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High-resolution Neanderthal settlements in mediterranean Iberian Peninsula: A matter of altitude?

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ABSTRACT

Neanderthals are widely known to be a resilient human species that successfully faced constant and strong environmental fluctuations modifying the landscapes they inhabited and the availability of their potential resources. It has been traditionally assumed that environmental features could strongly affect human behaviour due to the stretch relationship between their potential prey and the availability of habitats. Environmental changes would produce a high variability in the settlement patterns of the Neanderthal groups. However, the preponderant influence of environmental conditions on these human groups has recently been strongly questioned. This is especially true for the Iberian Peninsula, where latitudinal position and orographic features supported the persistence of environmental conditions that allowed the permanence of a wide range of biotopes and animal and vegetal resources. In the present study, we reconstruct the Neanderthal settlement patterns (i.e. duration and season) from four archaeological sites located in the Mediterranean area of the Iberian Peninsula: Arbreda Cave (Serinyà, Girona), Teixoneres Cave (Moià, Barcelona), Abric Romaní (Capellades, Barcelona), and El Salt (Alcoy, Alicante). We focus on identifying whether they show a high variability in settlement patterns and check for the existence of local influences, such as the altitude. To reach these objectives, we designed a multi-proxy approach combining tooth wear and dental cementum analysis of the main Neanderthal preys: *Cervus elaphus*, *Equus ferus*, *Equus hydruntinus*, *Bos primigenius* and *Capra pyrenaica*. Our results first suggest that local features (i.e. orography, altitude, and environment) appear to be predominant factors determining the main feeding behaviour of the ungulates hunted by Neanderthals. Additionally, seasonal environmental variations seem to have influenced horse migratory behaviour, involving altitudinal movements in search of high-nutritive pastures. Neanderthal survival strategies and settlement patterns seem to have been less affected by environmental particularities and more linked to selective prey procurement based on the seasonal resource availability. Therefore, the duration and seasonality of their settlement patterns and their

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mobility throughout the landscape indicate they had a high level of knowledge on the territory they inhabited, as well as on the behaviour and availability of their potential preys.

1. Introduction

Human behaviour related to subsistence procurement is a set of immediate and premeditated decisions for which environmental features, resource availability and social factors (among others) determine the choices taken for survival (Pyke et al., 1977; Binford, 2001; Miller and Barton, 2008; de la Torre et al., 2013). Some recent studies suggest however that environmental features could be less relevant to human survival strategies than previously expected (Ríos-Garaizar, 2008; Rios-Garaizar and Moreno, 2015). Indeed, it is widely known that humans developed a wide range of adaptive skills and strategies providing them advantages for survival in a broad range of habitats, and enabling them to overcome adverse conditions such as the succession of abrupt changes in the landscape (e.g. seasonal changes) or the scarcity of abiotic and biotic resources (Conard and Prindiville, 2000; Costamagno et al., 2006; Richter, 2006; Blasco et al., 2013a; Ilardo and Nielsen, 2018; Weinstein, 2018). On the other hand, if it is assumed that fauna have a close relationship with the surrounding habitat (Dugatkin and Reeve, 2000), then it is undeniable that the potential behaviour of human prey and the environmental stability of their habitats are important factors to consider (Kelly, 1992, 1995; de la Torre et al., 2013). Therefore, prey availability and ecology are still relevant factors in understanding human survival strategies in different environments (Mauss and Beuchat, 1904; Monks, 1981; Gourichon, 2004; Rendu, 2007; Fernández-Laso et al., 2011; Blasco et al., 2014).

Assessing the social behaviour of prehistoric groups is challenging, but research efforts in this field are now increasingly supported by the development of multi-proxy approaches and cutting-edge analytical tools. Accordingly, our main purpose in this paper is to reconstruct the Neanderthal settlement patterns from four Spanish Middle Palaeolithic sites located in the Mediterranean area of the Iberian Peninsula: Arbreda Cave (Gerona), Teixoneres Cave (Barcelona), Abric Romaní (Barcelona) and the El Salt shelter (Alicante) (Fig. 1).

