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After the Last Glacial Maximum in the refugium of northern Iberia: environmental shifts, demographic pressure and changing economic strategies at Las Caldas Cave (Asturias, Spain).

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Highlights

- Bone collagen $\delta^{13}C$ and $\delta^{15}N$ values used to reconstruct environments and faunal niches between 26-14kyr cal BP in N. Spain
- Harsh Solutrean conditions affected ibex habitats, and they moved to lower altitudes
- Improved Magdalenian conditions coincided with exploitation of wider ecological zones
- Increased Magdalenian human populations pressured resources, affecting subsistence strategies

Abstract

The Late Upper Palaeolithic of Europe, particularly the Last Glacial Maximum (LGM: 26-19kyr cal BP), was a time of dramatic climatic changes. Fauna, and the humans that preyed on them, were forced to adapt their behaviours in response to climate changes to survive. The Cantabrian Region of northern Spain was continuously inhabited during this period when many other areas of Europe were inhospitable. The site of Las Caldas (Asturias) was repeatedly occupied by hunter-gatherers during the Solutrean (26.1-20.3kyr cal BP) and Magdalenian (18.5-14.3kyr cal BP). This paper uses $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis of red deer (*Cervus elaphus*) and Spanish ibex (*Capra pyrenaica*) remains to reconstruct past environments, ungulate niches and habitats, and to understand how this impacted on their availability as a prey source. Results show that during the Solutrean, cold and potentially wet LGM conditions were experienced and ibex lived in lower altitudes, likely due to reduced vegetation on the higher mountain slopes, and even small glaciers on the higher mountain slopes. Improved environmental conditions in the Magdalenian allowed ibex to live in their preferred habitat of higher altitudes. Ameliorated Late Glacial conditions correspond with changing economic hunting strategies at the site. Humans exploited wider ecological zones, over larger distances, which coincides with population growth, and greater connectivity across the Cantabrian region. This research highlights the importance of characterising the complex interactions between humans, animals and environments during Late Pleistocene and how they responded to rapidly changing environmental conditions.

Key words

Cantabrian Spain , Las Caldas Cave, Last Glacial Maximum, Upper Palaeolithic, Archaeozoology, Stable Isotopes, Climate Change, Environmental change

1. Introduction

Understanding the adaptive strategies used by animals and humans during climatic and environmental changes in the past is fundamental for unravelling the complex interactions between different species and their environments. Such studies can provide clues to how current human population can adapt to the threats they face from climate change (Van De Noort, 2011; Sandweiss and Kelley, 2012).

During the Late Glacial Maximum (LGM) large ice sheets covered vast areas of northern Europe, impacting on the distribution of humans, plants and animals within the continent (Sommer and Nadachowski, 2006; Hofreiter and Stewart, 2009). The Cantabrian Region in the northern Atlantic strip of the Iberian Peninsula, along with other largely unglaciated southern European regions (southern France, Italy and the Balkans), and provided sufficient habitats for humans to successfully survive during the peak of the last Ice Age (Bocquet-Appel *et al.*, 2005; Banks *et al.*, 2006; Burke *et al.*, 2014; Burke, Riel-Salvatore and Barton, 2018). Specifically, the Cantabrian region was instrumental in facilitating the survival of salmon (Consuegera et al. 2002), red deer (Meiri *et al.*, 2013; Queirós *et al.*, 2019) and humans (Achilli et al. 2004; Fu et al. 2016) as determined genetically. After the LGM, these species were able to re-colonise northerly latititudes of as climate warned in Late and post-glacial Europe. In the southern refugia, hunter-gatherer populations survived and even thrived during the extreme periods of the LGM. Yet, detailed reconstruction of the specificenvironments surrounding persistently occupied sites is required.

Ice core records have shown global scale dramatic climatic fluctuations throughout MIS2 (Dahl-Jensen *et al.*, 2008; Rasmussen *et al.*, 2014; Seierstad *et al.*, 2014). Global ice sheet growth meant that eustatic sea level regression was around -134m between 29-21kyr BP, before rising by about 10-15m between 21-18kyr BP with the onset of deglaciation (Lambeck *et al.*, 2014). Specifically, in the North Atlantic between 24-19kyr cal BP, sea level was -120m relative to the current level (Siddall *et al.*, 2008; Clark *et al.*, 2009). Continental European-scale modelling of palynological evidence and sea temperatures have indicated that during the LGM, in general, there were large differences in seasonal temperatures in comparison to the present with summer temperatures thought to have been 5-10°C colder, and winter months 15-25°C colder, resulting in generally drier, steppic conditions (Jost et al., 2005; Kageyama et al., 2006).

Regarding the Iberian Peninsula, continental-scale studies of charcoal, reflecting past vegetation, have demonstrated that during the Solutrean, the Atlantic fringe of the Cantabrian region was relatively humid compared to relatively arid conditions in SE Spain and Portugal (Badal et al., 2014; Ochando et al. in press). Studies of continental pollen, marine core pollen and ostracod $\delta^{18}O$ analysis have suggested that during the LGM, the Iberian Peninsula was a refugium for deciduous trees (Naughton *et al.*, 2007), with *Quercus*, and mesothemophilious deciduous woods and evergreens consistently prevalent along the Iberian Atlantic fringe between 20-12kyr cal BP (Carrión *et al.*, 2010). Combined studies of Iberian microfaunal assemblages have suggested higher humidity levels during the LGM than was the case in many other areas of Europe, with the presence of species such as *Talpa europaea* and *Erinaceus europeaus* (Bañuls-Cardona *et al.*, 2014). The Iberian Peninsula was also a refuge for such Euro-Siberian microfaunal species as *Microtus oceconomus*, which even co-existed with thermo-Mediterranean taxa, indicative of milder conditions in the Iberian Peninsula during the LGM and beyond (Bañuls-Cardona *et al.*, 2014). Recent mammalian tooth $\delta^{13}C$ and $\delta^{18}O$ values from a range of LGM (26-20kyr cal BP) sites within the Iberian Peninsula have estimated precipitation and temperatures, and suggests differences in temperature of ~5°C and rainfall of 250mm per year beween Atlantic and Meditterean areas of SW Europe (Lécuyer *et al.*,2021), although some of these results from Northern Iberia should be viewed with care, as they pertain to materials from old excavations, where recent revisions of the chronologies suggest the need for caution (see- Marín-Arroyo *et al.* 2018). In Northern Iberia, where the Cantabrian Region is located, is thought, because of its oceanic climate, to have been less sensitive to environmental changes, and significantlevels of environmental variability due to high relief are considered to have played a role in the Late Pleistocene settlements (Schmidt *et al.*, 2012).

Within the Cantabrian region, several records have explored conditions in the Late Upper Palaeolithic. Marine offshore cores on the Basque continental shelf ostracod $\delta^{18}O$ values of *G. bulloides* and *L. lobatula*, and the

% of N. Pachyderma (sin.) and "Northern Guest" ostracods have informed on changing seawater temperatures, and the influx of melted glacial watermarked the end of the LGM at ~20.1kyr cal BP (Martínez-García *et al.*, 2014, 2015; Rofes *et al.*, 2014). These are valuable records on the impact of Late Glacial climate change, but are somewhat removed from the conditions experienced by terrestrial populations. In the montane zone of the Cantabrian region records temperature estimates from Calcium precipitation in Lake Enol sediments in the Province of Asturias have given temperatures of 1°C between 27-17kyr cal BP, with a small increase of around 1-2°C after this point until 13.5kyr, when temperatures rose again (Moreno, Valero-Garcés, *et al.*, 2010). Speleothem isotope records from El Pindal cave, also in Asturias (but in the coastal zone), have suggested that from 25-18kyr cal BP, the region was sensitive to high-frequency climatic changes. However inconsistencies between the $\delta^{18}O$ record and the Mg/Ca data indicate a high level of complexity in the records, with a need to understand these local conditions further (Moreno, Stoll, *et al.*, 2010). Whilst records such as these have provided valuable information on changing conditions in this refugium region, it is important to consider what environmental conditions were like in the vicinities of sites occupied by humans throughout this time. Reconstructing the local conditions experienced at key sites in Last Glacial refugia is fundamental to understand how different species were able to survive, using the network of ecological niches available to them in the region (Jones *et al.*, 2020), and how these influenced human economic strategies.

This paper explores how changes in the environment affected both faunal behaviour and human hunting strategies in the locality of Las Caldas cave in the western part of the Cantabrian region. Bone collagen $\delta^{13}C$ and $\delta^{15}N$ isotopic analyses are used and results are compared to changing economic strategies observable using the rich archaeozoological record from the site (Mateos Cachorro, 1999, 2002, 2003; Mateos, 2005, 2017; Altuna and Mariezkurrena, 2017a, 2017b).

1.1. Las Caldas Cave

Las Caldas Cave (Asturias), is an archaeological site with rich evidence of occupation levels spanning between 26kyr cal BP and 11Kyr cal BP. It has been described as "one of the most important sites to be researched continuously over the past several decades" (Straus, 2015: 164). Las Caldas was part of a network of sites within the Cantabrian region (Figure 1).

The site is a cave in the town of San Juan de Priorio, in a small cul de sac side-valley of the major Nalón River valley (5º 54' 48.20" W/43º 20' 4.68" N, 160m a.s.l.) 8 km to the east of Oviedo (Figure 1). The peri-glacial processes active in the area surrounding the site helped create undulating valley and mountain systems, with summits in the Picos de Europe above the upper Nalón basin reaching 2,100m (Corchón Rodriguez, 2017a, Figure 1). The site was initially excavated in 1971 and 1973 by F. Jordá, before further excavations by M.S. Corcoón throughout the 1980s, 90s and 00s focusing on three main areas; "Sala I", "Sala II", and the "Pasillo" (Corchón Rodriguez, 2017a). Of particular importance are the archaeologically rich, well-preserved and radiocarbon-dated levels that span from the Middle Solutrean to the Middle Magdalenian (26.1-14.3kyr BP)(Corchón Rodriguez, 1999; Corchón, 2004; Corchón Rodríguez and Cardoso, 2005; summarised in Corchón Rodríguez, 2017a), making it one of the most important Upper Paleolithic sites in the region (Straus, 2015b). Indeed, the extensive deposits relating to the Middle Magdalenian are unique and unrivalled in Asturias (Straus, 2018). Las Caldas's walls bearmodest cave art engravings and excavations at the base of the engraved panel have helped, attribute at least some of these engravings to the Middle Solutrean, with stylistic elements at the top of the panel being more consistent with Magdalenian origins (Corchón Rodriguez, 2017b).

