

What Neanderthals and AMH ate: reassessment of the subsistence across the Middle–Upper Palaeolithic transition in the Vasco-Cantabrian region of SW Europe

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Received 14 September 2020; Revised 1 February 2021; Accepted 5 February 2021

ABSTRACT: Recent research in northern Spain has revealed the disappearance of Neanderthal populations in the Vasco-Cantabrian region a few millennia earlier than in eastern and southern Iberia and discovered a short period of overlap with modern humans, at least, in terms of radiocarbon dates. However, the causes of Neanderthal decline understood as a regional and temporal process remain open. Despite the abundance of technological studies, modern-quality chronological dating, and the availability of archaeofaunal and palaeoenvironmental data, there is a lack of consensus about how climatic and environmental conditions could have affected ungulate prey and, therefore, Neanderthal subsistence strategies. In this paper, an analytical summary of the archaeofaunal and taphonomic data available for the Vasco-Cantabrian region, combined with the most recent chronological evidence, present general knowledge about animal biogeography and ecology during the Middle–Upper Palaeolithic transition, and provides an interpretation of the behaviour of both human species in the region. This work reviews the palaeomammal community of animals represented in the record as exploited by human groups in several caves and rock shelters and pointing to continuing lacunae in knowledge. Further research is needed to verify and potentially explain the apparent hominin population gap and the ultimate fate of the Neanderthals.

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KEYWORDS: Neanderthals; Anatomically Modern Humans (AMH); MIS3; Vasco-Cantabrian region; Archaeozoology

Introduction

The causes of Neanderthal decline are still an open debated issue in human evolutionary studies. In recent decades, multidisciplinary studies have been revealing novel and surprising discoveries about who Neanderthals were as humans, their efficiency in technology and hunting skills (Villa and Soriano, 2010; Aranguren *et al.*, 2018; Hardy, *et al.*, 2013, 2020), their diet breadth (Cortés-Sánchez *et al.*, 2011; Hardy and Moncel, 2011; Cochard *et al.*, 2012; Bocherens *et al.*, 2016; Terlato *et al.*, 2019; Zilhão *et al.*, 2020), their treatment of death (Pettitt, 2002; Rendu *et al.*, 2014), their artistic skills (Zilhão *et al.*, 2010; Peresani *et al.*, 2011; Hoffmann, *et al.*, 2018), and even their genome and how they interbred with our own species and with Denisovans (Hajdinjak *et al.*, 2018; Slon *et al.*, 2018). All these features expose a closer resemblance to our species than we had previously thought. But, despite a relatively short temporal overlap with anatomically modern humans (AMH) in different regions of western Eurasia, Neanderthals failed to survive, disappearing within less than 7,000 years of their first encounters with AMH (Higham *et al.*, 2014; Davies *et al.*, 2015; Hublin, 2015; Fewlass *et al.*, 2020). It is widely accepted today that the Neanderthal demise was not an identical and simultaneous continent-wide process. Regional and temporal variation must be considered globally to disentangle the understanding of the evolutionary history and mechanisms that shaped *Homo sapiens* survival, thus limiting the bias in our interpretations.

Iberia is one of the crucial areas for understanding how the human biological replacement occurred, specifically, the Vasco-Cantabrian region in northern Spain. This region, with more than 150 years of Palaeolithic research since the discovery of Altamira, contains one of the richest archaeological records of the presence of late Neanderthals and early modern humans, but in the form of artefacts only, in the absence of well-dated, diagnostic hominin remains. The abundant and well-preserved caves and rock shelters have provided abundant evidence on the archaeological record of both human species, mostly studied in terms of lithic technology and raw material procurement. However, a limited record of human remains exists in the region for the late Mousterian. Notably, El Sidrón in Asturias, dated to c. 49 k ¹⁴C a BP by several chronometric methods (Torres *et al.*, 2009; Wood *et al.*, 2013) contains some of the latest Neanderthal remains in Iberia. At the nearby site of La Güelga, several human teeth and bone fragments with Neanderthal features were found in Level 9-D interior (Menéndez *et al.*, 2014). The transitional Châtelperronian industry has been found at very few sites (Cueva Morín Level 10 in Cantabria (González Echegaray and Freeman, 1971), Labeko Koba Level IX in Guipúzcoa (Arrizabalaga, 2000) and Aranbaltza (Ríos-Garaizar *et al.*, 2012a). The lack of any human skeletal remains in this transitional period has prevented further interpretations relative to the makers of this technocomplex, who remain unknown today in Spain, in contrast to the French Châtelperronian levels at Saint-Césaire and Grotte du Renne, where Neanderthal skeletal remains were found. In Level 18B of El Castillo Cave, classified as 'Transitional Aurignacian' (Wood

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et al., 2018), there are several isolated deciduous teeth, with advanced states of wear that prevent a diagnostic species attribution, although some authors propose similarities in size and morphology with Neanderthals (Cabrera *et al.*, 2005; Garralda, 2006).

Recent research has revealed the earlier disappearance of Neanderthal populations in northern Atlantic Iberia than in the eastern and southern regions, where it occurred a few millennia later, although the last dates at Bajondillo cave (~45–43 k cal a BP) and Lapa do Picareiro (~41–38 k cal a BP) have documented a modern human presence in the southern and western margins of Iberia earlier than previously thought (Cortés-Sánchez *et al.*, 2019; Haws *et al.*, 2020). Recently, an overlap of Châtelperronian and early Aurignacian industries for around a millennium has been proposed (Marín-Arroyo *et al.*, 2018). The new chronological advances force us to re-review and rethink previous theories about Neanderthal extinction, including the Ebro Frontier hypothesis (Zilhão and Trinkaus, 2002; Zilhão, 2000, 2006; Cortés-Sánchez *et al.*, 2019) or the stratigraphic discontinuity between both human species (Mallol *et al.*, 2012). In the Vasco-Cantabrian region, the coexistence of the Châtelperronian with the early Aurignacian is not manifested by interstratification in the archaeological record; nor is this the case, according to the latest evidence, in France, with sequential stratigraphic positioning of these two technocomplexes in Saint-Césaire or Arcy-sur-Cure. The few sites with transitional industries are limited to usually small lithic assemblages and only rare osseous ones (notably Grotte du Renne). But today, hypotheses about Neanderthal decline due to the rapid and acute climatic oscillations of the late MIS3 (D'Errico and Goñi, 2003; Finlayson and Carrión, 2007; Fedele *et al.*, 2008; Finlayson *et al.*, 2006, 2008) with AMH already in the continent are still untested in this region. The reason for that is the scarce regional climatic proxies directly related to where humans lived. There are several available climatic proxies, but, for instance, macromammals are not generally detailed climatic indicators, as many of the species represented in regional archaeological contexts such as ox, bison, horse, red deer and ibex are eurytherms. When available, micromammal and pollen studies are more precise about the palaeoenvironment and palaeoclimate. Unfortunately, the lack of macrobotanical evidence is limited in archaeological assemblages for this transitional period.

Macromammals predominate, among the biological remains, as they were (at least mostly) accumulated by Neanderthals and AMH as part of their diet. Therefore, they provide direct and essential evidence to get at both subsistence and ecological settings. By focusing, on the one hand, on either herbivores exploited (or not) by humans and, on the other hand, on carnivores, precise information about subsistence strategies, resource availability and predators will be of relevance to recognise the behavioural choices adopted by Neanderthals and AMH, the role that carnivores could have played at different times, and the ecological niches exploited. At the same time, the mammals can be of relevance for climatic and environmental reconstruction and for showing the availability of animal resources in the region during late MIS3 (57–29 k cal a BP), reflecting turnovers in mammal palaeocommunities due to global climatic oscillations. In fact, a recent approach to climatic reconstruction by measuring δC^{13} , δN^{15} and δS^{34} stable isotopic values on ungulate collagen of animals consumed is providing insights about the Vasco-Cantabrian palaeolandscapes around such sites as El Castillo, Covalejos, Axlora, Amalda, Ekain, Labeko Koba and Aitzbitarte III in Cantabria and the Basque Country (Jones *et al.*, 2018, 2019).

