsula Mediterranean sites such as Nerja and Gorham's Cave (Pérez Ripoll 1992; Riquelme et al. 2008) which have been attributed to consumption by humans suggesting a similar taphonomic

pathway. However, the difference between $\delta^{15}\text{N}$ values of the human teeth and rabbit bones is higher than the common prey-predator offset in bulk collagen $\delta^{15}\text{N}$ value estimated at 3 to 5‰ (Bocherens & Drucker 2003). If humans mainly consumed rabbits, we would expect the nitrogen values of the analysed human remains to be enriched in the range of 5.9–11.3‰. Therefore, we argue that rabbits, albeit abundant in the zooarchaeological record, were not the most significant source of protein in the human diet, at least for these individuals. While not a dietary source, rabbits may have been a crucial resource for bone tools (Aura et al. 2016) or for fur, although direct evidence for these types of utilization have not been found at El Pirulejo.

Moreover, we argue that the high $\delta^{15}\text{N}$ value of the El Pirulejo humans cannot be solely attributed to the consumption of other terrestrial animals with high $\delta^{15}\text{N}$ values. The range of nitrogen isotope values of the human teeth are much higher than the aggregated values of terrestrial game in the Iberian Peninsula derived from the literature (**Figure 3**). Terrestrial herbivores, with high $\delta^{15}\text{N}$, include mammoth or reindeer, as well as carnivores such as lynx and bobcat (Bocherens et al. 2015). At El Pirulejo, there is no zooarchaeological evidence for the consumption of large herbivores (Cortés-Sánchez et al. 2014). Indeed, reindeer are absent in the Southern Iberian record, and mammoths are rarely associated with extreme cold periods (Álvarez-Lao & García 2012). Moreover, the extinction of the last mammoth in the Iberian Peninsula has been dated to 19 to 21 ka, which predates the site itself (Puzachenko et al. 2017). Indeed, in this study, the nine rabbit specimens analyzed showed low $\delta^{15}\text{N}$ values similar to the values of Magdalenian red deer from Northern (García-Guixé et al. 2009) and Eastern Iberia (Stevens et al. 2014) which had mean $\delta^{15}\text{N}$ values $\sim 3\text{‰}$ (see ellipses area in **Figure 3**).

Furthermore, *Carnivora* remains are scarce in the El Pirulejo record, with an average MNI percentage of $<1\%$ of the fauna (**Table 3**). Therefore, the consumption of carnivores cannot account for the elevated $\delta^{15}\text{N}$ of the human teeth. One rabbit specimen did have a $\delta^{15}\text{N}$ value of 6.3‰ , higher than many contemporaneous herbivorous mammals in Iberia (García-Guixé et al. 2009; Stevens et al. 2014). However, these levels are on

SPECIES	LEVEL	N	$\delta^{13}\text{C}$ VPDB (‰)	$\delta^{18}\text{O}$ VPDB (‰)
<i>Homo</i> (permanent tooth)	P/2	1	-13.6	-4.1
<i>Homo</i> (deciduous tooth)	P/2	1	-13.1	-2.5
<i>Oryctolagus cuniculus</i>	P/2	5	-12.9 ± 0.6	0.2 ± 2.5
<i>Oryctolagus cuniculus</i>	P/4	4	-13.5 ± 0.6	0.2 ± 2.5
<i>Oryctolagus cuniculus</i>	P/5	4	-12.2 ± 0.4	2.5 ± 4.0
<i>Oryctolagus cuniculus</i>	P/6	5	-12.8 ± 0.6	0.6 ± 1.6

Table 2 Carbon and oxygen isotopic composition of tooth enamel for the El Pirulejo humans and rabbits.