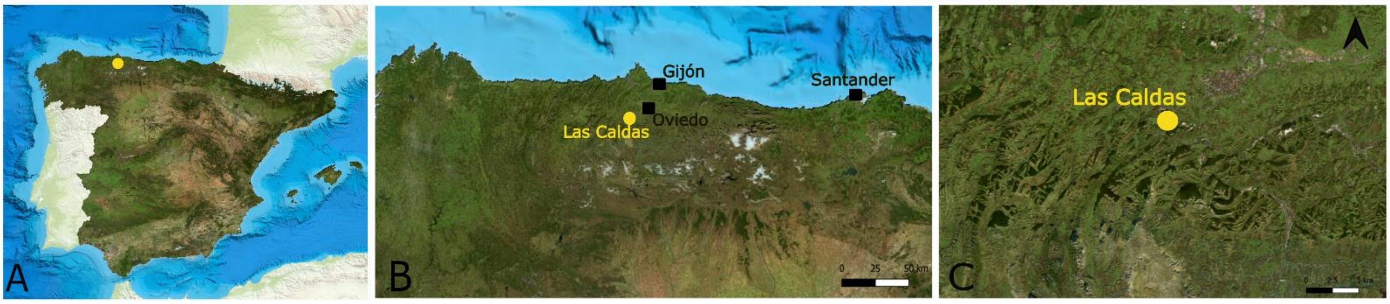


Figure 1: Map showing the location of Las Caldas (marked with a yellow spot) within Spain (A), the wider Cantabrian Region of northern Spain (B) , and the Nalón valley (C).

Archaeozoological and taphonomic analyses of the large quantities of faunal remains have provided extensive information on subsistence strategies and resource procurement (Mateos Cachorro, 1999, 2002, 2003; Altuna and Mariezkurrena, 2017b, 2017a; Mateos, 2017). In additon, spatial analysis has allowed for reconstruction of aspects of the human activities carried out throughout time, within the cave (Mateos Cachorro, 2003; Corchón, Ortega and Vicente, 2013; Corchón, Ortega and Rivero, 2016).

The archaeozoological evidence of Solutrean and Magdalenian human diet shows that red deer were the predominant food source, and there is evidence of large-scale red deer hunting. In addition, horse and ibex (Altuna and Mariezkurrena, 2017a; Mateos, 2017) were also consumed. Complete red deer carcasses were brought to the site for processing (Corchón *et al.*, 2013), and articulating red deer parts were found, indicating in-situ butchering during Solutrean Levels 18 and 9 (Corchón Rodríguez, 2017d). The Las Caldas economy followed the regional trend of red deer being a dominant Upper Palaeolithic prey across the Cantabrian Region, with supplementary species varying depending on site location (Altuna, 1986, 1995; Marín Arroyo, 2008; Marín-Arroyo, 2009a). Las Caldas is unusual in that, whereas most of the main regional Solutrean sites are located closer to the coast, it is located quite far inland (Straus and González Morales, 2012), between 40-50km from the LGM coast (Corchón Rodríguez, 2017b).

Regarding the wider environmental indicators from Las Caldas, in the Solutrean levels, pollen preservation is poor, with only two (out of 56) samples yielding well-preserved pollen (Corchón Rodriguez, 2017a). For the Magdalenian levels, and although preliminary interpretations of the pollen analysis were developed by Dupré, and presented at the Foix conference in 1987 (Fortea *et al.*, 1990), results are still pending. Initial interpretations, based on archaeological sediments, were noted during excavations and summarised in Hoyos (1995), but detailed studies are not available (Corchón Rodríguez, 2017c). Additional evidence, such as bird bones (Eastham, 2017), land snails (Aparicio and Esteban, 2017) and microfauna (Laplana et al., 2017) are recorded, but their presence within deposits is patchy, and many species present are not diagnostic of specific habitats, and further environmental indicators are required. Macro faunal remains are well-preserved, both within the Solutrean (Altuna and Mariezkurrena, 2017) and Magdalenian levels (Mateos Cachorro, 2002, 2003; Altuna and Mariezkurrena, 2017a; Mateos, 2017), meaning that bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of stable isotope analysis within different archaeological levels at Las Caldas can be used to explore changing environmental conditions, faunal species habitats, and their impact on human economic strategies.

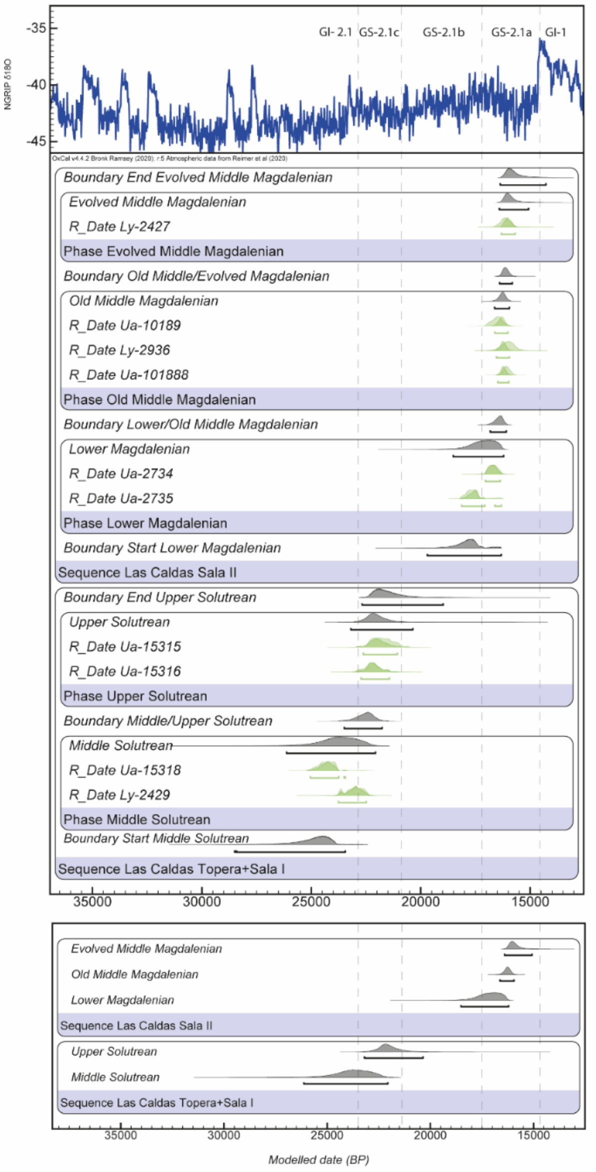


Figure 2: Modelled AMS radiocarbon dates from Las Caldas relevant to this study, including the: corte estratigráfico, Sala I and Sala II, modelled in OxCal v.4.4 (Bronk Ramsey, 2009) with the atmospheric data from IntCal20 (Reimer et al., 2020). and showing NGRIP isotopic record and key climatic events (Rasmussen et al., 2014).

1.2 Stable isotope analysis and palaeoenvironments

Biomolecular methodologies, specifically stable isotope analyses of macromammals, are invaluable for understanding past ecosystems and paleoenvironmental conditions in the areas surrounding archaeological sites (Jones and Britton, 2019), especially when traditional environmental indicators are not well-preserved, or are ambiguous or inconsistently recorded. Bone collagen δ^{13}C and δ^{15}N values of macrofauna reflect long-term consumed diet, and thus average environmental conditions experienced by animals during their lifetimes (Hedges, Stevens and Richards, 2004). There is a complex relationship between δ^{13}C and δ^{15}N values, and the factors that influence the isotopic values observed within soils, plants, and their subsequent consumers. The drivers that influence the δ^{13}C and δ^{15}N values in fauna can be a result of changing environmental conditions (e.g. temperature, precipitation, vegetation, CO_2 levels), or changing animal behaviour linked to localised environments, as summarised in Table 1. The dynamic interplay between isotope systems, faunal behaviour and habitat preferences means that trends in δ^{13}C and δ^{15}N values may affect species differently, and may not always be consistently reflected between geographical regions (Drucker *et al.*, 2008, 2011). Bone collagen δ^{13}C and δ^{15}N analysis have been applied to a wide range of Palaeolithic studies, informing on environmental conditions on continental (Richards and Hedges, 2003) or regional scales (Bocherens, Drucker and Madelaine, 2014), as well as identifying micro-environments, and the existence mosaic landscapes surrounding archaeological sites (Stevens *et al.*, 2014; Bocherens *et al.*, 2015; Jones *et al.*, 2018, 2019; Wong *et al.*, 2020; Reade *et al.*, 2021). Additionally, they have successfully been used to determine faunal ecosystems, food webs and habitats (Drucker *et al.*, 2011, 2017; Kuitems *et al.*, 2013; Bocherens *et al.*, 2015), and niche partitioning of species (Britton *et al.*, 2012; Schwartz-Narbonne *et al.*, 2019; Jones *et al.*, 2020). By viewing changes in the isotopic record with archaeozoological evidence, it is possible to explore how subsistence strategies changed with shifting environments is possible.