The preferential mobility strategies (e.g. circulating/radiating models) and the types of settlement patterns (e.g. logistical/residential models) performed by Neanderthal groups to make better use of available resources have been thoroughly discussed (Mortensen, 1972; Binford, 1980; Kelly, 1983, 1992; Costamagno et al., 2006; Grove, 2009; Delagnes and Rendu, 2011; Rios-Garaizar and Moreno, 2015; Clark and Barton, 2017; Marín et al., 2019). Indeed, the duration and season(s) (i.e. within the annual cycle) of the settlement stand out as key features that characterized the human settlements. Since Neanderthals seem to have been mainly organized into small groups (Henry et al., 2004; Burke, 2006a; Vallverdú et al., 2010; Hayden, 2012) and exhibited wide-ranging mobility throughout their inhabited territory (Macdonald et al., 2009; Fernández-Laso et al., 2011; Niven et al., 2012), it would be expected that highly variable settlement types (from short to long-term) could be identified (Farizy et al., 1994; Conard and Prindiville, 2000; Armand and Pubert, 2001a; Vaquero et al., 2001; Vallerdú et al., 2005; Burke, 2006a; Rivals et al., 2009b; Daujeard and Moncel, 2010; Daujeard et al., 2011; Moncel and Rivals, 2011; Bargalló et al., 2016; Sánchez-Hernández et al., 2016, 2019; Spikins et al., 2018). However, the occurrence of palimpsests is a conditioning factor that prevents the identification of single settlement events and limits interpretations regarding the duration and seasonality of human presence in a given place (Machado et al., 2013; Bargalló et al., 2016; Gabucio et al., 2018; Real et al., 2018). This aspect is especially problematic when assessing whether long-term settlement events are due to a real continued presence or are the result of a palimpsest effect. For this reason, we study the behaviour of the main prey (dietary patterns) as well as the hunting strategies (seasonality, targeted age classes) of Western Mediterranean Neanderthal groups to more efficiently assess their subsistence and mobility behaviour.

The duration and seasonality of settlements are also determined by the palaeoecological and environmental variables of a given region, and the strategies of the human groups surviving in these habitats. The numerous and abrupt climatic shifts (i.e. temperate to glacial periods) which occurred during the Middle Palaeolithic period resulted in changes in available resources, and presented constant challenges for fauna and flora adaptation and survival (Dansgaard et al., 1982, 1993; Heinrich, 1988; Hewitt, 2000; D'Errico and Goñi, 2003; Finlayson and Carrión, 2007). However, the Iberian Peninsula seems to have been subject to less extreme and more consistent environmental conditions, since relative climatic stability allowed the maintenance of a constant and wide variety of resources. Several studies point to evidence of resilient forests, which expanded and constricted according to the environmental fluctuations without totally disappearing, especially in regions ruled by Mediterranean influences (Burjachs et al., 2012; López-García et al., 2012, 2015; Allué et al., 2017, 2018; Fernández-García et al., 2018). This evidence is also supported by the stable ecology and distribution of the main Neanderthal prey within this region (Sánchez-Hernández et al., 2020).

The patterns of Neanderthal settlements have been explored through various zooarchaeological (Rosell et al., 2012b; Marín et al., 2017) and technological studies (Conard et al., 2012; Navazo and Carbonell, 2014), as well as more in-depth and specific approaches, such as animal dental wear (Rivals and Deniaux, 2005; Rivals et al., 2009a; Sánchez-Hernández et al., 2016) and stable nitrogen isotope analyses (Moncel et al., 2019; Wiβing et al., 2019). In the current study, we intend to further explore this issue by combining tooth microwear and dental cementum analyses in order to more accurately determine the duration and seasonality of human settlements, including in the context of relatively stable vegetal resources (Sánchez-Hernández et al., 2019). Both techniques deal with relatively short time intervals in an individual's life (Sánchez-Hernández et al., 2019, 2020). Through the study of the micro signals produced on the tooth enamel surface in a varying pattern according to the abrasive properties of the food ingested by animals day after day and season after season, tooth microwear provides information about the duration of procurement strategies of human groups, i.e. from short to long-term (Grine, 1986; Solounias and Semprebon, 2002; Rivals et al., 2009b). On the other hand, dental cementum analysis allows the identification of the season of the year in which the individual died, based on the study of the seasonal and incremental cementum bands deposited on the dental root (Klevezal and Kleinenberg, 1969; Gordon, 1988; Pike-Tay, 1991; Lieberman, 1993; Gourichon, 2004; Rendu, 2007).