Archaeozoological studies maintain a long tradition in the region, starting in the 1970s by the pioneer J. Altuna (1972),

with a palaeontological focus. Economic interpretations of the faunal records were also undertaken from the perspective of Americanist processual archaeology, beginning in the mid-1970s, notably with the syntheses of L.G. Freeman (1973, 1981) and L.G. Straus (1977, see also 1992, 2013) and the La Riera Cave Palaeoecological Project, for which Altuna was the mammalian archaeozoologist (Straus and Clark, 1986). It was not until the early 2000s, however, that taphonomic methods were broadly applied to regional archaeofaunal assemblages for multiple purposes: unravelling site formation processes, identifying the main bone accumulators and the role of humans and other non-human biological agents in the formation of the macrofaunal assemblages. Today, the role of taphonomy is undoubtedly a key aspect of archaeozoological studies, in combination with other approaches such as spatial analysis (Marín-Arroyo *et al.*, 2020; Sánchez-Romero *et al.*, 2020), diagenetic alteration studies and site catchment analysis, among others. These multidisciplinary techniques are providing a complete picture of the living conditions humans had to face. However, despite the abundance of MIS3 archaeofaunal assemblages, our understanding of the exploitation of the environment, the role of carnivores and the subsistence strategies undertaken by late Neanderthals and early modern humans in the region are blurred. This lack of knowledge has several causes: firstly, some key sites were excavated during the 1950s, 60s and 70s and were not or only poorly dated. Recent research to assess chronologically the Middle to Upper Palaeolithic transition and Early Upper Palaeolithic cultures in Vasco-Cantabrian region provided dates older and/or younger than expected. Examples of these are some levels in Llonín, Bolinkoba, El Cuco and Ekain (Marín-Arroyo *et al.*, 2018) forcing us to reevaluate their archaeological assemblages (Gutiérrez-Zugasti *et al.*, 2018; Ríos-Garaizar, 2020) and, in some cases, to discard some of them for revealing admixture caused either by carnivores, by other post-depositional processes not identified during the excavations or by curatorial problems as in the case in Morín, El Otero, El Ruso and Cobrante (Marín-Arroyo *et al.*, 2018). Secondly, many of the sites lack a complete archaeozoological study, providing brief quantification information such as numbers of remains and/or minimum numbers of individuals, but without taphonomic analysis or data about age and skeletal profiles, the identification of the main bone accumulator or of post-depositional processes.

In what follows, the available archaeozoological evidence from regional sites that have been recently chronologically reviewed and/or re-dated and, thus, have clear attributions to the late Mousterian, Châtelperronian and/or Aurignacian are summarised. The assumptions that Mousterian and Châtelperronian industries were of Neanderthal authorship and that the Aurignacian assemblages were made by modern humans are generally accepted in this paper. This work aims to identify the gaps in the knowledge about this transitional period in terms of mammal palaeocommunities that provide evidence about the subsistence strategies and environmental exploitation by Neanderthals and the first *Homo sapiens* in the region. This article is proposed as an incomplete review, as not all the culturally attributed levels from the region are included, but with those that are included, because dated, it will be possible to evaluate the most common ungulates represented in the assemblages and their role in the Neanderthal and early *Homo sapiens* diets, the identification of predators, the uses of the cave sites by humans and carnivores and the human nutritional choices made in each period. In addition, the role of the economic decisions taken in

relation to the topographic location of each site will be assessed.

Materials

The Vasco-Cantabrian region is constituted by the modern-day Spanish provinces of Asturias, Cantabria, Vizcaya, Alava and Guipúzcoa. Because they contain important sites relevant to this transitional period, to the latter three Peninsular Basque provinces can be added the traditional French Basque provinces of Labourd, Basse-Navarre and Soule, which form the western part of the Department of Pyrénées-Atlantiques. Geographically, this mid-latitude (c. 43–44° N) region is a well-defined entity backed to the south by the Cantabrian Cordillera with peaks of about 1500–2600 m.a.s.l and north the Cantabrian Sea–Bay of Biscay–Gulf of Gascony (Straus, 2015). The Vasco-Cantabrian region is some 350 km long on a west–east axis from the Nalón River in central Asturias to the Bidasoa in Guipúzcoa. The Basque sector is linked to Mediterranean Spain via the Ebro River Basin to the South of the Pyrenees. In general, the east–west-oriented tributaries of the main south–north river valleys create continuous avenues of communication as did the generally narrow coastal lowlands. During the Upper Pleistocene, prehistoric human settlement would have been necessarily organised along the main river valleys into well-defined territorial entities that presumably delimited economic activities and the relative intensity of social relations (Straus, 2015).

To evaluate the subsistence strategies and environmental exploitation carried out by late Neanderthals and early AMH in the Vasco-Cantabrian region, several key archaeological sites and levels attributed to the Mousterian, the Châtelperronian and the Aurignacian cultural technocomplexes based on their stratigraphic position, material culture and radiometric dates were selected. Although there are more archaeological levels corresponding to these periods, some were excluded from this study due to the lack of radiometric dates. These sites are situated in the modern-day provinces of Asturias in the west, Cantabria in the centre and the Spanish and French Basque Country in the east (Fig. 1). A total of 17 sites have been selected: La Viña, La Güelga and Llonín in Asturias, Esquilleu, El Castillo, Covalejos, Morín, El Mirón and El Cuco in Cantabria, Axlor, Arrillor, Labeko Koba, Ekain, Amalda and Aitzbitarte III in the Spanish Basque Country. Finally, from the

French Basque Country, Isturitz and Gatzarria were also included because they are very close to the Franco-Spanish border at the western end of the Pyrenees. The description of each site is provided in the Supplementary Information (SI1). For the Mousterian period, the macromammal data from 16 archaeological levels were included for this study: La Viña XIII basal, La Güelga D interior 9, Axlor IV, Arrillor Amk, El Castillo 20 C, El Mirón 130, El Cuco Vb, El Cuco X, El Cuco XIII, Llonín VIII Cono Posterior, Esquilleu VI, Amalda VII, Arrillor LMC, Arrillor Smk-I, Covalejos D and Gatzarria Cj. These levels have been initially grouped by their chronology according to their uncalibrated radiocarbon dates but later analysed individually. For the Châtelperronian levels, only two levels were considered: La Güelga D Interior Levels 1–2 grouped together for the remains scarcity and Labeko Koba IX Inferior. Finally, a total of 20 levels have been included for the Aurignacian, which are El Castillo 18B, El Castillo 18 C, Labeko Koba VII, El Castillo 16, Isturitz Proto-Aurignacian, La Güelga 5, Covalejos C, Covalejos B, El Cuco III, Aitzbitarte III ext Vb, Labeko Koba VI, Labeko Koba V, Labeko Koba IV, Ekain IXA, Isturitz Aurignacian 'intermédiaire', Isturitz Aurignacian ancient, Ekain IXB, La Viña XIII, XII and XI (Table 1). Despite being considered one of the key sites in the region, the lack of coherence in the chronology of Cueva Morín's Late Mousterian (Levels 11 and 12), Châtelperronian (10), and Proto-Aurignacian (Levels 8, 9) levels, as well as the lack of faunal data from Levels 11–12, excluded them from this study.

Methods

As stated above, this research was focused on the analysis of the macrofaunal remains from 17 archaeological sites and 38 selected levels (Table 1). By using the published literature, in combination with ongoing archaeozoological studies carried out by the authors of this paper within the SUBSILIENCE project (Marín-Arroyo, 2019), the methodology was focused on determining the relevance of the ungulates exploited for nutritional purposes and on comparing their exploitation as determined by choices made by the two human species throughout time. Identifying the role of carnivores represented in the faunal assemblages and evaluating the abundance and types of ungulate prey and from that, extrapolating information about Neanderthal and AMH subsistence strategies was also assessed.

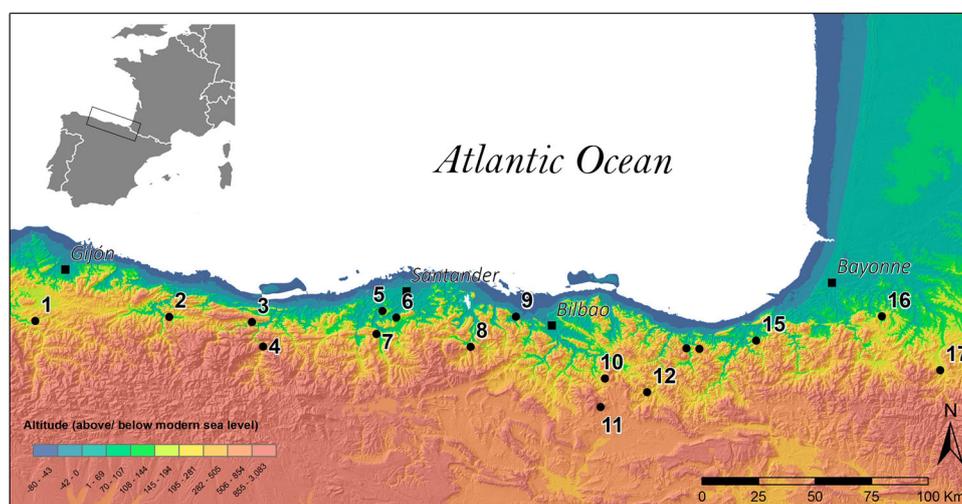


Figure 1. Location of the archaeological sites in the Vasco-Cantabrian region. 1. La Viña; 2. La Güelga; 3. Llonín; 4. Esquilleu; 5. Covalejos; 6. Morín; 7. El Castillo; 8. El Mirón; 9. El Cuco; 10. Axlor; 11. Arrillor; 12. Labeko Koba; 13. Ekain; 14. Amalda; 15. Aitzbitarte III; 16. Isturitz; 17. Gatzarria. [Color figure can be viewed at wileyonlinelibrary.com].