		Potential impact on $\delta^{13}C$ values	Potential impact on $\delta^{15}N$ values
Drivers linked to environmental change	Precipitation	Moisture availability and levels of precipitation have been observed as a major driving factor influencing plant $\delta^{13}C$ values, with a direct correlation between increasing annual precipitation and decreased $\delta^{13}C$ values (Farquhar *et al.*, 1989; Stewart *et al.*, 1995).	Mean annual precipitation can impact on plant $\delta^{15}N$ values. Areas with lower annual precipitation have been observed to result in higher $\delta^{15}N$ values than areas with mean annual rainfall (Austin and Vitousek, 1998; Handley, Austin, Robinson, et al., 1999; Amundson et al., 2003; Aranibar et al., 2004). This may be related to shifting diets, rather than physiological stress resulting from lack of water (Murphy and Bowman, 2006; Hartman, 2011). Recent global studies have shown a correlation between elevated $\delta^{15}N$ values and hot/dry ecosystems, and lower $\delta^{15}N$ values in cold/wet ecosystems based on studies of soil and plants (Craine, Elmore, *et al.*, 2015).
	Temperature	Temperature has been observed to be a factor influencing plant $\delta^{13}C$ values with lower temperatures producing lower $\delta^{13}C$ values at a range of altitudes and latitudes (Körner, Farquhar and Wong, 1991). Plants growing in temperatures lower than their optimal conditions is thought to reduce enzymatic reactions during photosynthesis, causing depleted $\delta^{13}C$ values (Tieszen, 1991). Although, It has been noted that isolating the impact of temperature from other factors is challenging (O'Leary, 1995), and both positive and negative correlations between $\delta^{13}C$ and temperature have been observed (Heaton, 1999).	In cold/or wet ecosystems (e.g. permafrost and glacial contexts), activity of microorganisms within soil is reduced, and can produce lower $\delta^{15}N$ values (Heaton *et al.*, 1986; Handley, Austin, Stewart, *et al.*, 1999). Soil and plant $\delta^{15}N$ values have been observed to decrease in association with lower mean annual temperatures on a global scale (Amundson *et al.*, 2003). Positive correlations between warmer temperatures and higher foliar $\delta^{15}N$ values have also been observed (Martinelli *et al.*, 1999; Amundson *et al.*, 2003; Pardo *et al.*, 2006), due to greater levels of nitrogen recycling being associated with colder and wetter ecosystems (Handley, Austin, Robinson, *et al.*, 1999), which has been observed on a global scale (Craine, Brookshire, *et al.*, 2015; Craine, Elmore, *et al.*, 2015).
	Tree cover	Areas of dense tree cover can result in decreased $\delta^{13}C$ values relative to those in open environments, due to reduced sunlight exposure and CO_2 recycling on the forest floor (Vogel, 1978; van der Merwe and Medina, 1989, 1991). This is termed the *canopy effect*.	
Drivers linked to faunal habitats and dietary preferences	Altitude	Changing CO_2 partial pressure, alongside changes in water use efficiency, and lower temperatures at higher altitudes results in plants growing at higher altitudes having been observed to produce elevated plant $\delta^{13}C$ values (Farquhar *et al.*, 1989; Körner, Farquhar and Wong, 1991; Hultine and Marshall, 2000; Zhu *et al.*, 2010).	Lower $\delta^{15}N$ values are typically associated with higher altitudes, due to lower levels of soil activity at elevated heights (Mariotti *et al.*, 1980).
	Lithology and soil type		Plant $\delta^{15}N$ values are directly affected by the type of nitrogen fixing mycorrhizae present (Brundrett, 2009). Differences in the mycorrhizae found within the soil, and associated play root systems of plants (Hobbie, Jumpponen and Trappe, 2005; Craine *et al.*, 2009; Craine, Brookshire, *et al.*, 2015) can impact on the $\delta^{15}N$ values of plants, and thus their consumers (see summary in Szpak, 2014). Soil acidity can impact on $\delta^{15}N$ values, with more acidic soils exhibiting lower $\delta^{15}N$ values (Mariotti *et al.*, 1980). Soil nitrogen content can vary depending on water table height, with water tables below 30cm typically producing higher $\delta^{15}N$ values, and water tables between 10-30cm resulting in lower nitrogen availability (Hefting *et al.*, 2004).
Drivers linked to changing faunal behaviour	Change in type or part of plant consumption	Notably, a shift from consuming C4 to C3 plants can impact on plant 13-C values (Vogel, 1993). The contribution of C4 plants to the landscape of Europe is negligible (Andres, 1992), and is unlikely to impact on observed $\delta^{13}C$ values within fauna from Palaeolithic Northern Spain. Different parts of plants exhibit variation in $\delta^{13}C$ values (and $\delta^{15}N$) (Ehleringer, Comstock and Cooper, 1987; Lightfoot *et al.*, 2016) and a shift in the part of plant consumed may affect herbivore $\delta^{13}C$ values.	A change in the parts of plants or types of plants being consumed by an animal can result in different (positive or negative) $\delta^{15}N$ values being observed (Michelsen et al., 1996; Högberg, 1997). Even plants growing in controlled conditions can show consider (Kolb and Evans, 2002; Szpak *et al.*, 2014; Mannino, Lightfoot and Stevens, 2016)
	Change in feeding location	Changes in the feeding locations of different species may be observable identifiable by comparing faunal isotopic results between different archaeological levels to identify. Factors such as changing altitudes, or feeding in more saline locations (Guy, Reid and Krouse, 1986; Van Groenigen and Van Kessel, 2002) can impact on the $\delta^{13}C$ values of plants, with elevated values being observed.	Long term, habitual changes in the feeding locations of animals may be reflected in bone $\delta^{15}N$ values, as a result of other factors mentioned above such as soil richness and lithology, or environmental differences between regions in rain shadows versus regions. This would be observable over a longer time scale. Potential different feeding locations identified within faunal $\delta^{15}N$ values was observed archaeologically within the Cantabrian Region during the Middle and Early Upper Palaeolithic (Jones *et al.*, 2018, 2019).

Table 1: A summary of the key factors that can affect the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of plants, and the animals that consume them, related to changes in the environment, faunal habitats, and ungulate dietary behaviour relevant to this study.

2. Methodology

Red deer (*Cervus elaphus*)-- the most commonly consumed species at Las Caldas-- and Spanish ibex (*Capra pyrenaica*)—the other staple food source--, were sampled for isotope analysis (Altuna and Mariezkurrena, 2017a; Mateos, 2017). In total 105 samples (41 ibex and 64 red deer) were analysed from 10 different levels, ranging from the Middle Solutrean to the Evolved Middle Magdalenian at different points in the archaeological sequence from the 'corte estratigráfico', 'Sala I' and 'Sala II' (Table 2, Figure 2). Levels selected for analysis were deposits that contained large numbers of faunal remains and had reliable and consistent, radiocarbon datesed, in correlation with lithic and bone tool typologies. All levels sampled are referred to the numbering system, and cultural attributions as published in the site monographs (Corchón Rodríguez, 2017a, 2017d). Levels sampled from within "Sala I", including the "corte estratigráfico" are referred to in Arabic numerals and levels within "Sala II" are referred to using Roman numerals. Specimens from "Sala II" evels IV, V, VII, VIII and IX were sampled from the collections held at the Department of Prehistory, Ancient History and Archaeology at the University of Salamanca. Bone specimens from levels 9, 11, 15, 18 and XII were sampled from the archive collections held at the Museo Arqueológico de Asturias. Adult animals, assessed using bone fusion evidence, were selected for analysis to prevent residual nursing signatures from causing inflated $\delta^{15}N$ values (Schurr, 1997, 1998; Fuller *et al.*, 2006), that may obscure environmental signatures. When possible, bone specimens selected displayed evidence of anthropogenic alteration, including cut marks and anthropogenic fractures for marrow extraction, to ensure that interpretations are related directly to periods of human activity were selected. Information about the bones sampled, and the stable isotope results achieved are available in SI1.

Archaeozoological data of Las Caldas are taken from recent publications (Altuna and Mariezkurrena, 2017a, 2017b; Mateos, 2017) to explore the changing importance of different species, use of animals and exploitation of habitat zones throughout the sequence to trends in the $\delta^{13}C$ and $\delta^{15}N$ data. The NISP and MNI data were used to calculate the Inverse Simpson's index to explore changing diversity in prey exploited at Las Caldas. The percentage of high-ranking prey (bovids, horse, red deer, ibex) in relation to low-ranking prey (fish, birds, chamois, roe deer, and hares/rabbits) was also calculated to explore exploitation strategies. The ratio of juveniles to adults was generated as an indicator of resource pressure. Skeletal profile representation using probabilistic Bayesian methods was undertaken following Marín-Arroyo and Ocio (2017) based on the % Minimum Animal Units (%MAU) to explore carcass transportation and attrition of the archaeozoological assemblage. The archaeozoological data used in this study are available in SI2-4.

Level/location	**Cultural attribution**	**Lab code**	**Date (uncal) BP**	**Calibrated dates (95.4% probability)**		**Red deer n=**	**ibex n=**
				From	**to**		
IV (Sala II)	Evolved Middle Magdalenian	Ly-2427	13,400 ± 150	14643	13747	6	5
V (Sala II)	Evolved Middle Magdalenian	-	-	-	-	6	6
VII (Sala II)	Old Middle Magdalenian	Ly-3318	12,869 ± 160	13950	12962	5	5
VIII (Sala II)	Old Middle Magdalenian	Ua-10189	13,640 ± 150 (AMS)	15036	14115	6	6
VIII (Sala II)	Old Middle Magdalenian	Ly-2936	13,310 ± 200	14633	13402		
IX (Sala II)	Old Middle Magdalenian	Ua-10188	13,370 ± 110 (AMS)	14671	13446	6	4
XI (Sala II)	Lower Magdalenian	Ua-2734	13,755 ± 120 (AMS)	15076	14372	7	
XII (Sala II)	Lower Magdalenian	Ua-2735	14,495 ± 140 (AMS)	16206	15391	7	2
9 (Sala I)	Upper Solutrean	Ua-15315	17,945 ± 370 (AMS)	20669	18865	7	2
11 (Sala I)	Upper Solutrean	Ua-15316	18,305 ± 295 (AMS)	20960	19500	7	0
15 (Sala I)	Middle Solutrean	Ua-15318	20,250 ± 235 (AMS)	23033	21877	7	7
18 (Sala I, Corte estratigráfico)	Middle Solutrean	Ly-2429	19,000 ± 280	21788	20444	7	3
					Total	71	40

Table 2: Stratigraphic levels and radiocarbon dates and the number of red deer and ibex samples taken from each level sampled for this study from Las Caldas. Radiocarbon dates are from (Corchón Rodríguez, 2017a, 2017d). Calibrations were achieved using OxCal 4.4 (Bronk Ramsey 2009) and IntCal 2020 curve (Reimer et al., 2020).

2.1. Analytical Methodology

Collagen extraction followed Richards and Hedges (1999) with an ultra-filtration step (Brown et al., 1988). Bone specimens were drilled and cleaned using abrasion. Samples were demineralised in 0.5M HCL at 6-8 °C for between 3-10 days, and then washed three times using de-ionised water before being gelatinised in a weak acidic solution (pH3 HCL) at 70 °C for 48 hours. Samples were filtered using 5–8 µm Ezee® mesh filters (Elkay Laboratory Products) and were ultra-filtered to retrieve the >30ka collagen chains. The >30ka fraction was then frozen and lyophilized for 48 hours. Between 0.2- 0.45mg of collagen was weighed into tin capsules for analysis of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios. Specimens were analysed in duplicate, using a Delta XP mass spectrometer coupled to a Flash EA 2112 elemental analyser.

The dataset for each level was tested for normality using the Shapiro-Wilk test, and the $\delta^{13}C$ and $\delta^{15}N$ data was not normally distributed. Despite this the parametric ANOVA test, combined with Tukey post-hoc pairwise comparisons were used, which has shown to be a valid method to use for data with non-normal distribution, when group size and sample sizes are unbalanced (Blanca *et al.*, 2017), and can be considered more robust when comparing unequal group sizes (Keppel and Wickens, 2004), such as those at Las Caldas. The paleontological software PAST was used to undertake the statistical analysis within this study (Hammer *et al.*, 2001). Values of p=<0.05 are deemed to be statistically significant. Statistical analysis of ibex remains from levels 18, 9 and XII were not undertaken due to small sample sizes, and no ibex specimens were available from level 11.

3. Results

3.1 Overview of the stable isotope results

Collagen preservation was exceptional, with results achieved from 104 of the 105 specimens. All samples were analysed in duplicate and results presented here are an average of these two values. For two specimens, only one aliquot was possible to analyse due to low collagen yields (SUBC11153 and SUBC11157). Replication was typically 0.1‰ or better for $\delta^{13}C$ values and 0.2‰ or better for $\delta^{15}N$ values. All of the samples had a C:N ratio between 2.9-3.6, indicative of in vivo collagen (DeNiro, 1985), with 98 of these complying with the more rigid criteria of 2.9-3.4 (Van Klinken, 1999). All specimens had a collagen yield >1%, despite being calculated from the >30ka fraction, rather than total collagen fraction, and specimens typically had >35%C and %N between 10-16%, all of which are indicative of well preserved, *in vivo* collagen (Van Klinken, 1999). Raw $\delta^{13}C$ and $\delta^{15}N$ data and quality indicators are provided in SI1.