Fig. 1. Location of the archaeological sites.

1.1. Archaeological sites

1.1.1. Arbreda Cave

Arbreda Cave is located in the foothills of the pre-Pyrenean area at an altitude of 211 m a.s.l., close to the municipality of Serinyà (Gerona, Spain). It belongs to the cave system namely “Paraje del Reclau”, a karstic system formed in travertine terraces as consequence of the lacustrine basin of Banyoles-Besalú (Julià, 1980; Roqué et al., 1999). The stratigraphy is formed by a broad Mousterian sequence from which levels I, J, K, L, M and N were included in the study. The Mousterian sequence shows a chronology ranging from 45,840 to 41,410 cal BP (^{14}C AMS) for upper level I (Maroto et al., 2012, 2005; 1996; Wood et al., 2014), to 120 ka BP (U/Th) for basal level N (Soler i Subils et al., 2012, 2014). The upper zone of level J is in contact with level I, whereas the lower zone lays above the level K dated by U—Th series to 71 ± 4 ka BP (Ajaja, 1994). The fossil record comprises a broad range of large mammals, where *Ursus spelaeus* is the most common carnivore taxa, and ungulates the dominant herbivores. *Cervus elaphus*, *Equus ferus* and *Bos primigenius* were the most common Neanderthal prey throughout the Mousterian sequence (Galobart et al., 1996; Maroto et al., 1996; Rufí et al., 2018; Soler i Subils et al., 2014). The lithic industry is mainly dominated by quartz and quartzite products of local origin and related to the Levallois technique (Maroto et al., 1996; Soler i Masferrer et al., 2004; Soler i Subils et al., 2014).

1.1.2. Teixoneres Cave

Teixoneres Cave is about 4 km away from Moià (Barcelona, Spain), at 760 m a.s.l. in the northeast area of the Iberian Peninsula, flanked to the north by the Pyrenees and to the east by the Mediterranean Sea. We selected the Unit III, which was in turn divided into two sub-units, i.e., IIIa and IIIb. The chronology of this unit ranged from >51 ^{14}C BP to 43.4 ka cal BP (Talamo et al., 2016). The faunal record, made up of 19 different taxa (Álvarez-Lao et al., 2017), showed a clear dominance of the ungulates *Cervus elaphus*, *Equus ferus* and *Equus hydruntinus*, and also includes several carnivore species, such as *Ursus spelaeus*, *Crocuta crocuta*, *Canis lupus*, *Vulpes vulpes*, *Lynx spelaea* and *Meles meles*. The lithic technology indicated two different reduction strategies with local raw material (i.e. quartz, limestone …) characterized by orthogonal and bifacial strategies, while Levallois and Discoidal were applied to the semi-local ones (mainly flint and quartzite) (Rosell et al., 2010, 2017; Bustos-Pérez et al., 2017; Picin et al., 2020).

1.1.3. Abric Romaní

Abric Romaní is a rock shelter situated in the locality of Capellades (Barcelona, Spain) at an altitude of 310 m a.s.l., and formed in Quaternary travertine called Cinglera de Capelló, a cliff about 50 m over the Anoia River. The archaeological site has a stratigraphic sequence of up to 20 m with 25 archaeological levels dated between 110 and 40 ka BP (Bischoff et al., 1988; Sharp et al., 2016; Vaquero et al., 2013), from which levels E, H and I were of interest to this study. The chronology for these levels was: 43.2 ± 1.1 ka BP (^{14}C AMS) for level E, 44.5 ± 1.2 (^{14}C AMS) to 46.6 ± 1.7 ka BP (U/Th) for level H, and 45.1 ± 3.1 to 48.6 ± 2.3 ka BP (U/Th) for level I (Bischoff et al., 1988; Vaquero et al., 2013). The faunal record of these levels indicates the preference of Neanderthals for *Cervus elaphus* and *Equus ferus*, the most represented ungulates (Rosell et al., 2012a; Marín et al., 2017). The lithic industry is characterized by raw materials of local and semi-local origin with a clear predominance of flint. This production is related to Discoid and Levallois strategies in levels E and H, while the Discoid method is more common in level I