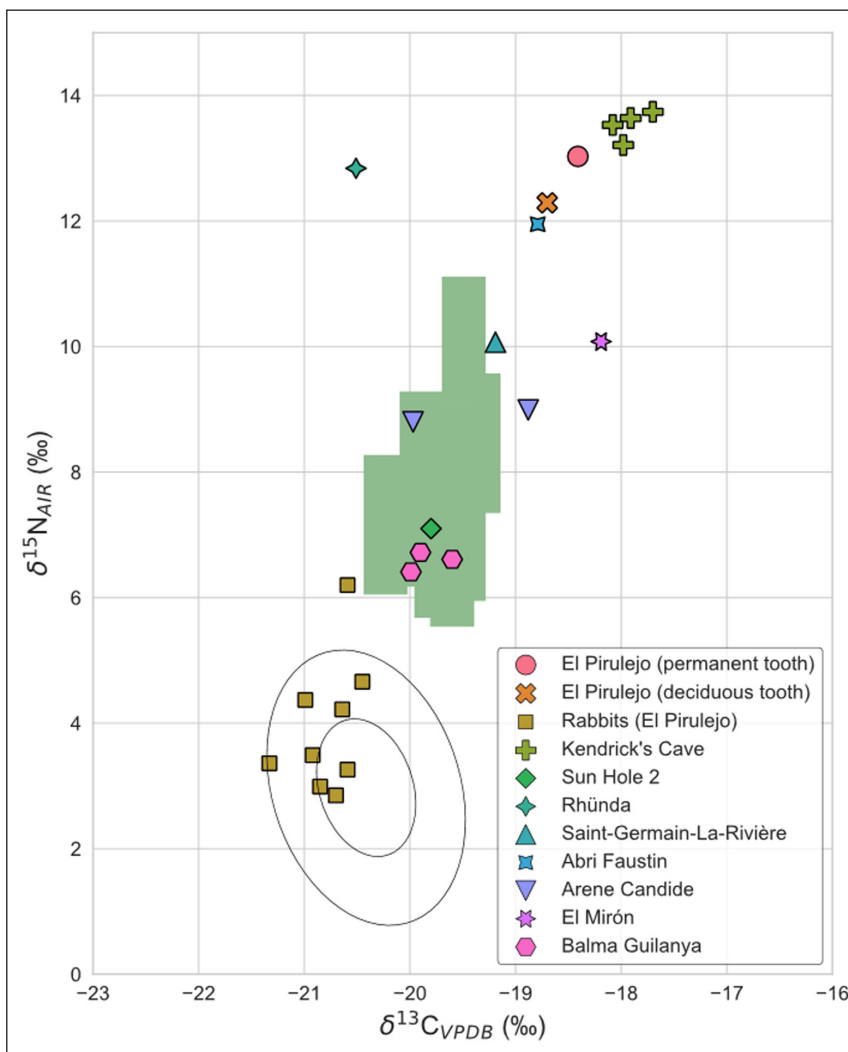


Figure 3 Carbon and nitrogen isotopic composition of the El Pirulejo (EIP) humans and rabbits and human remains from other sites of terminal Pleistocene Europe. Ellipses represent 99% and 95% of confidence intervals for isotope values observed for red deer, wild goat, and wild rabbit (n = 99 in total) in the initial Magdalenian to Azilian Iberian Peninsula (García-Guixé et al. 2009; Stevens et al. 2014). The colored area represents estimated 2 ranges of isotope values for human diets calculated based on the observed prey-predator enrichment factors for rabbits' bulk collagen (1.1 ± 0.2 for $\delta^{13}C$ and $3.8 \pm 1.1\text{‰}$ for $\delta^{15}N$) (Bocherens et al, 2015).

SPECIES	P/2			P/3			P/4		
	NR	%	NISP	NR	%	NISP	NR	%	NISP
<i>Lynx pardina</i>	3	0.19	1	2	0.04	1	1	0.01	1
<i>Felis sylvestris</i>	-	-	-	-	-	-	2	0.03	1
<i>Vulpes vulpes</i>	-	-	-	-	-	-	1	0.01	1
<i>Mustela nivalis</i>	-	-	-	1	0.02	1	-	-	-
<i>Carnivora sp.</i>	-	-	-	1	0.02	1	2	0.03	1

Table 3 Carnivora remains at El Pirulejo organized by archaeological levels. NR: Number of Rest. NISP: Number of Individual Specimens.

par with the high $\delta^{15}N$ values of herbivores reported at the Gravettian site of Serinyà caves (Drucker et al. 2021; Villalba-Mouco et al. 2018) or may be attributed to a high N availability in the environment (Craine et al. 2009), which is a factor determining plant $\delta^{15}N$ values.