3.2. Trends in $\delta^{13}C$ values

3.2.1. Red deer

The red deer $\delta^{13}C$ values range between -21.3‰ and -20.1‰ (Table 3, Figure 3). Red deer $\delta^{13}C$ values are typically lower in the Solutrean levels (18,15,11,9), and the $\delta^{13}C$ values seen in Levels 15 and 11 are statistically significantly different from all subsequent levels, except VIII and IV (Table 4). The lowest deer $\delta^{13}C$ values are seen in level 11 (mean value -21.1‰, Table 3, Figure 3). Standard deviation is typically lower in the lower part of the sequence (0.1-0.2‰ throughout the Solutrean and into the Lower Magdalenian), and the maximum standard deviation of 0.4‰ is observed in Old Middle Magdalenian level IX (Table 3, Figure 3). The red deer range is lowest in Middle Solutrean levels 18 and 15 (0.2‰ and 0.3‰ respectively) and in the Lower Magdalenian level IX (0.3‰, Table 4).

3.2.2 Ibex

The ibex $\delta^{13}C$ values range between -21.4‰ and -19.4‰ (Table 3; Figure 3). The ibex $\delta^{13}C$ standard deviation is typically between 0.1‰ and 0.3‰ red deer (Table 3). The largest standard deviation 0.5‰ in $\delta^{13}C$ ibex values is seen within level 18, despite only three individuals being analysed (Table 3; Figure 3). The lowest $\delta^{13}C$ for the ibex are also observed within level 18, with all three specimens having values that range between

-21.5‰ and -20.5‰ (Table 3; Figure 3). Within level 15, the values recorded are some of the lowest seen in the sequence (Table 3, Figure 3) and they were statistically significantly different from the ibex populations analysed in the latter part of the sequence of levels IX, VIII, VII and V (Table 5).

3.3.3 Comparison between the species

When comparing the two species, the ibex typically have elevated $\delta^{13}C$ values relative to the red deer within all levels where sufficient sample sizes were available (Table 3; Figure 3). Statistically significant differences between the $\delta^{13}C$ values of the two species were seen in all levels where sufficient sample sizes were available (Table 6). In Level 15, the ibex have $\delta^{13}C$ values 0.3‰ higher than the red deer from the same level (Table 3), and within levels IX to IV pertaining the Old and Evolved Middle Magdalenian, the mean values of the ibex are elevated by 0.5‰ (Table 3).

				$\delta^{13}C$					$\delta^{15}N$				
				Red deer									
	Cultural attribution	**Level**	**N**	**Mean**	**σ1**	**Min**	**Max**	**Range**	**Mean**	**σ1**	**Min**	**Max**	**Range**
SOLUTREAN	Middle	15	7	-20.9	0.1	-21.1	-20.8	0.3	6.5	0.6	5.3	7.2	1.9
		18	7	-20.8	0.1	-20.9	-20.7	0.2	6.1	0.5	5.2	6.6	1.4
	Upper	11	7	-21.1	0.2	-21.3	-20.6	0.7	4.2	0.6	3.1	5.0	1.9
		9	7	-20.8	0.2	-21.1	-20.5	0.6	4.2	0.3	3.9	4.6	0.7
MAGDALENIAN	Lower	XII	7	-20.7	0.1	-20.9	-20.6	0.3	6.1	0.6	5.5	7.2	1.7
	Old Middle	IX	6	-20.5	0.4	-20.9	-20.1	0.8	5.4	0.6	4.7	6.3	1.6
		VIII	6	-20.8	0.3	-21.2	-20.5	0.7	5.5	0.7	4.6	6.4	1.8
		VII	5	-20.4	0.2	-20.6	-20.2	0.4	6.0	0.5	5.3	6.6	1.3
	Evolved Middle	V	6	-20.4	0.2	-20.8	-20.2	0.6	5.1	0.3	4.8	5.6	0.8
		IV	6	-20.7	0.3	-20.9	-20.2	0.7	5.8	0.7	5.2	7.1	1.9
				Ibex									
	Cultural attribution	**Level**	**N**	**Mean**	**σ1**	**Min**	**Max**	**Range**	**Mean**	**σ1**	**Min**	**Max**	**Range**
SOLUTREAN	Middle	15	7	-20.6	0.3	-21.0	-20.2	0.8	5.8	0.4	5.5	6.6	1.1
		18	3	-20.9	0.5	-21.4	-20.5	0.9	7.0	0.9	6.3	8.0	1.7
	Upper	9	2	-20.0 -20.6	- -	- -	- -	- -	3.8 3.7	- -	- -	- -	- -
MAGDALENIAN	Lower	XII	2	-19.7 -20.0	- -	- -	- -	- -	6.5 7.5	- -	- -	- -	- -
	Old Middle	IX	4	-20.0	0.1	-20.0	-19.9	0.1	6.3	1.3	4.8	7.5	2.7
		VIII	6	-20.0	0.3	-20.4	-19.6	0.8	5.1	1.1	4.1	7.2	3.1
		VII	5	-19.9	0.3	-20.1	-19.4	0.7	4.7	0.6	4.1	5.4	1.3
	Evolved Middle	V	6	-19.9	0.2	-20.2	-19.6	0.6	5.3	1.0	3.9	6.3	2.4
		IV	5	-20.2	0.3	-20.6	-19.9	0.7	4.5	0.6	3.9	5.4	1.5

Table 3: Summary statistics results of bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of red deer and Spanish ibex from each level at Las Caldas. Where only two results are available both values are displayed in the mean column.

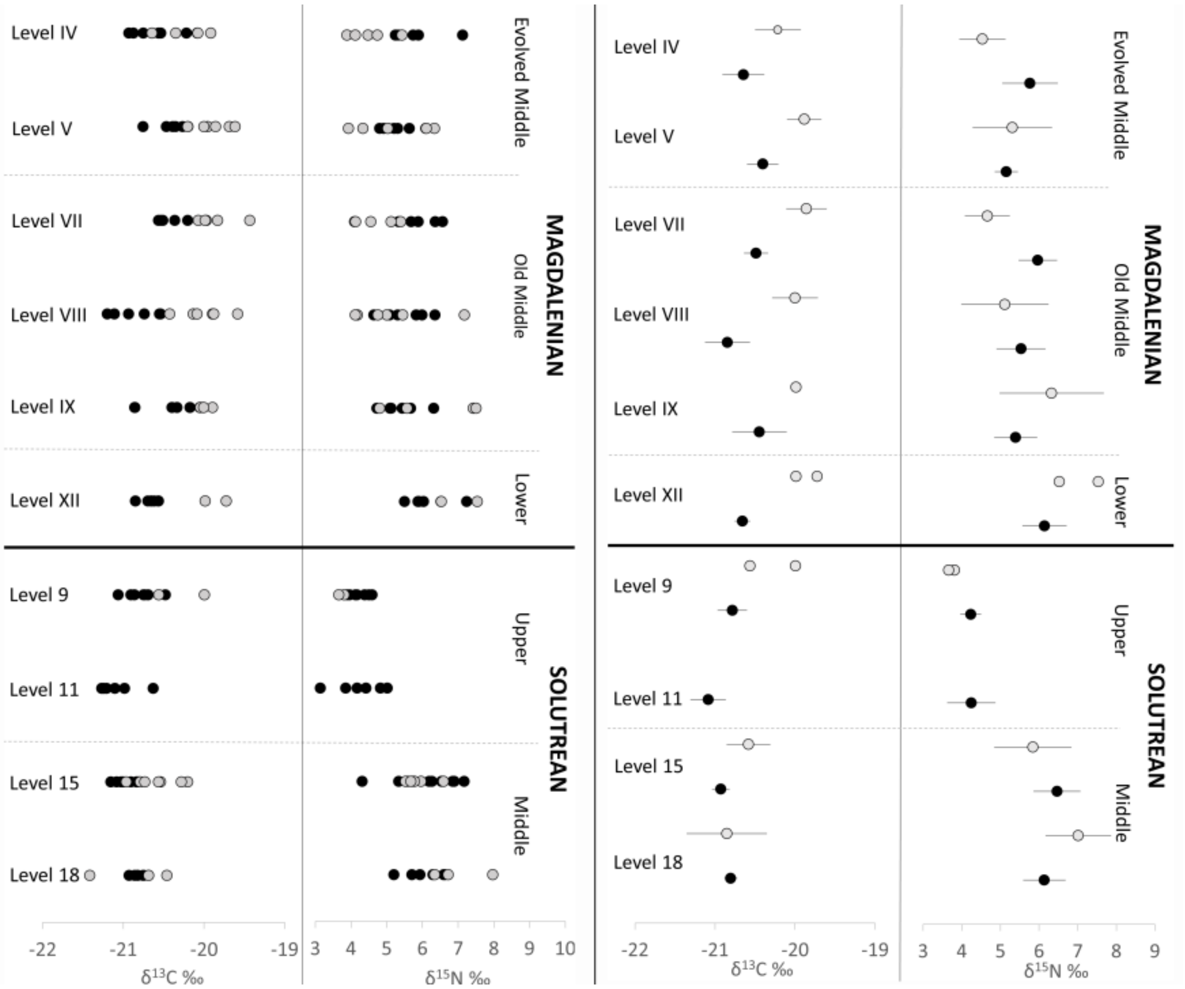


Figure 3: The bone collagen $\delta^{13}C$ and $\delta^{15}N$ of red deer (black circles) and ibex (grey circles) for each archaeological level sampled at Las Caldas. The left-hand side of the figure shows each individual plotted. The right-hand side of the graph shows the mean values, with error bars depicting 1σ from the mean.

	Cultural attribution		**SOLUTREAN**				**MAGDALENIAN**					
			Middle		**Upper**		**Lower**	**Old Middle**			**Evolved Middle**	
		Level	**18**	**15**	**11**	**9**	**XII**	**IX**	**VIII**	**VII**	**V**	**IV**
SOLUTREAN	**Middle**	**18**		0.996	0.917	0.999	0.805	**0.046**	1	**0.042**	**0.023**	0.650
		15	0.995		0.398	1	0.999	0.323	1	0.280	0.202	0.989
	Upper	**11**	**0.000**	**0.000**		0.479	0.087	**0.001**	0.564	**0.001**	**0.000**	**0.046**
		9	**0.000**	**0.000**	1		0.996	0.258	1	0.223	0.155	0.975
MAGDALEINIAN	**Lower**	**XII**	0.963	1	**0.000**	**0.000**		0.805	0.989	0.737	0.650	1
	Old Middle	**IX**	0.093	0.506	**0.021**	**0.013**	0.718		0.202	1	1	0.917
		VIII	0.257	0.810	**0.005**	**0.003**	0.939	1		0.175	0.117	0.952
		VII	0.984	1	**0.000**	**0.000**	1	0.713	0.930		1	0.867
	Evolved Middle	**V**	**0.011**	0.119	0.151	0.106	0.233	0.998	0.952	0.246		0.805
		IV	0.684	0.993	**0.001**	**0.000**	1	0.972	0.999	0.999	0.614	

Table 4: The p-values from the statistical analysis comparing red deer between each level at Las Caldas. The upper part of the table displayed in white shows the results from comparisons of the $\delta^{13}C$ values achieved. The values in the lower half of the table shaded in grey shows the results for the comparisons of the $\delta^{15}N$ values. Statistically significant values ($p=<0.05$) are displayed in bold.