(Morant and García-Antón, 2000; Vaquero et al., 2001, 2012; Chacón et al., 2006; Marín et al., 2017).

1.1.4. El Salt

El Salt, which is the most south-eastern site of the study, is 2 km away from Alcoy (Alicante, Spain). Located in the foothills of the Sierra de Mariola, at an altitude of 680 m a.s.l, it is a rock shelter of travertine origin close to the Serpis River. The sequence was divided into 13 units that were grouped into 4 segments (Fumanal, 1994). We will focus on Unit X (subdivided into sub-units Xa and Xb) dated to 52.3 ± 4.6 cal ka BP (Galván et al., 2014a, Galván et al., 2014b). The faunal assemblage from this unit comprises a wide number of species, with *Cervus elaphus*, *Capra pyrenaica* and *Equus ferus* as the main prey of Neanderthal groups (Machado and Pérez, 2016; Pérez et al., 2017). The lithic assemblage is mainly composed of local raw material (i.e. flint and limestone) with a centripetal Levallois technique as the main knapping system and, to a lesser extent, discoidal and non-directional Levallois techniques (Machado-Gutiérrez et al., 2011; Machado and Pérez, 2016; Machado et al., 2017).

2. Material and methods

For the current research, various ungulate dental assemblages have been sampled from the four archaeological sites described above: the Teixoneres and Arbreda caves, and the Abric Romaní and El Salt shelters. A total of 297 molars from at least 5 different taxa (*C. elaphus*, *E. ferus*, *E. hydruntinus*, *Bos/Bison* and *C. pyrenaica*) were studied and provided reliable results for mesowear, microwear and cementum (Table 1; see also Table S1 in the supplementary data).

2.1. Dental wear

2.1.1. Tooth microwear

Tooth microwear is a high resolution and non-destructive technique that provides data about the feeding activity of an individual in the last days/weeks of its life (Solounias and Semprebon, 2002). The procedure identifies and quantifies the signals produced on the dental enamel surface during the chewing process (i.e. scratches and pits) by intrinsic (phytoliths) and extrinsic (e.g. dust, grit, sand) particles present in the food ingested by the studied individual. The resulting microwear pattern varies according to the properties of the food ingested, and is also characterised by a fast turnover since each new food intake generates a new signal pattern in a process referred to as the “Last Super Effect” (Grine, 1986). Therefore, the microwear pattern is produced in a short-term period, so this method highlights the diet on a short temporal scale (i.e. hours/days). Consequently, the observed microwear pattern reflects the diet effect of an individual at the time of its death, as well as the surrounding and seasonal environmental conditions at the same time (Solounias and Semprebon, 2002). We quantified the two main signals identified over the enamel surface: scratches (elongated features of differing widths, depths and refractivity) and pits (circular features of different diameters and depths) (Solounias and Semprebon, 2002; Semprebon et al., 2004). Nevertheless, only the number of scratches is considered for the purpose of the present research. We recorded the density of scratches for each individual, i.e., the number of scratches (NS), which varies according to the season of death. Based on the analytical protocol elaborated by Rivals et al. (2015) using large modern and fossil collections, the study of the variation of the numbers of scratches on the enamel of a set of individuals allows identification of the duration of the ungulate procurement events (i.e. hunting events within the annual cycle) through the combination of the sample-size corrected coefficient of variation (CV*) and the standard deviation (SD) (Rivals et al., 2015). In terms of time window, the procurement events were classified into three categories: short/seasonal events, long events (longer than one season), and separated events (two at least) in non-contiguous seasons (Rivals et al., 2015). These categories were respectively designated as zones A, B and C on the theoretical model established by plotting the CV* and SD values on a bivariate graph (*ibid.*). Finally, we used the number of scratches (NS) for characterizing the diet of an individual during the few days/weeks prior to its death. When transformed into microwear values (i.e., low scratch range (LSR)), these data allow distinguishing between the three main dietary groups: browser, grazer, and mixed feeder. The LSR was obtained by identifying the percentage of individuals from a population or taxon ranging from 0 to 17 scratches per unit of observation (Solounias and Semprebon, 2002; Rivals et al., 2007b; Rivals and Semprebon, 2010). The populations comprising 72.7–100% of individuals showing between 0 and 17 scratches were classified as browsers, while those with less than 22.2% were considered grazers. Mixed feeders overlapped with the previously described groups (i.e. from 20.9 to 70%) depending on the daily amount of attritive/abrasive items consumed (e.g. grasses, leaves or shrubs) (Solounias and Semprebon, 2002; Semprebon and Rivals, 2007; Semprebon et al., 2011).