Table 1. Archaeological sites and levels included in this study organised by cultural periods and radiocarbon chronology based on their uncalibrated dates BP.

Culture Date BP	Mousterian			Châtelperronian			Aurignacian			
	>45,000	49-46,000	45-42,000	40,000	38-37,000	46-45,000	43-42,000	39-36,000	35-32,000	32-30,000
Archaeological levels	La Viña XIII basal	Castillo 20C	Lionin VIII Cono Posterior	La Güelga D Int 1-2	Labeko Koba IX inf	El Castillo 18B	El Castillo 18C	Labeko Koba VII	La Güelga 5	Ekain IXB
	Axlor IV	El Miron 130	Esquilleu VI					El Castillo 16	Covalejos C	La Viña XIII
	Arrillor Amk	El Cuco Vb	Amalda VII					Isturitz Proto-Aurignacian	Covalejos B	La Viña XII
		El Cuco X	Arrillor LMC						El Cuco III	La Viña XI
		El Cuco XIII	Arrillor Smk-I						Aitzbitarte III ext Vb	
			Covalejos D						Labeko Koba VI	
			Gatzarría Cj						Labeko Koba V	
			La Güelga D9 Int						Labeko Koba IV	
									Ekain IXA	
n levels	3	5	8	1	1	1	1	3	11	4
									Isturitz Aurignacian "intermediaire"	
									Isturitz Early Aurignacian	

To do so, firstly, a compilation of published archaeozoological and taphonomic data was assembled, including the number of identified specimens (NISP) and minimum number of individuals (MNI) values, prey age, and taphonomic interpretation of each assemblage. Analytically those data were processed by taking a series of analytical steps. First, to assess the diet breadth, the Inverse of Simpson's Index was calculated for the NISP and MNI values, respectively, when available. It quantifies taxa diversity by considering richness and evenness. The greater the diversity of ungulate species, the higher the value. Next, the ratio between juvenile and adult individuals was estimated to measure the pressure on low-return younger prey. The ratio of high to low prey ranks to evaluate the selection of the prey hunted was also calculated. That ratio was used to assess what kind of ecological areas (coastal plains, broad river valleys, wooded areas and mountainous zones) were exploited, based the topographic location of each site by calculating the relationship between mountain areas, fluvial/coastal plains and forested areas. Roe deer, chamois and wild boar were considered low-ranked species, while the rest of the ungulate prey were considered to be high-ranked (red deer, ibex, horse, bovines (bison and/or aurochs)). This classification was based on the travelling times from a central point and the economic input obtained from the prey according to previous studies in the region during the Palaeolithic (Marín-Arroyo, 2009a). The ratio of carnivores to ungulates was calculated to observe the changing representation of carnivores throughout time. A separation between large, medium and small-sized carnivores was achieved to differentiate the role that medium-sized and large carnivores, especially, could have had as prey accumulators among the faunal assemblages. According to the body size of the carnivores, these were grouped into three categories: large carnivores includes *Ursus spelaeus*, *Ursus arctos*, *Panthera leo*; medium-sized includes *Panthera pardus*, *Crocota spelaea*, *Crocota crocuta*, *Canis lupus* and *Cuon alpinus*; and small-sized are *Felis silvestris*, *Vulpes vulpes*, *Vulpes lagopus* and *Meles meles*. To evaluate the role that large and medium-sized carnivores could have had in the accumulation of ungulate prey, a ratio between the group of *Panthera leo*, *Panthera pardus*, *Crocota spelaea* and *Crocota crocuta* in relation to all the other carnivores represented by level was calculated.

Lastly, the calculations of the catchment area around each site, for 1.2 and 2.15 h (calculated with the ISOCRONAS software based on a Digital Elevation Model for the area of study according to previous studies in the same region; see Marín-Arroyo, 2009c) were correlated with the types of ungulate prey prominently represented at each site. Catchment areas associated with steep, rocky terrain and lowland (sometimes woodland)-adapted animals were defined and topographically characterised for the different sites. The verification of hunting specialisation at each site, based on the surrounding environment, is based on the correlation between the topographic factor and the preferred type of hunted game. The *topographic factor* is defined as the quotient between the montane surface at a distance of less than 1.2 h and the plain surface at a distance of less than 2.15 h from each site. This factor quantifies the susceptibility of the environment near the settlement to sustenance rocky species. The higher this quotient, the higher the proportion of montane areas and the greater the hunting possibilities of its associated species. On the other hand, the *hunting preference* is calculated as the quotient between the NISP or MNI identified in the fossil record as taxa associated with the montane habitat *vis à vis* those of the plain. The ibex and chamois are montane-adapted species. The ibex is not exclusive to high mountains, but is well-adapted to all mountains with rocks, while the

chamois is an ecotonal species, which lives on the border between the forest and the supra-forest pastures, and usually uses the steep and rocky areas as an escape and refuge; the red deer, the roe deer, the giant deer, the fallow deer and the wild boar are animals that could have inhabited wooded areas (though not exclusively) and the mammoth, the woolly and steppe rhinoceros, the reindeer, the horse and the bovines are generally animals that favour open landscapes. The use of the NISP or the MNI to characterise the hunting specialisation recorded in a faunal record is not an easy decision, since neither constitutes an entirely valid quantification measurement. In reality, the actual number of individuals hunted and consumed should be used, but it is a value that is not archaeologically available, thus we must use the correlation of the NISP and the MNI, since both values considered at least constrain the numbers of individuals that are represented. Within each area, it is possible to discriminate between the montane and lowland/plains areas by classifying the space in areas with a slope greater than or less than 30°, estimating the area associated with each of them by quantifying the respective cells.

During the data analysis process, several limitations were found, as follows. Some of the sites lack taphonomic studies, but when available, the taphonomic information was of relevance to determine the alternation of carnivores and humans in caves and to understand the role of human species in ungulate assemblage accumulation. On the sites where taphonomic data related to anthropogenic and natural agencies were not available, the relevance of the other archaeological evidence recovered in each level was evaluated to consider the anthropic origins of the macromammal assemblage. Other limitations were the absence of MNI or NISP values (and, for most of them, the lack of MNE) and prey age data in several levels within each cultural period. Nevertheless, it would have been of relevance to unravel the type of ungulate prey transport that was done by humans during the time of formation of each level. Unfortunately, the uniformity or absence of the data on skeletal profiles representation limited the achievement of this kind of analysis so far.

Results

Chronological data

A compilation of 82 published radiocarbon dates, 75 of them done with ultrafiltration methods, for the levels and sites included in this study was assembled. To plot and analyse the macromammal data chronologically, only those levels with radiocarbon dates were included in this research. Table S1 presents the complete list of the radiocarbon dates. Except for three dates obtained on *Patella vulgate* from El Cuco, all the other dates were done on mammal bone collagen. For those dates on shells, the delta R marine reservoir correction used was -235 ± 135 (Monge Soares *et al.*, 2016). Fig. 2 shows all the calibrated dates in order of age, so there are no constraints on these data and modelling is not creating or imposing a pattern. Archaeological levels with radiocarbon dates lacking a standard deviation were excluded from this plot, including La Viña XIII basal, Axlor IV and Arrillor Amk.

The results in Fig. 2 show how some of the older dates corresponding to the Mousterian extend beyond the radiocarbon ages when plotted, as they have considerable standard deviations. In this case, one of the two dates of El Cuco X is plotted as the last Mousterian; however, a difference of almost 4,000 years between two of the dated shells from this level was noticed. Therefore, this