3.4 Trends in δ^{13}N values

3.4.1 Red deer

Red deer δ^{15}N values range between 3.1‰ and 7.2‰. The standard deviation for red deer δ^{15}N values for each level was between 0.3‰ and 0.7‰ (Table 3; Figure 3). Within the Middle Solutrean (levels 18 and 15, 26.1-22.1kyr BP), the δ^{15}N values of the red deer are 2‰ higher than those seen within the Upper Solutrean (levels 11 and 9, 23.2-20.3kyr cal BP) (Table 3; Figure 3). The δ^{15}N values drop in the Upper Solutrean to be the lowest seen within the sequence (Figure 3). There is no overlap in the δ^{15}N values for the Middle Solutrean and the Upper Solutrean (Table 3; Figure 3), and statistically significant differences between these two periods were also observed (p=0.000 for each test, Table 4). In the following part of the sequence, from the Lower Magdalenian (Level XII, 18.5-16.2kyr BP) onwards, the mean δ^{15}N values increase again by around 2‰ (Table 3; Figure 3). The δ^{15}N values remain at this higher level throughout the Early Middle Magdalenian and into the Evolved Middle Magdalenian (Table 3; Figure 3). The only exception to this is level V. The red deer mean δ^{15}N values were 0.9‰ lower than in level VII, and 0.7‰ lower than in level IV (Table 3; Figure 3), although no statistically significant differences between the populations were observed (Table 4).

3.4.2 Ibex

Ibex δ^{15}N values range between 3.7‰ and 8.0‰ (Table 3), and the δ^{15}N standard deviations are generally higher than for the red deer, between 0.4‰ and 1.3‰ (Table 4; Figure 3). The two Upper Solutrean ibex from level 9 also have lower values than those earlier in the sequence (3.8‰, 3.7‰) (Figure 3), mirroring the trends seen within the red deer. Higher δ^{15}N values are then observed in the ibex again in the Old- and Evolved- Middle Magdalenian (level IX, 16.6ky cal BP onwards), which is consistent with the red deer trends.

3.4.3 Comparison between the species

When comparing the δ^{15}N values of the red deer and ibex for each level, where sufficient samples were available, the two species have similar mean values within levels 15, IX, and VIII within the earlier part of the sequence (Table 3; Figure 3). Statistically significant differences between the red deer and the ibex were identified within levels VII, and IV, where the ibex had δ^{15}N values 1.3‰ lower than the red deer (Table 6) with little overlap in values of the two species (Table 3; Figure 3).

	Cultural attribution	**level**	**SOLUTREAN**				**MAGDALENIAN**					
			Middle		**Upper**		**Lower**	**Old Middle**			**Evolved Middle**	
			18	**15**	**11**	**9**	**XII**	**IX**	**VIII**	**VII**	**V**	**IV**
SOLUTREAN	**Middle**	**18**	■	x	x	x	x	x	x	x	x	x
		15	x	■	x	x	x	**0.018**	**0.008**	**0.001**	**0.001**	0.219
	Upper	**11**	x	x	■	x	x	x	x	x	x	x
		9	x	x	x	■	x	x	x	x	x	x
MAGDALENIAN	**Lower**	**XII**	x	x	x	x	■	x	x	x	x	x
	Old Middle	**IX**	x	0.973	x	x	x	■	1.000	1.000	1.000	0.872
		VIII	x	0.769	x	x	x	0.377	■	0.976	0.995	0.879
		VII	x	0.277	x	x	x	0.104	0.971	■	1.000	0.442
	Evolved Middle	**V**	x	0.908	x	x	x	0.534	1.000	0.899	■	0.537
		IV	x	0.171	x	x	x	0.062	0.905	1.000	0.778	■

Table 5: The p-values, from the statistical analysis, comparing ibex between each level at Las Caldas. The upper part of the table displayed in white shows the results from comparisons of the δ^{13}C values. The values in the lower half of the table, shaded in grey, show the results for the comparisons of the δ^{15}N values. An X is used to denote levels where insufficient data were available for statistical analysis to be undertaken. Statistically significant values are displayed in bold.

	Archaeological level					
Isotope	15	IX	VIII	VII	V	IV
$\delta^{13}C$	**0.028**	**0.026**	**0.001**	**0.004**	**0.001**	**0.022**
$\delta^{15}N$	0.090	0.156	0.473	**0.006**	0.739	0.013

Table 6: The p-values from the statistical analysis comparing red deer and ibex $\delta^{13}C$ and $\delta^{15}N$ values, within each archaeological level at Las Caldas, where sufficient sample sizes were available. Values in bold denote statistically significant results.

	SOLUTREAN								**MAGDALENIAN**											
	Middle				**Upper**				**Lower**		**Old Middle**				**Evolved Middle**					
Level	**18**		**15**		**11**		**9**		**XII**		**IX**		**VIII**		**VII**		**V**		**IV**	
Taxon	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Mammuthus primigenius	1	1	0	0	1	1	8	1	0	0	0	0	0	0	0	0	0	0	0	0
Equus sp.	60	3	151	5	851	12	38	1	559	10	980	14	389	5	115	3	32	2	70	2
Bovinae	0		2	1	49	5	2	1	12	1	7	2	9	1	7	1	2	1	2	1
Cervus elaphus	764	11	781	8	4028	28	393	7	502	8	3729	169	1112	10	2980	17	1118	5	1671	10
Rangifer tarandus	0	0	2	1	2	1	0	0	2	1	1	1	1	1	0	0	0	0	0	0
Capreolus capreolus	0	0	0	0	0	0	0	0	1	1	20	9	27	5	8	1	6	1	1	1
Capra pyrenaica	33	2	72	4	266	6	18	2	32	3	1479	14	382	8	1600	10	689	5	1010	6
Rupicapra rupicapra	0	0	0	0	44	4	2	1	9	1	303	9	215	5	304	7	165	5	292	5
Totals	858	17	1008	19	5241	57	461	13	1117	25	6519	218	2135	35	5014	39	2012	19	3046	25

*Table 7:*NISP and MNI of major herbivore species exploited at Las Caldas from the levels sampled in this study *(data from Altuna and Mariezkurrena, 2017a, 2017b; Mateos, 2017, see SI2 for full faunal septrum of NISP and MNI values)*

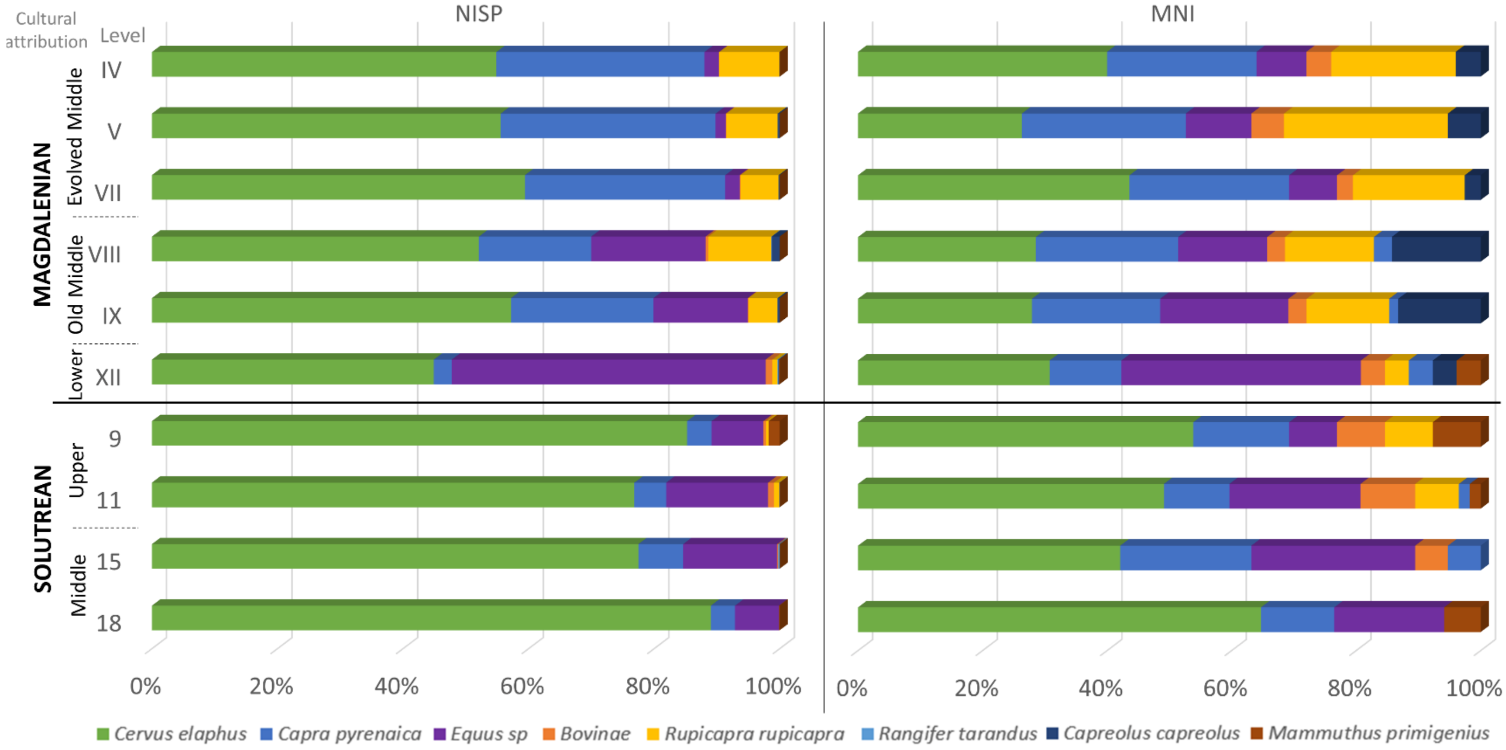


Figure 4: NISP (left) and MNI (right) percentage proportions of herbivore species hunted at Las Caldas for each of the archaeological levels sampled in this study