The selection of the teeth is conditioned by a number criteria in accordance with the protocol described by Solounias and Semprebon (2002) and Semprebon et al. (2004). The selected lower and upper molars must be in a good state of preservation (at least on the occlusal surface), present a visible wear facet on the enamel surface, and belong to adult individuals. A direct observation of the occlusal surface at the stereomicroscope at 35× allows to identify microscopic alterations of a post-mortem nature (e.g. abrasion, erosion or trampling among other) following Teaford standard criteria (Teaford, 1988). These alterations are easily distinguishable from the feeding signal because they strongly modify the enamel surface and present a different morphology (King et al., 1999; Martínez and Pérez-Pérez, 2004; El-Zaatari, 2010). The occlusal surface was subsequently cleaned using acetone and then 96% ethanol in order to remove sediment residues, dirt or chemical compounds from the enamel tissue that could impede or prevent the microscopic analysis. The microscopic sampling process consisted of two successive steps. First, the occlusal surface was replicated with a high-resolution silicone (vinylpolysiloxane) while the upper part of the molar crown was covered by a low-resolution silicone to form the negative mould. Secondly, this mould was filled with a transparent epoxy in order to create the positive cast. The enamel surface recorded on these casts was then observed using a Zeiss-Stemi 2000C stereomicroscope with an ocular reticule, focusing on a 0.16 mm^2 area of analysis.

Table 1
Summary of dental sample size.

Site	Dental Wear			Cementochronology	
	Samples	Mesowear	Microwear	Samples	Cementum
Teixoneres	154	99	128	8	7
Arbreda	72	23	67	5	4
Abric Romaní	34	16	27	1	1
El Salt	37	15	36	0	0
Total	297	153	258	14	12

“Samples” refers to the number of selected teeth to be analysed. Mesowear, microwear and cementum data correspond to the teeth suitable for the analyses and which yielded results.

2.2. Tooth mesowear

Tooth mesowear is a non-destructive technique that describes the relative degree of attritive-abrasive tooth wear produced by intrinsic (phytoliths) and extrinsic (dirt, dust and grit) items present in the feeding bolus (Fortelius and Solounias, 2000). Throughout the lifetime of an individual, the morphology and height of the tooth buccal apices are affected and modified by interactions with dietary items on a relatively long temporal scale, i.e. months or years (Fortelius and Solounias, 2000). Given the fact that the attritive-abrasive properties vary according to the diet consumed by an individual, the three main ungulate dietary groups can be categorized through the morphology of the tooth cusps. The low abrasive and highly attritive diet of browsers (feeding mainly on leaves and shrubs) produces high relief and sharp apices, whereas the highly abrasive and lower attritive diet of grazers (feeding on grasses) creates lower relief and rounded or blunt apices. The intermediate attritive-abrasive values of mixed feeders produce diverse patterns more or less oriented towards the dietary preferences of each individual (e.g. a little more browser than grazer, or the reverse). The degree of cusp wear is quantified using the mesowear scoring procedure elaborated by Fortelius and Solounias (2000) from the study of extant and extinct ungulate populations, and modified by Mihlbachler and collaborators (2011). The scores grade seven stages of wear, where 0 indicates high relief and sharp apices and 6 refers to no relief and absolutely blunt apices. The tooth selection criteria take into account the age of the individual, discarding those belonging to senescent or young individuals (highly worn and unworn teeth respectively) (Fortelius and Solounias, 2000; Rivals et al., 2007a). In addition, general preservation of the cusps is considered: cusps must present an optimal structural preservation without evidence of breakage or damage (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003).