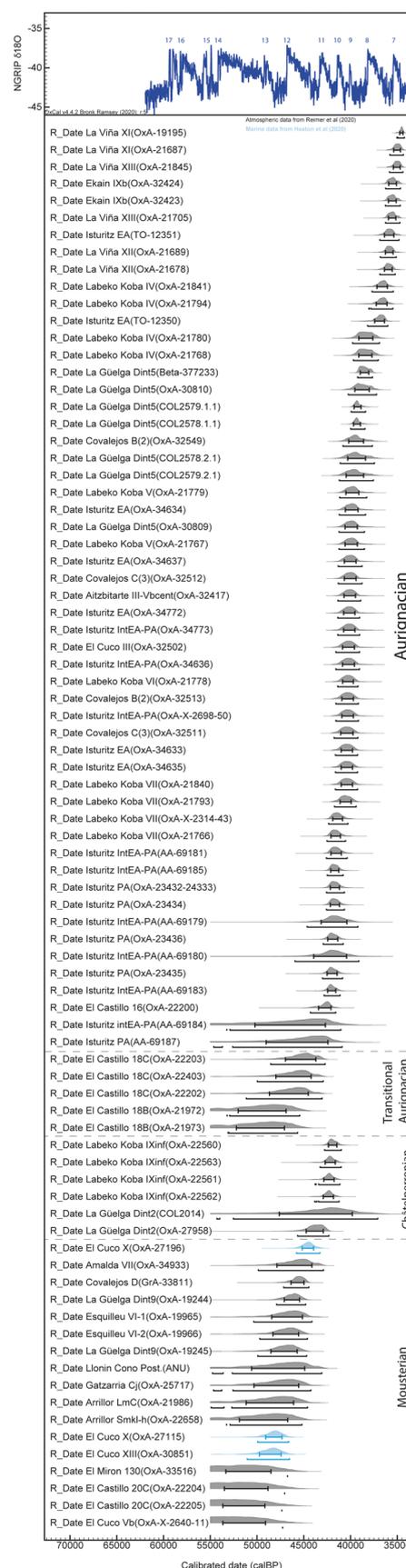


Figure 2. Plot of dated AMS ^{14}C -dated Mousterian, Châtelperronian and Aurignacian assemblages, using OxCal4.4.2 software (Bronk Ramsey 2009) with the INTCAL20 calibration curve (Reimer *et al.* 2020) and the marine data from Heaton *et al.* (2020) for the Northern Hemisphere. Dates on shells are in light blue. Further information about these sites and samples is provided in Appendix S1 and Table S1. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)].

evidence must be considered with caution. Excluding this date of El Cuco X, Amalda VII is shown to be the latest Mousterian in the Vasco-Cantabrian region (Marín-Arroyo *et al.*, 2018). For the Châtelperronian, only two levels were included, Labeko Koba IX inf and levels 1–2 of La Güelga D interior. In La Güelga one of the dates goes beyond the timing determined for this cultural technocomplex in the region of 38 000–37 000 ¹⁴C a BP (Marín-Arroyo *et al.*, 2018) and is dated at 40 300 ± 1200 ¹⁴C a BP (OxA-27958). The archaeologists at this site proposed the attribution of these levels to a Châtelperronian technocomplex due to some guiding fossils highly characteristic of this period (Châtelperron points) (Menéndez *et al.*, 2018). Unfortunately, the lack of coherence in the dating of the other Châtelperronian level 10 identified in Cueva Morín and the absence of faunal assemblage in Aranbaltza prevented its inclusion in this analysis.

Despite the fact that the term 'Transitional Aurignacian' is only used at El Castillo, it was considered relevant to differentiate the levels for which it was coined – 18B and 18C – whose dates overlap with dates for the late Mousterian at other regional sites. However, they have been plotted separately and their faunal data have been grouped within the Aurignacian period for this study. After El Castillo Levels 18B and 18C, the Proto-Aurignacian levels of Isturitz, El Castillo 16 and Covalejos C and B follow in age. The following Aurignacian levels are plotted without consideration of the various subdivision designations that have been given to them (i.e. Early, Initial or Classic) to avoid confusion in the use of such typological attributions, by different archaeologists, that go beyond the scope of this work.

Quantification values of macromammals represented

Many of the levels provided both NISP and MNI values, but not all of them (Table 2). However, the values have not been compared among them and they can only be considered as relative, not absolute, indicators of abundance. The percentages of ungulates and carnivores from the total NISP and MNI were calculated for each level (Fig. 3). The results indicate that ungulates predominate over carnivores with relative frequencies of between 45% and 100% for NISP (average value: 89%) and 47% to 100% for MNI (average value: 79%). By contrast, carnivores represented between 0% and 55% for NISP (average value: 11%) and 0% to 53% for MNI (average value: 21%). Raw data are presented in Tables S2 and S3.

Among the herbivores, *Mammuthus primigenius* appears at the end of the Late Mousterian and during the Aurignacian. The few identified specimens do not imply either their consumption or hunting. Two species of Rhinocerotidae are present: *Dicerorhinus hemitoechus* during the Mousterian and in the 'Transitional Aurignacian' at El Castillo, and *Coelodonta antiquitatis*, which is more abundant in the Châtelperronian level of Labeko Koba. Equids are present by two species: *Equus ferus*, which is widely represented throughout the studied period, with similar proportions during Châtelperronian and Aurignacian and less abundant during the Mousterian; and *Equus hydruntinus*, exclusively identified in the Aurignacian level of Covalejos B and at Isturitz. According to the MNI, Cervidae are highly represented, mostly by *Cervus elaphus* that appears significantly in all the studied levels, representing 36% during the Mousterian, 45% in the Châtelperronian and 55% during the Aurignacian. *Capreolus capreolus* and *Rangifer tarandus* appear as well, but in limited amounts compared with red deer. Reindeer is not represented during the Mousterian and is only found in the oldest levels during the Aurignacian. *Dama dama* is solely identified in the Mousterian level of Covalejos D. *Bos/Bison* sp. are represented in similar

proportions by ~12% during the transition. *Capra pyrenaica* and *Rupicapra rupicapra* are highly represented in the Mousterian and decrease drastically in the Aurignacian. Looking at the %MNI, chamois is more common than ibex. Nevertheless, these montane species are scarce during the transition. *Sus scrofa* is minimally present.

Among the carnivores, all in terms of NISP, *Ursus spelaeus* is highly represented during both the Mousterian and Aurignacian, and *Ursus arctos* appears, minimally, only during the Aurignacian. *Panthera leo* is rare during the Mousterian and Aurignacian. However, *Panthera pardus* is relatively well-represented during the Mousterian, but afterwards, it appears only anecdotally. Except in the Châtelperronian, when *Felis silvestris* is not found, this small felid appears in minuscule amounts across the transition. Lynx is not documented. Both hyena species are represented unequally across the three periods, especially during the Châtelperronian, with 92% (from a single level of Labeko Koba IX which was as a hyena den deposit). *Canis lupus* appears during the Mousterian and in the Aurignacian, but is absent from the Châtelperronian assemblages. *Cuon alpinus* appears in the Mousterian of Llonín VIII and Amalda VII. *Vulpes vulpes* is represented during the three periods and *Vulpes lagopus* appears exclusively in the Aurignacian level of Labeko Koba VII. In some sites, there is not a clear distinction between these two fox species, so both are recorded together. *Meles meles* is only represented during Mousterian. According to the MNI, *Crocuta* sp., *Ursus spelaeus*, *Vulpes vulpes* and *Panthera leo* are the most common carnivores. *Panthera pardus* is limited in number of individuals (Table S2 and S3).

Taphonomy data

Of the 17 sites included in this study, 12 provided some taphonomic information about the assemblage accumulators, diagenesis and biostratigraphic processes that occurred at each level. Those sites are La Viña (Rasilla *et al.*, 2020, n.d.; Wood *et al.*, 2014), Llonín (Sanchis *et al.*, 2019), Esquilieu (Yravedra and Gómez-Castanedo, 2014), El Castillo (Luret *et al.*, 2020), Covalejos (Yravedra *et al.*, 2016), El Mirón (Marín-Arroyo *et al.*, 2020), Amalda (Sánchez-Romero *et al.*, 2020), Aitzbitarte III (Altuna *et al.*, 2011, 2017), Ekain (Ríos-Garaizar *et al.*, 2012b), Labeko Koba (Ríos-Garaizar *et al.*, 2012b; Villaluenga *et al.*, 2012), Isturitz (Soulie, 2013) and Gatzarria (Ready, 2013). Due to the differences among sites, the analysis was not focused on the percentages of cut or gnawing marks; rather, the general interpretation of each level.

In some sites, apart from the role of human groups evidenced by the artefacts, hearth structures, the density and type of materials and the direct evidence of butchering activities on mammal carcasses and thermo-alterations, carnivores also played a significant role in the accumulation and disturbance of some of the ungulate prey, especially those of medium- to small-sized animals. In Level VIII, Cono Posterior of Llonín, Sanchis *et al.*, (2019) propose that the cave was occupied alternately by hyenas, leopards and other carnivore species, as well as by Neanderthals for short, sporadic episodes of hunting red deer and some caprines. Hyenas would mostly have been scavenging leftovers from humans and also introduced some bear remains, while leopards would have killed and transported caprines to consume them at the site. The same pattern is repeated in Amalda VII, where the multidisciplinary approach to the taphonomy of the faunal remains, together with spatial analysis and radiocarbon dates on gnawing and cut-marked bones revealed that large (bovids) and medium-sized mammals (red deer and ibex) were brought to the site by

Table 2. Summary of the total number of identified specimens (NISP) and minimum number of individuals (MNI) values and their percentages per level and sites are presented in Table S2 and S3. Note that not all the levels had both NISP and MNI values.