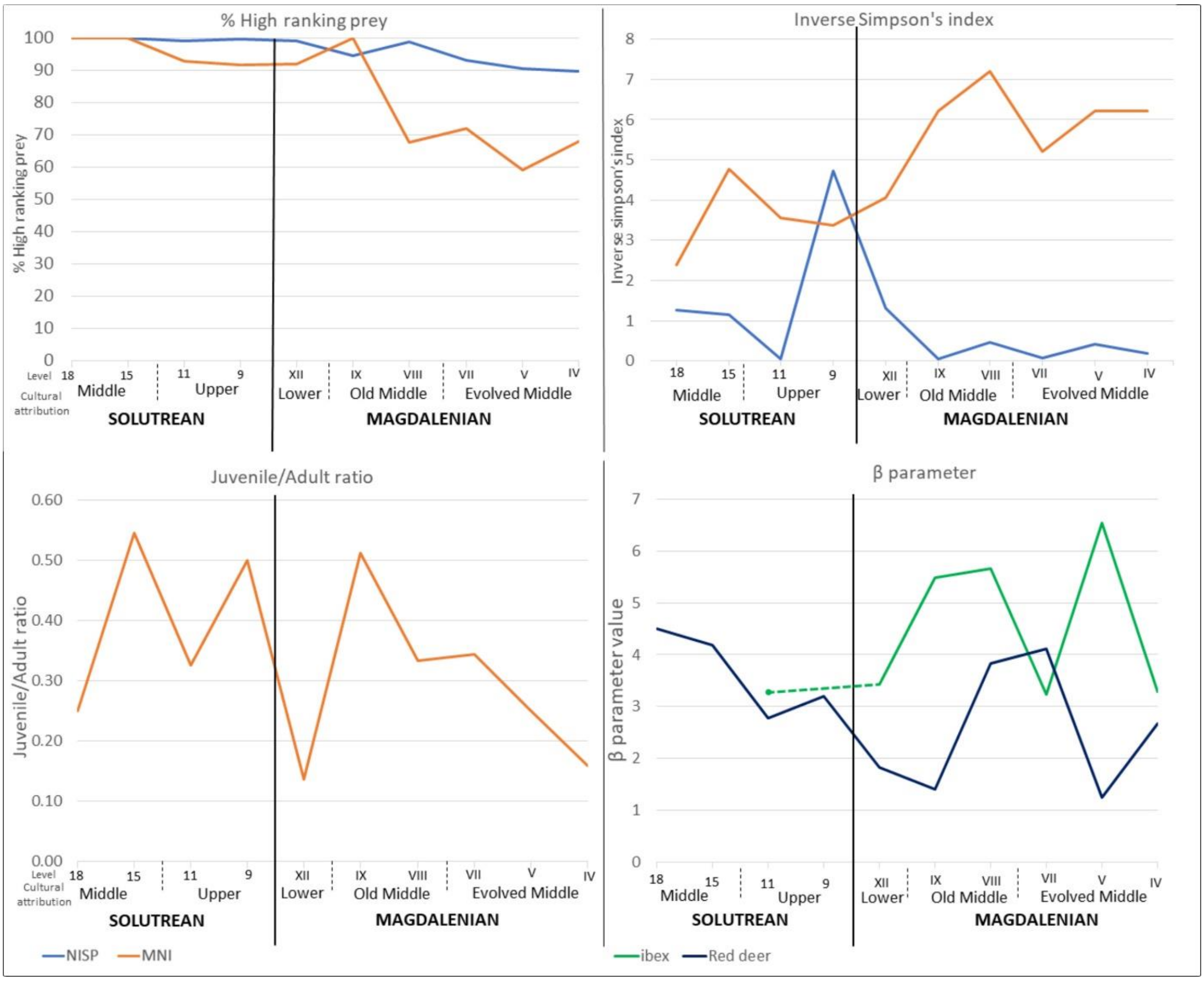
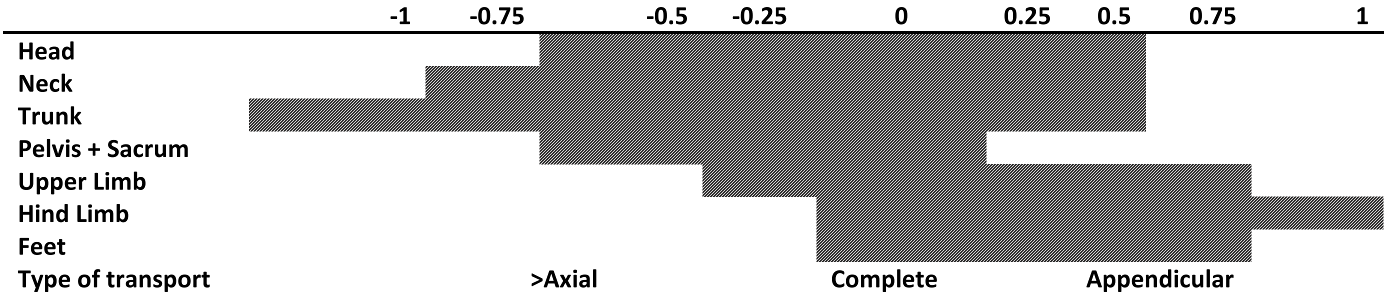


Figure 5: The % high-ranking prey (Upper left), Inverse Simpson's index (Upper right) both NISP and MNI, the combined juvenile/adult ratio of all species (lower left) and the β parameter (Lower right) showing faunal skeletal attrition for red deer and ibex, with higher values indicating higher levels of attrition, and lower values indicating lower levels of attrition. Original data from Altuna and Mariezkurrena, 2017a, 2017b; Mateos, 2017, see SI 2-4 for values used to create these indices.

				α parameter		β parameter		Archaeozoologial data			
		Level	Species	Median	95% credibility interval	Median	95% credibility interval	MNE	MNI	Total Adults	Total Juv.
SOLUTREAN	Middle	18	Red deer	0.06	-1.1	4.51	0.46-9.34	117	11	9	2
		15	Red deer	0.05	-1.01	4.19	0.64-8.99	116	8	5	3
	Upper	11	Red deer	0.04	-1	2.77	0.35-7.62	618	28	20	8
		11	Ibex	-0.04	-1.02	3.28	0.33-8.43	65	6	5	1
		11	Horse	-0.08	-1.08	4.81	0.71-9.33	129	12	9	3
		9	Red deer	0.07	-1.01	3.19	0.31-8.05	84	7	4	3
MAGDALENIAN	Lower	XII	Red deer	0.05	-1.09	1.82	0.11-6.32	92	8	6	2
		XII	Ibex	0.11	-1.3	3.42	0.2-8.31	111	3	3	0
	Old Middle	IX	Red deer	-0.12	-1.04	1.41	0.06-6.35	491	19	21	13
		IX	Ibex	0.02	-1.05	5.49	0.68-9.55	243	14	15	0
		IX	Horse	-0.04	-1.11	3.06	0.22-8.0	110	14	7	9
		VIII	Red deer	-0.04	-1.21	3.83	0.33-8.31	143	10	22	12
		VIII	Ibex	0.09	-1.25	5.66	0.67-9.69	62	8	13	0
		VIII	Horse	-0.13	-76.58	4.04	0.27-8.39	55	5	4	1
	Evolved Middle	VII	Red deer	0.09	-1.15	4.12	0.28-8.97	489	17	31	17
		VII	Ibex	0.11	-1.11	3.23	0.23-8.33	293	10	23	1
		V	Red deer	-0.17	-1.17	1.25	0.05-6.14	100	5	3	1
		V	Ibex	0.27	-1.08	6.55	0.82-9.83	107	5	7	0
		IV	Red deer	-0.07	-1.13	2.67	0.16-7.56	154	10	17	6
		IV	Ibex	-0.10	-1.06	3.29	0.31-8.0	145	6	15	1

Interpretation of different transport strategies corresponding to α values



Interpretation of bone survivorship corresponding to β values

β value	0	1	2	3	4
Survival (%)	100	50	26	15	8

Table 8: Results of the Bayesian analysis of skeletal representation for each level at Las Caldas, α parameter and β parameter values, alongside MNI, MNE and quantities of known adults and juveniles. The α parameter used to explore human transport strategies and the β value shows the attrition of the faunal assemblages for each level. Interpretations for both the Bayesian α parameter and β parameter values are shown in the lower part of table, following Marín-Arroyo and Ocio (2017).

4. Discussion

4.1. Vegetation cover in the Las Caldas environs

All red deer and ibex $\delta^{13}C$ values from Las Caldas are within the expected range for herbivores eating C_3 plants, in open environments, outside of the canopy effect (van der Merwe and Medina, 1989, 1991). This is consistent with the findings from other stable isotope studies from the wider Cantabrian region during the Late Upper Palaeolithic (Stevens *et al.*, 2014; Domingo *et al.*, 2015; Rofes *et al.*, 2015; Jones *et al*. 2020). At Las Caldas, the microfaunal assemblage derived from species that dwell in open environments were identified and no woodland species were represented, supporting this interpretation of generally lower tree cover (Laplana *et al.*, 2017). Vegetation reconstructions based on pollen evidence have also indicated that the Iberian Peninsula was by no means heavily wooded throughout the LGM, although pockets of trees survived, predominantly in the southern regions (Naughton *et al.*, 2007; González-Sampériz *et al.*, 2010; Badal *et al.*, 2014). These results belie the frequently held notion that red deer in the Cantabrian Paleolithic context necessarily signified wooded conditions (see Straus 1981).

4.2. Shifting conditions in the Solutrean and Magdalenian

The changing $\delta^{13}C$ and $\delta^{15}N$ values of the red deer throughout the sequence indicates changes in environmental conditions. The lower $\delta^{15}N$ values observed in the deer, and supported by the values of the two ibex in the Middle Solutrean (26.1-22.1kyr BP, levels 15 and 18), compared to the Upper Solutrean (23.2-20.3kyr cal BP, levels 11 and 9) suggests that the environment changed between the Middle and Upper Solutrean times. Multiple biogeochemical factors can affect $\delta^{15}N$ values of soils, plants, and their consumers (Table 1), and the soil, and plant $\delta^{15}N$ values are a complex reflection of the environmental conditions, mycorrhizal communities and wider processes of nitrogen fixation (Szpak, 2014; Craine, Brookshire, *et al.*, 2015).

Moisture availability and rainfall, can impact on $\delta^{15}N$ values (Cormie and Schwarcz, 1996; Austin and Vitousek, 1998; Amundson *et al.*, 2003; Aranibar *et al.*, 2004; Murphy and Bowman, 2006), and an inverse correlation between precipitation and plant $\delta^{15}N$ values has been observed (Hartman and Danin, 2010). Additionally, temperature can create a positive correlation between foliar $\delta^{15}N$ values and temperature (Martinelli *et al.*, 1999; Amundson *et al.*, 2003; Pardo *et al.*, 2006). Lower $\delta^{15}N$ values can be an indication of bioactivity within the soil, being decreased within colder and/or wetter environments, affecting the processes of microorganisms in the soil (Handley, Austin, Stewart, *et al.*, 1999), and decreased $\delta^{15}N$ values have been shown to correlate with low mean annual temperatures (Martinelli *et al.*, 1999; Amundson *et al.*, 2003; Pardo *et al.*, 2006). More recent global studies of soil $\delta^{15}N$ values have been shown to correlate with mean annual temperatures and mean annual precipitation, with results showing a depletion in ^{15}N within cold or wet ecosystems, and enrichment in ^{15}N associated with hot or dry ecosystems (Craine, Elmore, *et al.*, 2015). The lower $\delta^{15}N$ values could be indicative of cold and potentially wet conditions during the Upper Solutrean at Las Caldas, within levels 11 and 9 (23.2-20.3kyr cal BP), in comparison to the preceding Middle Solutrean levels. Bone collagen $\delta^{15}N$ values from the site of El Mirón (Ramales de la Victoria, Cantabria c. 250km from Las Caldas) between 27-20kyr cal BP, were noted as being lower and were attributed to colder conditions (Stevens *et al.* 2014), which is consistent with the findings from Las Caldas.