We suggest that the $\delta^{13}C$ and $\delta^{15}N$ values for El Pirulejo human teeth support the use of aquatic food resources as a staple food in the diet of the inhabitant of the cave (Schoeninger & Moore 1992; Tauber 1981). Values for $\delta^{13}C$ and $\delta^{15}N$ of the El Pirulejo human teeth are among

the most enriched values among contemporaneous human remains in Western Europe dated between 18–12 ka (Bietti 1987; Drucker et al. 2016; Drucker, Henry-Gambier & Lenoir 2005; García-González et al. 2015; García-Guixé et al. 2009; Richards et al. 2005). Indeed, the most comparable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to those of El Pirulejo are those from the human remains from Kendrick's Cave, UK, dated to ~12 kyr BP (–17.7 – –18.1‰ and 13.4–13.9‰, respectively) interpreted as a signal of marine food consumption (Richards et al. 2005). Similarly, we argue that the diet of human occupants of El Pirulejo, as in Kendrick's cave, included a combination of terrestrial with aquatic dietary resources. A socio-economic network between inland and coastal regions during the terminal Pleistocene Southern Iberia is also evinced in ornaments made on fluvial or marine mollusks present at the site (Asquerino, 1992; Cortés-Sánchez et al. 2014). Aquatic resources may be freshwater in origin or anadromous fish, which while marine, are harvested in rivers (Bocherens & Drucker 2006).

The quantitative estimation of aquatic food consumption is challenging when local baseline isotope values for the resources are unknown (Dufour, Bocherens, & Mariotti 1999; Rey et al. 2019). Such analyses are precluded in El Pirulejo, where fish remains were not found. Nonetheless, our data point to a qualitative indication of aquatic resource consumption by humans. Our conclusions are consistent with studies pointing to an intensification and broadening the dietary breadth by the inclusion of freshwater and marine aquatic species in human diet across the southwestern Mediterranean region from Solutrean to the Magdalenian periods and even further in later periods (Cortés-Sánchez et al. 2008). This change in diet may be related to the decrease in terrestrial animal food resources throughout the Upper Palaeolithic (e.g., Cortés-Sánchez et al. 2008; Nakazawa et al. 2009) similar to these described in other regions in Europe (e.g., Morin 2008), as well as to the high spatial mobility of humans between coastal and inland locations as suggested by the acquisition of lithic materials (Cánovas-Calle et al. 2018) and marine and fluvial seashell ornaments (Asquerino 1992).

4.2. CARBON AND OXYGEN ISOTOPE ANALYSIS ON TOOTH ENAMEL CARBONATES

Herbivore $\delta^{13}\text{C}$ values reflect the proportion of vegetation types and photosynthetic pathways of the plants they eat. As small mammals are typically non-migratory, their $\delta^{13}\text{C}$ values reflect a local signal rather than the complex signal of different climate gradients typical of migratory taxa. Indeed, leporid lagomorphs (rabbits and hares) typically spend their lives in areas 0.4–200 ha in size (Chapman & Willner 1978; McNab 1963), and they are generalist herbivores (Martins, Milne & Rego 2002).

Results of rabbit $\delta^{13}\text{C}$ from El Pirulejo indicate significant differences across levels. The $\delta^{13}\text{C}$ value of rabbits decreased between levels P/5–P/6 to levels P/4–P/2, suggesting an increase in denser vegetation over time. This pattern mirrors the increase in *Pinus* and Mediterranean forest pollen from at Lake El Padul (a continuous paleoenvironmental record for the last 200 kyr at 80 km from the studied site), from ca. >5% during the Greenland Stadial-2a to more than 80% at the onset of the B-A (Camuera et al. 2018). This increase in Mediterranean forest is coetaneous with a significant climate warming in Southern Iberia (García-Alix et al. 2014).

The $\delta^{18}\text{O}$ values of rabbits from El Pirulejo do not differ significantly across studied stratigraphic units and are higher than the $\delta^{18}\text{O}$ values of the human teeth. The interpretation of carbonate $\delta^{18}\text{O}$ values of leporids is complex (Figure 4, Supplementary file 1: S1). The difference in $\delta^{18}\text{O}$ values between the taxa may indicate a consistent difference in water sources (e.g., meteoric water vs. consumed vegetal material). As leporids are non-obligate drinkers, they ingest water from other sources in addition to meteoric water. Thus, carbonate $\delta^{18}\text{O}$ values of leporids may correlate negatively with relative humidity (Somerville, Froehle & Schoeninger 2018). While not significantly different from older levels, we note that the most negative $\delta^{18}\text{O}$ values across the stratigraphic sequence are P/4 to P/2. The values could indicate a humid refugium in inland Southern Iberia in the Cordoba/Jaen and Granada uplands (Camuera et al. 2021) during the dryer condition of H1 predicted by bioclimatic models (Jennings et al. 2011). Moreover, if the rabbits were ingesting meteoric water, the oxygen isotope values would correlate positively with temperature; thus, the negative $\delta^{18}\text{O}$ values would be consistent with the colder conditions of H1.