	NISP per period			MNI per period			%NISP per period			%MNI per period		
	Mousterian	Châtelp	Aurignacian	Mousterian	Châtelp	Aurignacian	Mousterian	Châtelp	Aurignacian	Mousterian	Châtelp	Aurignacian
	<i>Mammuthus primigenius</i>	10	0	45	0	0	6	0.17	0.00	0.27	0.00	0.00
<i>Dicerorhinus hemioitechus</i>	27	0	14	7	0	3	0.45	0.00	0.08	3.30	0.00	0.46
<i>Coleodontia a.</i>	7	92	5	0	7	1	0.12	7.35	0.03	0.00	13.73	0.15
<i>Equus ferus/Equus sp.</i>	259	210	2562	17	6	71	4.29	16.79	15.52	8.02	11.76	10.97
<i>Equus hydruntinus</i>	0	0	6	1	0	1	0.00	0.00	0.04	0.47	0.00	0.15
<i>Bos/Bison sp.</i>	728	143	1773	21	7	76	12.05	11.43	10.74	9.91	13.73	11.75
<i>Megaloceros giganteus</i>	2	0	15	0	0	7	0.03	0.00	0.09	0.00	0.00	1.08
<i>Cervus elaphus</i>	2929	792	10354	77	23	351	48.50	63.31	62.72	36.32	45.10	54.25
<i>Rangifer tarandus</i>	0	14	611	2	2	18	0.00	1.12	3.70	0.94	3.92	2.78
<i>Capreolus capreolus</i>	71	0	292	15	1	34	1.18	0.00	1.77	7.08	1.96	5.26
<i>Dama dama</i>	1	0	0	1	0	4	0.02	0.00	0.00	0.47	0.00	0.62
<i>Capra pyrenaica</i>	1025	0	55	22	0	9	16.97	0.00	0.33	10.38	0.00	1.39
<i>Rupicapra rupicapra</i>	978	0	763	46	4	61	16.19	0.00	4.62	21.70	7.84	9.43
<i>Sus scrofa</i>	2	0	12	3	1	5	0.03	0.00	0.07	1.42	1.96	0.77
Total Ungulates	6039	1251	16507	212	51	647						
<i>Ursus spelaeus</i>	239	3	813	16	2	53	43.53	5.00	46.99	39.02	28.57	37.32
<i>Ursus arctos</i>	0	0	2	0	0	3	0.00	0.00	0.12	0.00	0.00	2.11
<i>Panthera leo</i>	1	0	6	0	0	0	0.18	0.00	0.35	0.00	0.00	0.00
<i>Panthera pardus</i>	118	0	1	2	0	1	21.49	0.00	0.06	4.88	0.00	0.70
<i>Felis silvestris</i>	3	0	11	2	0	4	0.55	0.00	0.64	4.88	0.00	2.82
<i>Crocuta spelaea</i>	25	0	46	3	0	10	4.55	0.00	2.66	7.32	0.00	7.04
<i>Crocuta crocuta</i>	1	55	185	2	4	22	0.18	91.67	10.69	4.88	57.14	15.49
<i>Canis lupus</i>	56	0	40	7	0	13	10.20	0.00	2.31	17.07	0.00	9.15
<i>Cuon alpinus</i>	3	0	0	2	0	0	0.55	0.00	0.00	4.88	0.00	0.00
<i>Vulpes vulpes</i>	101	2	624	7	1	34	18.40	3.33	36.07	17.07	14.29	23.94
<i>Vulpes lagopus</i>	0	0	1	0	0	1	0.00	0.00	0.06	0.00	0.00	0.70
<i>Meles meles</i>	2	0	1	0	0	1	0.36	0.00	0.06	0.00	0.00	0.70
Total Carnivores	549	60	1730	41	7	142						
Grand Total	6588	1311	18237	253	58	789						

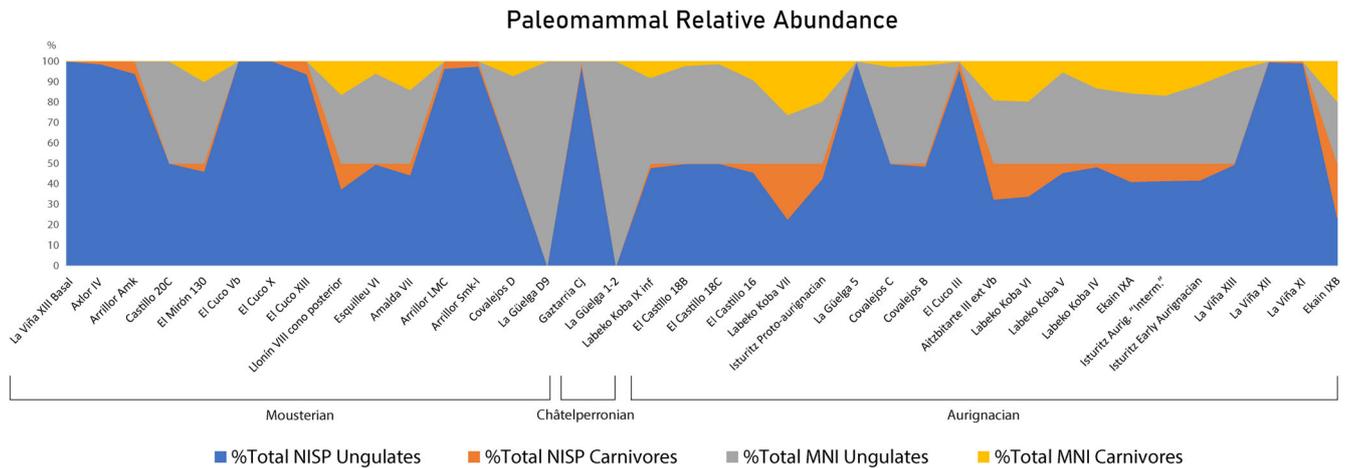


Figure 3. Palaeomammal relative abundance according to the percentages of number of identified specimens (NISP) and minimum number of individuals (MNI) values for each archaeological level organised by chronometric order and cultural period. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)].

Neanderthals and small-sized mammals probably by medium-sized carnivores (Sánchez-Romero *et al.*, 2020). The Châtelperronian level of Labeko Koba IX inf was interpreted as an occasional hyena den with gnawing marks on *Coelodonta antiquitatis*, but wolf and fox also modified the assemblage. However, the modifications by Neanderthals were also recognised on *Cervus elaphus*, *Equus ferus* and Bovine specimens. In the case of *Megaloceros*, the study revealed that this giant deer might also have been brought by humans (Villaluenga *et al.*, 2012). Along its whole sequence, *Crocota crocuta* continues to be present in significant amounts, indicating the recurrent use of the site as a den. In fact, 58% of the hyena remains found in the transition were found here (Villaluenga *et al.*, 2012; Ríos-Garaizar *et al.*, 2012b). In El Mirón, medium-sized carnivores were probably the accumulation agents, especially in the Mousterian levels where artefacts were scarce, suggesting only a short, ephemeral Neanderthal visit (Marín-Arroyo *et al.*, 2020).

Ratio of prey accumulator/non-accumulator carnivores

The ratio of prey accumulator/non-accumulator carnivores was calculated to observe the presence of responsible carnivores for accumulating medium-sized and small ungulate prey. Those ratios were calculated, when possible, for the NISP and MNI values (Table 3). The results indicate that the average value of the ratio is 0.1 during the Mousterian, 0.05 during the Châtelperronian and 0.3 during the Aurignacian. The overall average for the three periods is 0.2. These results proved what the taphonomic studies also show. During the Mousterian, Amalda VII and Llonín VIII have the highest values, while during the Châtelperronian, Labeko Koba IX inf shows the highest value of the studied period, while there are no published data about carnivores in La Güelga, although the presence of panther is attested (Menéndez *et al.*, 2014). During the Aurignacian, according to the NISP, Labeko Koba VII has the highest values, followed by Ekain IXB, Aitzbitarte III Vb and Labeko Koba VI. And according to the MNI, Labeko Koba VII and VI, Ekain IXB, Aitzbitarte III Vb and Isturitz show the highest values.

Inverse of Simpson Index

The results of the Inverse of Simpson Index provide interesting results that have been compared throughout time for those

sites with several transitional levels (Table S4). When sites only had one cultural level, the values were compared by period. This index provides information about the diet breadth achieved by human groups. In general terms, the average values are relatively constant along the transition (Table 4). It must be noted that during the Mousterian in Amalda VII, chamois was mostly brought to the site by medium-sized carnivores (Sánchez-Romero *et al.*, 2020). When chamois is excluded, then the index is higher. This is explained because chamois represents 63% of the assemblage and the other specimens, including horse, bovid and ibex represent 6–7% and red deer 17%. Similarly, in levels of Labeko Koba, Llonín and El Castillo, prey accumulator/non-accumulator carnivore ratios are high, which implies that the prey likely brought to the sites should be excluded before interpreting human choices and actions. Doing that, the general values are relatively constant by period when considering both the NISP and MNI values. These data reflect the exploitation on average of two to three specimens. In this case, it is red deer that is complemented somewhat by the presence of some equids and bovines.