The increased $\delta^{15}N$ values from the Lower Magdalenian (level XII, 18.5-16.2kyr cal BP) and subsequent levels in the sequence, suggests an improvement in conditions, with potentially warmer temperatures observed from that point onwards in the sequence. The appearance of roe deer from level XII onwards is indicative of tempering conditions, and increased areas of woodland (Figure 4, Table 7). Similar patterns have been seen in other regions, for example at the site of El Mirón in Cantabria, higher $\delta^{15}N$ values were seen after the LGM (20-14.5 kyr cal. BP) interpreted as relating to increased temperatures in the region (Stevens *et al.*, 2014). Studies of reindeer and horse from SW France demonstated $\delta^{15}N$ values were seen after 26kyr cal BP, with values increasing again after 17kyr cal BP (Drucker *et al.*, 2003), demonstrating a similar response of plant (and thus animal) $\delta^{15}N$ values to these globally cold conditions of the LGM.

The lower $\delta^{13}C$ values of red deer throughout the Solutrean levels (26.1-20.3kyr cal BP), in comparison to the Magdalenian (18.5-14.3kyr cal BP) sequence, also suggests shifting conditions. A negative correlation between plant $\delta^{13}C$ values and temperatures have been observed in some studies (Körner, Farquhar and Wong, 1991; Tieszen, 1991), although both positive and negative associations between $\delta^{13}C$ values and temperature have been noted, and isolating temperature from other factors is a challenge concerning the understanding plant δ^{13}C values (O'Leary, 1995; Heaton, 1999). Water availability is also thought to impact on plant δ^{13}C values (Heaton, 1999; Dawson et al., 2002), with lower δ^{13}C values being produced in wetter conditions (O'Leary, 1995; Diefendorf *et al.*, 2010; Kohn, 2010). Thus, the lower δ^{13}C values of the Solutrean at Las Caldas could also be reflecting these colder/wetter conditions, as suggested by the δ^{15}N values, before conditions improved in the Magdalenian (as seen in level XII onwards), when temperatures increased. Other records from the site are limited, but microfaunal evidence is interpreted as showing colder and wetter conditions generally in the Solutrean compared to the later parts of the sequence, with a decrease in humidity from the Solutrean to the Magdalenian levels (Laplana *et al.*, 2017). The decrease in δ^{13}C values seen at El Mirón between 20-18.5kyr cal BP is interpreted as being link to wetter conditions (Stevens *et al.*, 2014). These results are consistent with the findings of the δ^{13}C and δ^{15}N analysis from the studies at Las Caldas.

Considering the δ^{13}C and δ^{15}N values, in light of wider regional proxies, can help with interpretation and contextualisation of the results achieved. Regarding vegetation cover, offshore core MD95-2039 from the NW of the Iberian Peninsula between ~25-18.5kyr cal BP, corresponding to the Solutrean levels at Las Caldas, contained increased quantities of aboreal pollen, heath, and *quercus* that suggest moister conditions, although not as cold as seen during parts of MIS3 (Roucoux *et al.*, 2005). It has been proposed that during the LGM precipitation in Iberia may have been higher than seen today, due to West wind drift (Beghin *et al.*, 2016; Ludwig *et al.*, 2016), although this is not consistently observed in all proxy records (González-Sampériz *et al.*, 2010; Moreno *et al.*, 2012), and local variability due to distinctive geographical and topographical conditions is important to evaluate. When considering regional proxies, between ~25.2 to 20.5kyr cal BP, which broadly correspond to the Middle and Upper Solutrean levels at Las Caldas, the El Pindal speleothem isotope record suggests relatively cold and/or dry conditions, although it is noted that this period was not as dry as observed during the Heinrich events (Moreno, Stoll, *et al.*, 2010). Following on from this there is a hiatus in the speleothem record between~20.5-16.8kyr cal BP, at El Pindal cave thought to be due to a period of intense cold/or dry conditions, suggesting lower temperatures than the peak of the LGM (Moreno, Stoll, *et al.*, 2010). However, part of this phase relates to a break in the sequence sampled at Las Caldas. Rainfall and temperature reconstructions based on δ^{13}C and δ^{18}O analysis of large mammal teeth between 25-16kyr cal. BP has suggested higher rainfall levels of ≈550 mm yr^{-1} in Atlantic LGM Northern Spain, in contrast to ≈250 mm yr^{-1} in the Mediterranean façade, with mean air temperatures of between 6-10°C and 14-15°C respectively in the two regions (Lécuyer *et al.* 2021), supporting the hypotheis for possible cold and or/wet conditions being expressed in the Cantabrian Region during the LGM. However the northern Iberian results should be viewed with caution, as most of them stem from materials obtained in very old or substandard excavations with stratigraphic mixture and insufficient dating evidence. Recent revisions of regional chronologies with critical evaluation of stratigraphic sequences and high-quality AMS dating, suggest the need for great prudence in such generalizations (see Marín-Arroyo *et al.* 2018). From 20.1kyr cal BP increased numbers of *N. pachyderma* (sin.) present in cores taken from the Basque continental shelf appears to correlate with the melting of ice sheets in Europe (Rofes *et al.*, 2014, 2015; Martínez-García *et al.*, 2015). Pollen evidence available from multiple offshore records suggest that, from 20kyr cal BP, mesothermophilic tree species appear (Carrión *et al.*, 2010), supporting the possibility of improved, warmer conditions following the conclusion of the LGM. This is observed by the increase in δ^{13}C and δ^{15}N values from the Magdalenian onwards in the vicinity of Las Caldas from 18.5 kyr BP onwards. The El Pindal speleothem sequence, from 16.8 to 11.6 kyr cal BP, relating to the Magdalenian activity at Las Caldas, reflects an increase in both temperature and humidity (Moreno, Stoll, *et al.*, 2010), which is consistent with the findings of the stable isotope results.

In summary, when considering the stable isotope results from Las Caldas in light of the wider environmental proxies available, pertaining to the Northern Iberian Peninsula, the lower δ^{13}C values appear to reflect generally cold, and potentially moist conditions throughout the Solutrean. The decrease in $\delta^{15}N$ values in levels 11 and 9 (23.2-20.3kyr cal BP) suggests a possible shift in conditions to become even colder/wetter at that time in the locality surrounding Las Caldas. A climatic improvement is seen from the Lower Magdalenian levels analysed (18.5kyr cal BP) onwards, with warmer conditions experienced in the elevated $\delta^{13}C$ and $\delta^{15}N$ values, reflecting trends observed in the broader environmental proxies.

4.3. Reconstructing the ecological niches of ibex and red deer hunted at Las Caldas

The difference in the $\delta^{13}C$ values of the red deer and ibex within Middle Solutrean level 15 and 18 (26.2-22.1kyr cal BP), and in the Magdalenian part of the sequence (levels IX, VIII, VII, V and IV, 18.5-14.3kyr cal BP), suggests niche partitioning of the two species. In levels 15 and 18, the $\delta^{13}C$ values of the ibex are not as high as seen later in the sequence. Indeed, the lowest $\delta^{13}C$ values are observed within level 18, suggesting that the ibex niche shifted from the Solutrean to the Magdalenian. Altitude is likely to be the factor affecting these values, given the preference of ibex to inhabit higher altitudes when conditions allow this (Freeman, 1973; Schroder and Kofler, 1984; Wiersema, 1984; Martínez and Martínez, 1987; García-González and Cuartas, 1992; Martínez, 2002). Elevated $\delta^{13}C$ values are seen in plants growing at these higher altitudes (Tieszen *et al.*, 1979; Körner, Farquhar and Roksandic, 1988; Körner, Farquhar and Wong, 1991). Archaeologically for instance, increased tooth carbonate $\delta^{13}C$ values of Middle Palaeolithic ibex from Valdegoba (Burgos, on the high plateau of Old Castile, northern Spain) were interpreted as resulting from animals grazing at higher altitudes (Feranec *et al.*, 2010). The lower ibex $\delta^{13}C$ in the Solutrean, relative to the Magdalenain levels, suggests that the ibex were habitually occupying lower altitudes than seen later in the sequence, and could be indicative of more impoverished conditions. Higher altitudes typically have lower diversity and density of plant species (Montalvo *et al.*, 1993), which would be further reduced during periods of cold climate. This fact may explain why ibex were living at lower altitudes during the Solutrean. However, from the Lower Magdalenian onwards, the shift in the ibex $\delta^{13}C$ increase, relative to the individuals analysed from the Solutrean, suggests that there may have been an improvement in environmental conditions at altitude, with sufficient vegetation to support ibex in their preferred niche of higher and rocky escarpments.

At Las Caldas, the consistently lower $\delta^{13}C$ values of red deer, relative to ibex, suggest that red deer were routinely inhabiting lower altitudes, reflecting the two species' different ecological niches, and were likely hunted in different parts of the landscape. This contrasts with results of studies of other contemporaneous regional sites. For instance, the late Last Glacial site of La Riera in the coastal zone of Asturias, located 100km away to the NE of Las Caldas, where deer and ibex were feeding at similar altitudes, as no difference in $\delta^{13}C$ values was seen between the two species in either the Solutrean or Magdalenian (Jones et al. 2020), and suggest that a mosaic environments (the site is on the coastal plain but is near the base of a steep, rocky mountain range) may have facilitated survival in the Cantabrian Region. Distinctive micro-environmental biomes, surrounding archaeological sites, may have helped fauna survive by adapting in different ways, making them suitable prey for Late Glacial hunter-gatherers. The presence of Late Pleistocene mosaic environments have also been observed isotopically in the Upper Paleolithic cave sites of the Swabian Jura (southwestern Germany) with its deep, cliff-lined valleys (Wong *et al.*, 2020) and during the Magdalenian at Kůlna Cave in the gorge-rich Moravian karst of the Czech Republic (Reade *et al.*, 2021). Diversity in habitatsmay have played an important role in enabling humans and animals' continued presence in the late Upper Palaeolithic throughout Europe.

The red deer is the dominant prey species at Las Caldas (Figure 4, Table 8), despite climatic and environmental fluctuations, which is a testament to its resilience. Red deer are flexible in their diet and habitats. As intermediate feeders, they can both graze and browse (Gebert and Verheyden-Tixier, 2001). Studies of Mediterranean red deer show how well they can alter their diet between drier and wetter years, according to the availability of different resources (Bugalho and Milne, 2003). Their ability to adapt to environmental conditions may explain their reliability as a prey species in the region, particularly during the more difficult conditions of the Middle and Upper Solutrean levels 18, 15, 11 and 9, in which red deer accounted for at least 75% of the NISP at Las Caldas (Figure 4). A combination of both red deer's flexibility and favourable conditions for survival in the Cantabrian region, may help explain the species' constancy throughout the Upper Palaeolithic. Additionally, the exploitation of supplementary species during the later Upper Palaeolithic in the region, e.g., horse and later ibex at Las Caldas (Figure 4), and ibex at La Riera (Altuna, 1986), and El Mirón (Marín-Arroyo, 2009b), appears to have been fundamental to human survival, ensuring economic stability, even during climatically challenging times. Diverse mosaic environments in the region, produced by the high relief topography, of mountains and deep valleys adjacent to a narrow coastal zone may have played an important role in the survival of different species during climatic and environmental changes.