2.3. Cementochronology

The dental cementum analysis is a method used for determining the age and season of death of an individual (Scheffer, 1950; Klevezal and Kleinenberg, 1969; Lieberman, 1991; Pike-Tay, 1991; Gourichon, 2004). It is based on the study of the dental cementum, an avascular and mineralized tissue mainly composed of hydroxyapatite crystals and collagen fibres (Boyde and Jones, 1972; Williams and Elliott, 1989; Lieberman and Meadow, 1992), and located in the most external surface of the tooth root (Lieberman and Meadow, 1992; Burke, 1993; Gourichon, 2004). The main function of the cementum is to anchor the root to the periodontal ligament and avoid its displacement or loss within the alveolar bone (Schmidt and Keil, 1972; Lieberman and Meadow, 1992; Lieberman, 1993). Structure, composition and organization of this tissue show a great complexity that contributes to the recognition of five different categories of cementum (Schroeder, 1986). Of these categories, the present research focuses on the acellular extrinsic fibre cementum (henceforth shortened to acellular cementum, AC) which is deposited continuously and regularly on the upper part of the root surface throughout the life of the tooth, following predictable seasonal cycles of rate deposition (Pike-Tay, 1991; Lieberman and Meadow, 1992; Burke and Castanet, 1995; Bosshardt and Schroeder, 1996). These growth changes result in the deposition of two optically and structurally different cementum bands over a year (Klevezal and Kleinenberg, 1969; Burke and Castanet, 1995; Gourichon, 2004; Naji et al., 2015). The first, the translucent band (TB), is characterized by a fast growth and low mineralization rate which generally takes place during seasons of good environmental conditions (e.g. spring and summer) (Lieberman, 1991, 1994; Pike-Tay, 1991; Gourichon, 2004). The second, the opaque band (OB), is thinner, darker than the TB, and characterized by a slow growth and high mineralization rate. It is formed during the months of the year when environmental conditions are least favourable (generally the winter time) (Lieberman, 1991, 1994; Pike-Tay, 1995; Gourichon, 2004).

This alternating growth pattern allows the determination of the age and season of an individual's death, since one pair of TB and OB is deposited per year. Inferring the age of death requires identifying the eruption time of the studied tooth and the total number of pairs of bands observed within the cementum layer. The season of death, which is of interest for our research, is estimated by identifying the nature of the last cementum band (LCB) formed at the time of death: TB or OB (i.e., good season or bad season). When the LCB corresponds to a TB, the degree of completeness of this band can be assessed by calculating the growth rate of the LCB compared to the average thickness of the preceding complete translucent bands. Therefore, the time of death can be more accurately determined for the TB at the beginning, middle and late parts of the 'good season' by assuming constant deposition rates of up to one-third of the mean thickness (1–33.3%), one-to two-thirds (33.4–66.6%) and more than two thirds (66.7–100%), respectively (Gourichon, 2004). This procedure is not applicable to the OB because of its thinness.