Role of high versus low prey-ranked species

From the 38 levels, 30 sets of NISP and 24 sets of MNI values were available. For those levels, it was possible to estimate the high to low prey ratio of ungulate species, according to Marín-Arroyo (2009a, 2010) defined for the Palaeolithic in the region (Table S5). Only 19 levels had both values. The role of high prey species is a constant along the transitional periods, with slight variations per site, indicating hunting of high-productivity prey. Subtle differences between the Mousterian and Aurignacian are observed. There are no discrepancies between the ratio calculated with NISP or MNI. It is highly significant that, while in the Vasco-Cantabrian region the high prey is predominantly dominated by red deer, distantly followed by bovines and horse, at the Pyrenean site of Isturitz, equids, bovines and reindeer play the role as high-ranked prey species, despite its topographic location, with 99% of areas with a slope lower than 30°, similar to other sites in the region, such as Covalejos, where red deer is the most represented taxa. At the nearby site of Gatzarria, the role of equids and bovines is significantly lower. In Fig. 4, the different levels are plotted. The maximum values estimated

Table 3. Values of the prey accumulator/non-accumulator carnivore ratio calculated on the number of identified specimens (NISP) and minimum number of individuals (MNI) for each level.

		Ratio accumulator NISP	Ratio accumulator MNI
Mousterian	La Viña XIII basal	-	-
	Axlor IV	0.01	-
	Arrillor Amk	0.07	-
	Castillo 20C	-	-
	El Miron 130	0.09	0.25
	El Cuco Vb	-	-
	El Cuco X	-	-
	El Cuco XIII	0.07	-
	Llonin VIII Cono Posterior	0.34	0.49
	Esquilleu VI	0.01	0.13
	Amalda VII	0.13	0.39
	Arrillor LMC	0.04	-
	Arrillor Smk-I	0.03	-
	Covalejos D	0.01	0.17
	La Güelga D9	-	-
	Gatzarria Cj	0.02	-
Châtelperronian	La Güelga 1-2	-	-
	Labeko Koba IX inf	0.05	0.19
Aurignacian	El Castillo 18B	0.01	1.05
	El Castillo 18C	0.00	1.03
	El Castillo 16	0.10	1.23
	Labeko Koba VII	1.21	2.10
	Isturitz Proto-Aurignacian	0.18	1.66
	La Güelga 5	-	-
	Covalejos C	0.00	1.06
	Covalejos B	0.03	1.04
	El Cuco III	0.04	-
	Aitzbitarte III ext Vb	0.54	1.62
	Labeko Koba VI	0.48	1.65
	Labeko Koba V	0.10	1.12
	Labeko Koba IV	0.04	1.36
	Ekain IXA	0.22	1.45
	Isturitz Aurignacian "intermédiaire"	0.21	1.50
Isturitz Aurignacian ancient	0.20	1.29	
La Viña XIII	0.00	0.00	
La Viña XII	0.00	-	
La Viña XI	0.50	-	
Ekain IXB	1.14	1.65	

by NISP and MNI that are from the Isturitz Proto-Aurignacian and Labeko Koba VI, respectively, were chosen as the basis with which to calculate and plot the percentages of the other sites. The complete data per level are in Table S5.

Unfortunately, the limited age data prevented further insights about the nutritional stress that age of prey exploited can reveal. However, it is true that the higher values have been found at sites where the ratio of carnivore accumulation is higher. The available data are presented in Table S6.

Table 4. Average, minimum, maximum and mean values of the Inverse of Simpson Index based on number of identified specimens (NISP) and minimum number of individuals (MNI) values for all the levels included by cultural period.

	Mousterian		Châtelperronian		Aurignacian	
	NISP	MNI	NISP	MNI	NISP	MNI
Average	2.18	3.09	2.23	3.35	2.03	3.15
Minimum	1.33	2.16	2.23	3.20	1.17	1.35
Maximum	3.78	3.80	2.23	3.50	3.22	5.45
Mean	2.02	3.20	2.23	3.35	1.99	3.06

Environmental exploitation

The palaeomammal assemblages provide some insights about the climatic and environmental conditions in the studied area. Cold-adapted animals are represented by *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Rangifer tarandus* (Tables S1 and S2). Mammoth appears with minimal numbers of remains during the late Mousterian, it is absent during the Châtelperronian and occasionally represented again during the Aurignacian. The woolly rhinoceros is only represented during the Mousterian and Châtelperronian Level IX inf of Labeko Koba, which might have been accumulated during a cold period, as reindeer is also present. Reindeer is absent during the Mousterian, and more abundant during the Aurignacian between 39 to 32 k ¹⁴C a BP period.

By looking at the whole spectrum of herbivores, classified as favouring either open landscapes, wooded or mountainous areas, it is observed that, in general, in the Vasco-Cantabrian region woodland-adapted animals tend to dominate, although during the Aurignacian there is an equilibrium between open landscapes and woodland animals (note, however, that this woodland focus may be overstated because red deer can and does comfortably live in both open grass- or heathlands and wooded areas (Straus, 1981). This could be due to the colder and relatively more arid conditions evidenced during the Aurignacian, with probably more open landscapes in the region (Jones *et al.*, 2018, 2019).

The results of the correlation between the topographic factor calculated per site and the hunting preferences for each archaeological level reveal that during the Mousterian there was a positive and significant correlation between the prey selected and the surrounding environment for both NISP and MNI values. However, during the Aurignacian there is a positive but non-significant correlation for these values (Table 5). These results might suggest that, while Neanderthals were highly influenced in the hunting selection by the surrounding environment, modern humans might have taken more selective decisions on the exploitation of the prey, independently of the sites where they lived. For modern humans, this would have implied moving longer distances from a site, something that could have been motivated as well by the function of the site, with either long-term residential or short-term occupations. Figs. 5 and 6 show the catchment areas from each site for walking times of 1.2 and 2.15h and data are presented in Tables S7 and S8. Due to the limited data for the Châtelperronian, it was not possible to make these calculations.

Discussion

Archaeozoological data indicate that red deer is the most abundant and exploited taxon in this particular region.

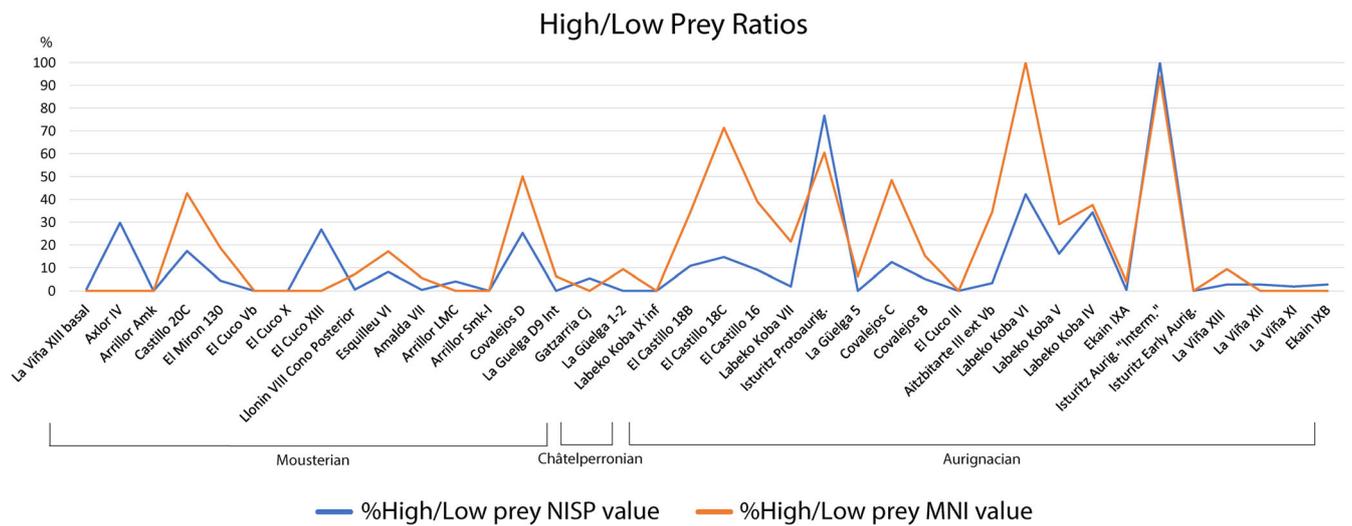


Figure 4. Ratio between high- and low-prey rank for number of identified specimens (NISP) and minimum number of individuals (MNI) values on sites and archaeological levels studied. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)].

However, the local differences between the Vasco-Cantabrian region and Isturitz (in the western Pyrenean sectors) are interesting, with abundant exploitation of equids and reindeer followed by bovines in Isturitz during the Aurignacian, in contrast to the fauna of the western sites.