4.4. Shifting economic strategies and mobility to environmental change

The shift towards improved conditions during the end of the Solutrean and the onset of the Magdalenian coincides not only with a technology change but also in the proportions and types of prey species exploited (Figure 4). An increase in ibex NISP occurs from level IX onwards, as ibex once again began to inhabit their preferred habitat of rocky excarpments and suggests an amplification of hunting zones into mountainous rocky regions, that had been previously under-exploited. Maximum travelling time to procure ibex, based on from sites in Northern Spain, is estimated to be around 1-2 hours (Marín-Arroyo, 2009). Las Caldas lies in a small side- valley, with steep cliffs lining a narrow stretch of the Nalon upstream (south) of the site, which would have been ideal habitat for ibex around 6km distant be well within the human hunting range (Figure 1).

The exploitation of a wider variety of environmental zones during the Magdalenian is further evidenced by chamois being more strongly represented, accounting for between 5-10% of , a species which typically have a preference for forests (Acevedo *et al.*, 2005), and today in central Spain preferentially inhabit mesic mountain forests (Virgós and Tellería, 1998), the ungulate NISP between levels IX to IV (Figure 4). Modern-day chamois within the neighbouring province of Cantabria have been shown to have as diet comprised of predominantly grass-forb and shrub, with animals inhabiting subalpine meadows and shrublands (Pérez-Barberia *et al.*, 2014), with very low frequencies in forested areas (Perez-Barberia and Nores, 1994). This is indicative of more meadow and steppic environments being exploited in the Late Glacial. Roe deer is a species which typically has a preference for forests (Acevedo *et al.*, 2005), and today in central Spain preferentially inhabits mesic mountain forests (Virgós and Tellería, 1998). Procurement of roe deer in the Magdalenian points to the exploitation of this new and expanding Late Glacial habitat. The representation of species from a range of environmental biomes indicates that not only was a rich mosaic of habitats available during the Magdalenian, but humans were routinely exploiting a variety of different habitats (incluing the littoral at sites near the coast, such as La Riera Straus and Clark 1986). The Magdalenian faunal assemblage at Las Caldas suggests that these hunters exhibited greater flexibility in the strategies they employed, procuring species from a range of habitats as they expanded their hunting ranges towards the mountainous and forest zones, facilitated by more sophisticated hunting technologies observable within the material culture recorded in these levels (Mateos, 2017). The appearance of specialised tools, such as spearthrowers, appearing at the site from the Upper Solutrean onwards (Corchón Rodríguez and Martínez, 2017), would have enabled more intensive hunting over larger distances. Targeting of resources from different environmental zones may have helped to increase encounter rates and maximise hunting returns.

The Bayesian models of skeletal representation can help to inform on carcass transportation, hunting ranges and attrition (Table 8). Analysis of the horses suggests that they were being brought to the site as complete carcasses, based on their α parameter values of around 0, in the three levels where data are available (Upper Solutrean level 11, and Old Middle Magdalenian levels IX and VIII) (Table 9), suggesting that they were hunting at closer distances on the broad fluvial plain of the Nalón valley downstream of Las Caldas. Horses decline in importance, notably in the Evolved Middle Magdalenian (Table 7, Figure 4), which could suggest that they were not being encountered in such large numbers in the site's immediate locality. The lower frequencies of horses, a previous staple at the site, might have contributed to the need for hunters to exploit wider ecological zones to find sufficient nutrition.

The skeletal profile analysis of the red deer and ibex suggests that throughout the Solutrean red deer and ibex were predominantly being brought to the site complete, implying that they were being transported over relatively short distances (Figure 5; Table 8). This is also true for Magdalenian levels XII, IX, VIII, VII, IV (Table 8). Complete carcass representation of major prey species were noted within the Magdalenian deposits at Coímbre cave in Asturias (Álvarez-Alonso *et al.*, 2016), indicative of similarities in landscape use and travelling distances across a wider area. A notable exception to significant carcass transport was seen in level V, where there is a tendency towards transporting more axial elements of red deer, and more appendicular parts of ibex (Table 8), indicative of either more selective transport of body parts, or more intensive processing at the kill sites. The more intensive processing of carcasses is indicative of greater transport distances, with hunters having to travel longer to find the resources that they needed and suggests that there was more pressure on the environment during this time. In the Cantabrian Region, it has been proposed that populations moved between base camps, and specialised logistical sites in the Cantabrian Region during the Magdalenian (Straus 1986; Marín-Arroyo, 2009b, 2009a) (Straus and Clark, 1986) to make full use of available resources and ensure survival, which may have occurred when encounter rates became too low within the maximum hunting ranges.

Despite somewhat improving environmental conditionsduring the Magdalenian and with ibex shifting back to their preferred montane habitat, the archaeozoological evidence suggests greater pressure on resources. A high level of bone fragmentation, even of small bones including phalanges for marrow extraction was noted within levels VIII (Middle Magdalenian), XII (Lower Magdalenian) (Mateos Cachorro, 2002, 2003). The Bayesian analysis of the skeletal profiles provides further detail on this. The β parameter values of ibex show an opposite trend to the red deer in the Magdalenian (Figure 5, Table 8), indicative of higher levels of attrition of red deer bones relative to ibex. This could suggest more intensive processing of the larger red deer bones for grease and marrow extraction. Intensive bone processing is a trend seen within other Middle Magdalenian occupations in the Cantabrian Region (Nakazawa *et al.*, 2009), indicative of more intense pressure on resources. Other indicators of resource stress are observed at Las Caldas, such as an increase in the exploitation of low-ranking prey beginning in the Old Middle Magdalenian as seen in the MNI and to a lesser extent the NISP (Figure 5). Greater diversity in species exploitation is suggested by the increasing inverse Simpson’s index values for MNI (Figure 5). During the Magdalenian, marine shells and crustaceans were also present (Corchón *et al.*, 2008), and during the Middle Magdalenian, there is evidence of fishing for salmon and trout at the site (Corchón 2005; Corchón 2006), pointing to the exploitation of wider resource bases. The ratio of juveniles to adults shows a sharp decline in lower Magdalenian level XII (Figure 5). The ratio increases again in the old Middle Magdalenian (level IX) (Figure 5) suggesting additional pressure on hervibore populations, likely linked to increased numbers of human groups in the region during this period of ameliorated conditions. The ratio of juveniles to adults then drops again, between levels VII-IV, as the Middle Magdalenian progressed (Figure 5). It is possible that increased hunting ranges, wider resource exploitation and intensive extraction of nutrition from animals captured, might have inadvertently provided have helped to mitigate some of the pressures on faunal populations, when these levels were occupied at Las Caldas.

The δ^{13}C and δ^{15}N results show that despite improved conditions in the Magdalenian, with animals inhabiting their preferred niches, there was a need for more intensive exploitation of the primary regional game species and exploitation of a wider range of habitat biomes. This fact suggests that human population increase may be responsible for the shifting economic strategies observed, rather than environmental change, corroborating findings at other contemporary regional sites such as La Riera and El Mirón (Straus 1977; Marín-Arroyo, 2009a; Jones *et al.*, 2020). An increase of ~15 sites per millennia in the Cantabrian Region during the Magdalenian is indicative of rapid population growth (Straus, Bicho and Winegardner, 2000a, 2000b), undoubtedly putting additional pressure on resources, despite ameliorated conditions allowing animals, such as ibex, to thrive in their preferred niches. Greater population mobility is also seen during the Magdalenian, potentially linked to these improved environmental conditions, and the necessity to travel larger distances to obtain sufficient food supplies to feed an ever-growing population. Engraved and perforated marine mammal teeth (Corchón Rodriguez and Alvarez Fernández, 2008) and whale-bone ornaments (Lefebvre *et al.*, 2021) suggesting movements to the coast and/orPyreneo-Cantabrian down-the-linetrade/exchange networks. Longer distance transportation of lithics attests to more significant movement of populations with some lithic artifacts found at Las Caldas deriving from the Western (French) Pyrenees (Corchón, Tarriño and Martínez, 2007; Corchón Rodríguez, 2017a), a characteristic observed across the wider Cantabrian region during the Magdalenian (Tarriño, Elorrieta and García-Rojas, 2015; Fontes, Straus and González Morales, 2016). Shifting environmental conditions have been proposed as a possible model to explain the extensive distances covered to exploit raw material in the Lower Magdalenian (Fontes, Straus and González Morales, 2016). This hypothesis is supported by the isotopic evidence from Las Caldas. Opening up of new environments and amplified ecological biomes may have drawn hunter-gatherers to the region and allowed successful breeding of existing populations in the region. Ultimately this would have resulted in producing larger human populations, in addition to facilitating greater levels of connectivity across the Franco-Cantabrian region.

5. Conclusions

The stable isotope analysis of red deer and Spanish ibex at Las Caldas has demonstrated that environmental shifts occurred from the Solutrean (26.1-20.3kyr cal BP) to the Magdalenian (18.5-14.3yr cal BP), as reflected by changing bone collagen δ^{13}C and δ^{15}N values, impacting on both animal and human behaviour. During the Solutrean, the environment was hostile, with lower δ^{13}C values in all levels, and by the lower δ^{15}N values in the Upper Solutrean reflecting cold and potentially wet conditions. Additionally, the lower δ^{13}C values of the ibex during the Solutrean suggests that they were living at lower altitudes, which is outside of their preferred habitats. In the Magdalenian, climatic amelioration is expressed by increased δ^{13}C and δ^{15}N values. The higher δ^{13}C values of the ibex show that their niche shifted and they started living at higher altitudes again, likely due to lessened snow cover and increased vegetation on higher slopes. Improved conditions may have been a draw for human populations to the area, as well as possible increased birth rates due to greater security in nutrition. Ameliorated conditions and larger human populations in the Magdalenian coincide with changing economic strategies, as habitats and biomes for various fauna improve, and a greater diversity in species is exploited. Some evidence of resource pressures is also seen at this time, with an intensification of carcass processing, and exploitation of more low-ranking prey species, despite improved environmental conditions. This fact is hypothesized to be due to the need to feed larger populations. The presence of the resilient and stable prey of red deer, alongside a supplementary species (horse or ibex), may explain why this region was able to serve as a refugium during the LGM for a host of different flora, fauna and humans.

This research provides valuable insights into the changing environmental conditions experienced during the Last Glacial Maximum in the Cantabrian Region, and how this impacted on the faunal populations, and the humans who were hunting them. Characterising the shifting niche and habitat preferences, resulting from environmental change during the Palaeolithic, can help us understand the pressures facing faunal species in the world today, and the complex interactions occurring between humans, animals and the environments they inhabitated.

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