The sample preparation protocol followed a petrographic thin section procedure (Gordon, 1988; Lieberman et al., 1990; Pike-Tay, 1991; Burke and Castanet, 1995; Gourichon, 2004; Rendu, 2007), which had been modified by one of us (LG) for preserving the majority of the tooth by sampling one single root and cutting two or more sections per sample. The selection criteria focused on teeth showing well preserved cementum tissue from a macroscopic point of view: absence of fractures or other taphonomic alterations on the root surface. Once selected, only the tooth root was embedded in an epoxy resin. When the resin was dry, the root was separated from the tooth using a low speed precision diamond saw (Buehler Isomet). The same machine was employed to cut the root into thin slices (500–900 μm thick) orthogonal to the cementum surface. The slices were glued on a glass slide and then abraded to a thickness of 50–80 μm using an automatic grinding machine (Buehler Petrothin). The objective was to obtain an appropriate thickness to observe all the histological features by using a polarized transmitted light microscope Leica 2500P. The microscopic observations were made through three different lights: plane-polarized (i.e. "natural light" henceforth), cross-polarized and, cross-polarized light plus a half-wave plate (λ plate). The cementum bands were observed at ×100, ×200 and ×500 magnifications.

3. Results

3.1. Tooth microwear

3.1.1. Teixoneres Cave

All the studied taxa from Teixoneres Cave showed similar mortality patterns in both sub-units except *E. hydruntinus*, which plots in two distinct zones on the graph (Fig. 2; Table 2). In sub-unit IIIa, *C. elaphus* ($n = 15$) is characterized by a low coefficient of variation (CV*) and a low standard deviation (SD), i.e., its low variability plots this population within zone A but close to the boundary of zone B (Table 2; Fig. 2A). Zone A corresponds to a short/seasonal procurement event, but since these results plot nearby the zone B boundary, it is not possible to indicate the duration of the procurement event ($p > 0.05$). The equids, *E. ferus* ($n = 29$) and *E. hydruntinus* ($n = 19$), show low variability (with respect to both CV* and SD) and these results are plotted within zone A, indicating a short/seasonal procurement event (Fig. 2A). In sub-unit IIIb, *C. elaphus* ($n = 42$) and *E. ferus* ($n = 12$) both show low variability,