Among the carnivores represented, curiously, *Ursus spelaeus* is the most common one, followed by *Crocuta* sp., *Vulpes vulpes* and *Canis lupus*, while the other carnivores appear in very low percentages. The presence of cave bear proves the use of the caves for hibernation, with alternating cave use by humans and carnivores (notably hyenas). In general, the significant presence of carnivores within the mammal assemblages is greater during the Aurignacian than during the late Mousterian and Châtelperronian.

The archaeozoological analysis of the different sites from the Vasco-Cantabrian region is, in most cases incomplete. However, recent works have been able to provide new information about human subsistence of both Neanderthals and AMH. Thus, the macromammal assemblage from Covalejos Cave (Levels D, C and B) exhibit the same taxonomic representation, with red deer as the main prey with a predominance of adult individuals. These data highlight that Neanderthals kept similar hunting strategies over time, showing continuity in subsistence strategies with AMH (Yravedra *et al.*, 2016). This conclusion coincides with other authors who do not observe important cultural and subsistence changes until the end of the Upper Palaeolithic (Butzer, 1986; Clark and Lindly, 1989a, b;

Marshack, 1989; Hoffecker and Gleghorn, 2000; Patou-Mathis, 2000; Yravedra, 2002). In El Castillo, located in the same river valley of Covalejos, the macrofaunal spectrum of Mousterian Level 20 and the Transitional Aurignacian levels (18B and 18C) from recent excavations is similar in all of them. Coinciding with Covalejos, red deer is the dominant species showing a main mortality profile of adults and mature adults. Nevertheless, the proportion of red deer is higher during the 'Transitional Aurignacian' than in the Mousterian, the former being almost monospecific (Luret *et al.*, 2020). While the cultural attribution of Level 18 is still subject to debate (Zilhão and D'Errico 1999; Wood *et al.*, 2018), Luret *et al.* (2020) propose that there is a change between a non-specific hunting strategy in Level 20 and a hunting strategy specialised in red deer in Level 18, claiming that those results demonstrate their cultural attribution. This also highlights a difference between the Middle and Upper Palaeolithic subsistence strategies contradicting Covalejos's interpretations (Yravedra *et al.*, 2016). Despite these subsistence data, it is clear that the chronology of Level 18 falls within the Mousterian boundaries (as shown above, Fig. 2) and more detailed studies are necessary to clarify this 'Transitional Aurignacian' and the transitional subsistence strategies in El Castillo.

The ratio of carnivore accumulators varies throughout time and it was relevant to discern the role of carnivores in the assemblages. These results were corroborated in levels at Llonín, Labeko Koba and Amalda, where the presence of carnivore accumulators, as well as proven disturbance on the herbivore assemblages brought in by humans to the site was, taphonomically, tested. Another example of alternate carnivores/Neanderthals was found at El Esquilieu. Neanderthals focused on the hunting of ibex and chamois during specific periods of the Middle Palaeolithic occupation. These species inhabited the surrounding mountainous terrain reflecting the remarkable adaptability of Neanderthals; in particular, the ability to exploit the mountain environments (Yravedra and Gómez-Castanedo, 2014; Yravedra and Cobo-Sánchez, 2015). According to Yravedra and Cobo-Sánchez (2015), the presence/absence of ibex and/or chamois does not seem to depend on chronology or climatic conditions, but it is affected by the topography. This coincides with the idea proposed by Altuna (1990: 233), and it has been confirmed statistically with the results presented in this paper, suggesting that the faunal spectra of Mousterian sites could be considered to be strongly linked to the surrounding environment. However, this focus on hunting

Table 5. Spearman's correlation coefficient and subsequent significance for the relation between the topographic factor and the hunting preference, obtained by the number of identified specimens (NISP) and minimum number of individuals (MNI) values of the Mousterian and Aurignacian deposits. In bold, significant and positive correlation.

Orographic factor versus Hunting preference		
	Mousterian	Aurignacian
NISP		
n	10	6
r Spearman	0.709	0.536
p	0.022	0.215
MNI		
n	6	7
r Spearman	0.886	0.559
p	0.019	0.192

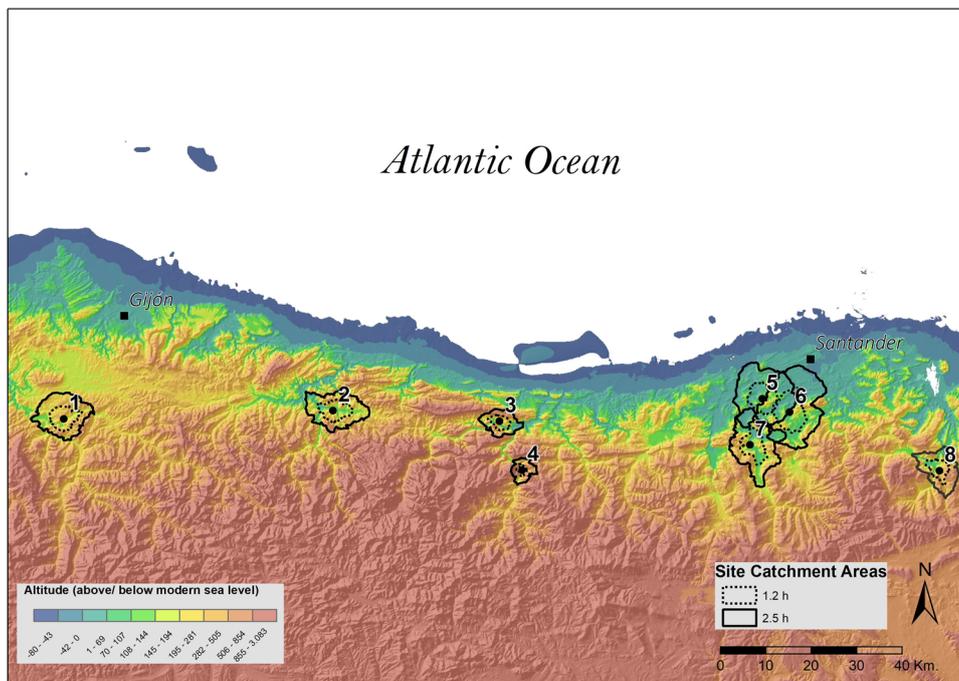


Figure 5. Catchment areas for 1.2 and 2.15 hours walking distances from sites in Asturias and Cantabria calculated using the method described in the text. Archaeologica site numbers: 1. La Viña; 2. La Güelga; 3. Llonín; 4. Esquilieu; 5. Covalejos; 6. Morín; 7. El Castillo; 8. El Mirón. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

mountain species has rarely been documented among Neanderthals and has traditionally been regarded as typical of AMH hunting behaviour (Freeman, 1973; Straus, 1987; Gamble, 1987). Although ibex is often present at Mousterian sites, it has traditionally been linked to the action of carnivores such as at Llonín cave (Sanchis *et al.*, 2019). Some other Mousterian sites have also shown chamois and ibex presence such as at Arlanpe (Ríos-Garaizer *et al.*, 2015), Venta la Perra, Arrillor, etc. (Altuna, 1989; Yravedra, 2000; Castaños, 2005). But, at the moment, there are no taphonomic details published about the

cause of its accumulation. Therefore, combined occupations of Neanderthals and carnivores seems a common occurrence during MIS3 and is consistent with the evidence found at Vasco-Cantabrian Middle Palaeolithic sites (Villaluenga *et al.*, 2012; Ríos-Garaizar *et al.* 2012b; Yravedra and Gómez-Castanedo, 2014; Sanchis *et al.*, 2019; Sánchez-Romero *et al.*, 2020). However, more research is needed at those sites where the ratio is high, but where the taphonomic evidence of carnivore activities is indicated as scarce, such as at Isturitz and El Castillo. These archaeological sites are complex palimpsests,