5. CONCLUSION

Our data support the inclusion of aquatic food resources and increased food resource diversity among hunter-gatherers in Southern Iberia during the Magdalenian. We showed that Palaeolithic humans at El Pirulejo lived in a shifting environment associated with the H1 to B-A transition by using an upland refugium and various food sources, including aquatic ones, even inland. This study agrees with previous ones that suggested a socio-economic network among human groups between inland and coastal regions in the terminal Pleistocene Iberian Peninsula.

In the future, the discrimination, if not quantitative, between terrestrial, freshwater, and marine food consumption should be addressed, which would also benefit the calibration of reservoir effects on the ^{14}C age of human remains.

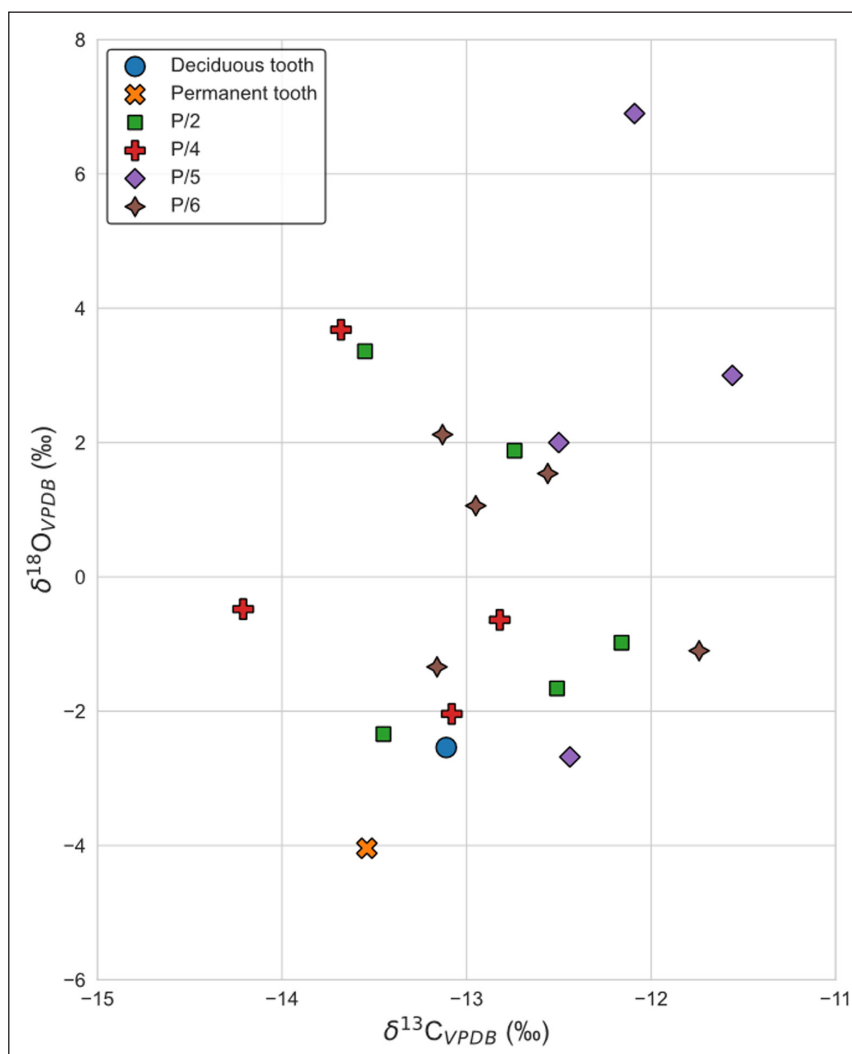


Figure 4 Carbon and oxygen isotopic composition of El Pirulejo human and rabbit tooth enamel.

DATA ACCESSIBILITY STATEMENT

Presented in this paper.

ADDITIONAL FILE

The additional file for this article can be found as follows: Supplementary material.

- **Supplementary material.** Table S1. DOI: <https://doi.org/10.5334/oq.109.s1>

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

MC-S and FJJE initiated the project; YIN and MB performed the experiments; and RPG YIN, MC-C, FJJE analyzed the data, MDS-V analyzed the chrono-cultural sequence, JARC completed the taxonomic identification. All authors wrote and edited the manuscript.

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