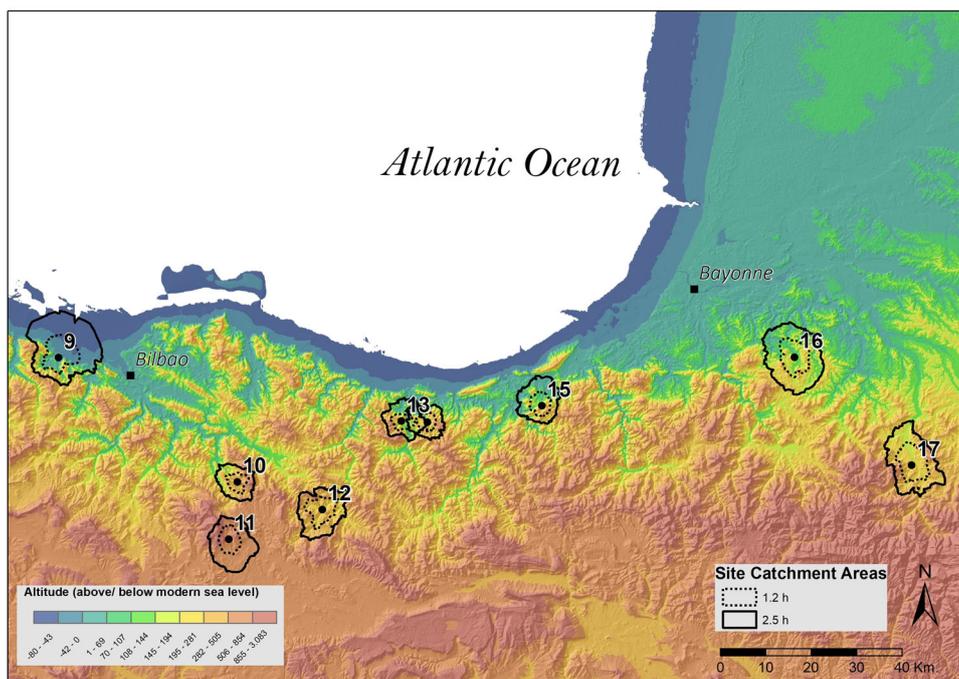


Figure 6. Catchment areas for 1.2 and 2.15 hours walking distances from sites in the Basque Country and south Aquitania, calculated using the method described in the text. Archaeological site numbers: 9. El Cuco; 10. Axlor; 11. Arrillor; 12. Labeko Koba; 13. Ekain; 14. Amalda; 15. Aitzbitarte III; 16. Isturitz; 17. Gatzarria. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)].

and it is not always clear how to differentiate the role of carnivores as primary or secondary agents.

Across the transition, the palaeomammal assemblages reflect environmental conditions with episodes of marked glacial conditions indicating open vegetation (steppe-tundra, grassland, heath) and a limited representation of trees that, when present, were scattered pines and junipers. But during the interglacials, the mammal spectrum seems to have adapted to those environments accordingly and the cold species disappeared. It is interesting to note the identification of *Equus hydruntinus* in Covalejos and Isturitz exclusively. *E. hydruntinus* is considered a species adapted to semi-arid steppe conditions (Burke *et al.*, 2003; Orlando *et al.*, 2006) and even to dry Mediterranean habitats. In the Aurignacian and Mousterian levels (B and J) of Covalejos, its presence/absence coincides precisely with more arid/humid moments (Jones *et al.*, 2019). Nevertheless, in the Vasco-Cantabrian region this small equid has never been identified before and the closest evidence of its presence is found only in Burgos (in Valdegoba, Galería de las Estatuas and Cueva Millán) (see Sanz-Royo *et al.*, 2020). *Dama dama* is also only found in Covalejos. Fallow deer were cited by Breuil and Obermaier (1935) in Altamira as '*Cervus dama*', and recently by Rosas *et al.* (2011) in the Mousterian level of Galería del Osario in El Sidrón. However, in none of these sites is it discussed how the determination of this species was made. So, a careful review of this atypical ('Mediterranean') taxa for Northern Atlantic Spain (fallow deer and hydruntine) would be recommended.

Conclusions

This work is a starting point for the systematic analysis of these and other cave sites in which the existence of various archaeological layers dated during the Late Middle and Early Upper Palaeolithic have been defined. This incomplete review identify, in general terms, aspects of human subsistence and, from the same mammals, insights about environmental and climatic indicators at the time late Neanderthals and AMH were living in the Vasco-Cantabrian region. This work has identified gaps of knowledge that prevent us from: (1) getting a complete regional understanding of the subsistence achieved by both human species, (2) obtaining an accurate comparison between them, and (3) observing a diagnostic diachronic evolution.

The summary of the macromammal assemblages represented at the Vasco-Cantabrian archaeological sites, dated to the Mousterian, Châtelperronian and Aurignacian, provided data from 17 sites; specifically, 38 levels with 82 radiocarbon dates. The processed information provides a general perspective on the palaeomammal community existing in the region between 50,000 and 34,000 cal a BP, covering the period from Greenland Interstadial 13 to Greenland Stadial 7.

The archaeozoological data indicated that red deer is the most abundant and exploited taxon in this particular region, as it will be until the Late Pleistocene. In terms of subsistence, the results indicate how Neanderthals were influenced in their hunting decisions by the topographic location of each site, somewhat in contrast to the case of Aurignacian modern humans. This would have implied longer travel times for AMH, favoured by their particular anatomy (Weaver and Steudel-Numbers, 2005; MacDonald *et al.*, 2009) and motivated either to the biotope abundance in the site's proximity or just the preference for hunting diverse prey independent of the distance, which allowed them more efficient exploitation of specific distant taxa. AMH would have relied more heavily on logistic mobility than Neanderthals, leading to greater travel

distances during their expeditions which, in turn, would mean less residential mobility (Wallace and Shea, 2006; Marín-Arroyo, 2013). The skeletal profiles' transport will provide insights on whether the body size of carcasses and hunting location played a greater role in transport decisions, probably involving more intense butchering at the kill site.

More research from an archaeozoological point of view is needed to collect data about the age selection of the ungulate prey, the type of exploitation of the carcasses, and skeletal transport, which will provide relevant information about the Neanderthal and modern human subsistence strategies in the region and discern whether Neanderthals might have suffered any episodes of nutritional stress. The diverse multidisciplinary analysis on the Neanderthal skeletons found at El Sidrón notes how famished they were, suggesting cannibalism as a consequence of that (Rosas *et al.*, 2006).

The ongoing ERC-CoG SUBSILIENCE project aims to complete this review by achieving further research in the region that can provide a general understanding of the foraging behaviours of late Neanderthals and AMH and, as well, to fulfil the lack of regional and local climatic proxies directly related to the surrounding areas where humans lived. The expected result will help to determine the potential implications for regional patterns of resource exploitation, subsistence strategies and environmental-human relationships that may have been involved in the demise of the Neanderthals and the evolutionary success of AMH.

Acknowledgements and funding. This research is funded by the European Research Council under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement No. 818299-SUBSILIENCE project (<https://www.subsilience.eu>) and the Ministerio de Ciencia, Innovación y Universidades (ABRUPT - HAR2017-84997-P) to ABMA. ASR's PhD is supported within the SUBSILIENCE project. The authors would like to thank J. García Sanchez (Instituto de Arqueología-Merida, CSIC-Junta de Extremadura) for technical assistance with catchment areas analysis and Figs. 1, 5 and 6. Special thanks to L. Agudo (EvoAdapta-University of Cantabria) for her technical assistance and G. Terlato for comments on the final version of the manuscript. The authors wish to acknowledge L. Straus for editing the manuscript and for his suggestions to improve this manuscript, as kind and effective as always.

Author contributions—The design was conceived by AB.M.A. The site/levels selection for radiocarbon dating was performed by both authors. AB.M.A. built the OxCal model. AB.M.A. and A.S.R. compiled the bibliographic and numerical data of the archaeological and faunal data. Both authors discussed the results and write the discussion and contributed to the Supplementary Information. AB.M.A. design and wrote the paper with contributions from A.S.R.

Additional information

Supplementary information accompanies this paper in the Wiley online library.

The authors declare no competing financial interests.

Data availability statement

The data that support the findings of this study are available in the supplementary material to this article.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Supporting information appendix with a detailed description of each archaeological site mentioned in this study.

Appendix S2. Bibliographic references of the radiocarbon dates included in Table S1.

Table S1. Radiocarbon AMS dates of the archeological sites and levels included in this study, as shown in Figure 2. UF refers to an ultrafiltration protocol. AMS radiocarbon of ABA (Acid-Base-Acid) protocol applied to charcoal samples. Calibrated dates with the IntCal20 calibration curve (Reimer *et al.* 2020) and the marine data from Heaton *et al.* (2020) for the Northern Hemisphere. Radiocarbon dates on shells have not been calibrated given the lack of information on the ΔR of the ocean reservoir effect for that period in the region (Gutiérrez-Zugasti *et al.* 2018).

Table S2. Total number of identified specimens (NISP) values per archaeological level organised by cultural period.

Table S3. Total minimum number of individuals (MNI) values per archaeological level organised by cultural period.

Table S4. Individual values of the Inverse of Simpson Index based on number of identified specimens (NISP) and minimum number of individuals (MNI) values per level and by cultural period.

Table S5. Individual values of the ratio between high and low prey rank species based on number of identified specimens (NISP) and minimum number of individuals (MNI) values per level and by cultural period.

Table S6. Individual values of the ratio between juvenile and adult ungulates based on minimum number of individuals (MNI) values per level and by cultural period, where age data were available.

Table S7. Catchment areas in km² surrounding each site for 1.2 h and 2.15 h together with the value of their topographic factor, calculated using the method described in the text.

Table S8. Topographic factor (montane area within a distance of under 1.2 h/lowland area within 2.15 h) and hunting preference (quantification of montane taxa/lowland taxa) for number of identified specimens (NISP) and minimum number of individuals (MNI) values for each site by cultural period.

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