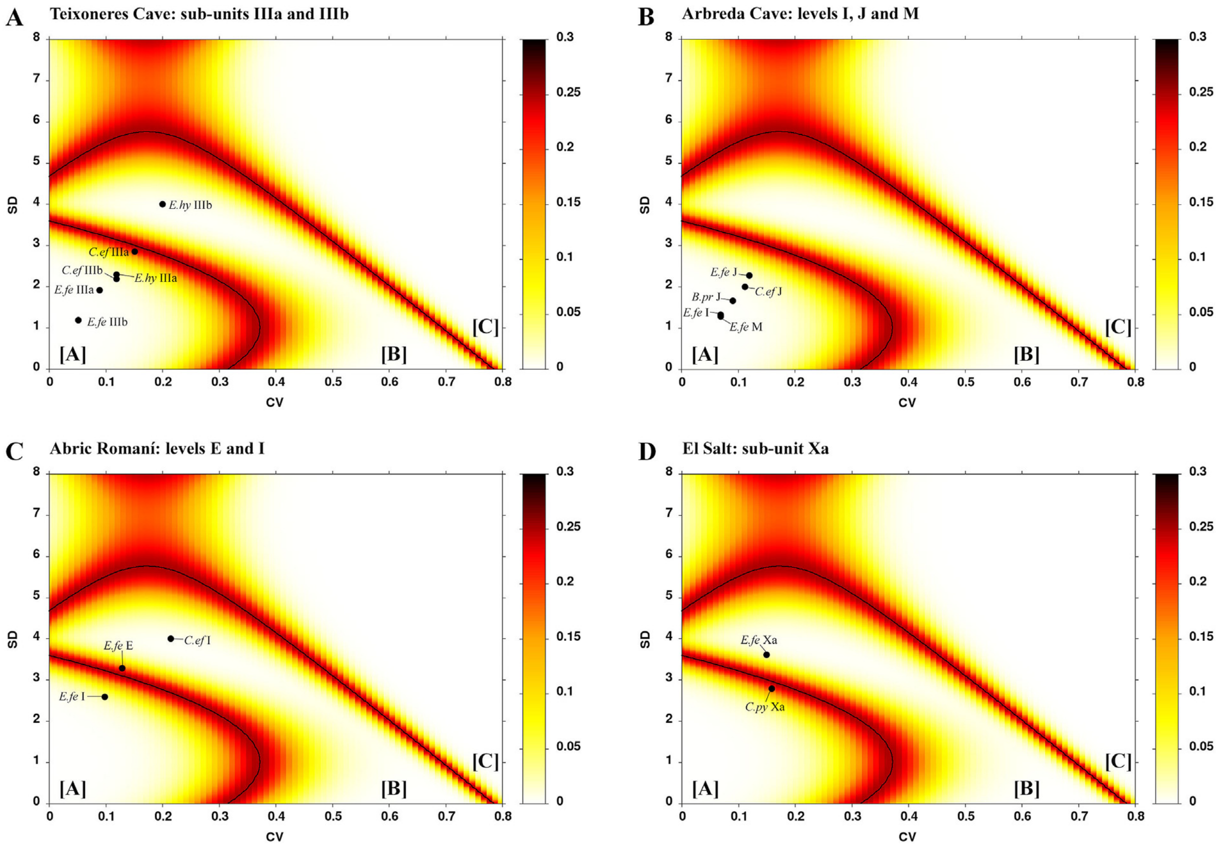

Fig. 2. Microwear data for *Cervus elaphus*, *Equus ferus*, *Equus hydruntinus*, *Bos primigenius* and *Capra pyrenaica* from the Teixoneres (sub-units IIIa and IIIb), Arbreda (levels I, J and M), Abric Romaní (levels E and I) and El Salt (sub-unit Xa) archaeological sites. Bivariate plot: standard deviation (SD) and coefficient of variation (CV*) calculated based on the number of scratches. Boundary lines between the three areas with the error probability (heat map). A = Seasonal or shorter events; B = Longer than one season; C = At least two separated events that occurred in different non-contiguous seasons.

Table 2
Summary of microwear data of all the selected sites.

Locality	Level	*Cervus elaphus*			*Equus ferus*			*Equus hydruntinus*			*Bos primigenius*			*Capra pyrenaica*		
		N	CV*	SD	N	CV*	SD	N	CV*	SD	N	CV*	SD	N	CV*	SD
Teixoneres	IIIa	15	0.16	2.88	29	0.09	1.84	19	0.12	2.36	–	–	–	–	–	–
	IIIb	42	0.12	2.20	12	0.05	1.09	11	0.2	4	–	–	–	–	–	–
Arbreda Cave	I	3	–	–	6	0.07	1.37	–	–	–	3	0.15	2.52	–	–	–
	J	14	0.12	2.03	10	0.11	2.17	–	–	–	5	0.1	1.68	–	–	–
	K	1	–	–	1	–	–	–	–	–	2	–	–	–	–	–
	L	2	–	–	4	0.1	1.89	–	–	–	–			–	–	–
	M	2	–	–	6	0.07	1.37	–	–	–	3	0.04	0.76	–	–	–
	N	–	–	–	3	0.1	1.73	–	–	–	2	–	–	–	–	–
Abric Romaní	E	3	0.27	4.36	5	0.14	3.33	–	–	–	–	–	–	–	–	–
	H	3	0.28	6.61	2	0.12	3.18	–	–	–	–	–	–	–	–	–
	I	6	0.23	4.03	8	0.11	2.62	–	–	–	–	–	–	–	–	–
El Salt	Xa	4	0.2	3.74	22	0.15	3.58	–	–	–	–	–	–	7	0.16	2.82
	Xb	–	–	–	3	–	–	–	–	–	–	–	–	1	–	–

The CV* and SD values correspond to *Cervus elaphus*, *Equus ferus*, *Equus hydruntinus*, *Bos primigenius* and *Capra pyrenaica* from the Teixoneres (sub-units IIIa and IIIb), Arbreda (levels I, J and M), Abric Romaní (levels E and I) and El Salt (sub-units Xa and Xb) archaeological sites. Abbreviations: N = number of specimens; CV* = corrected coefficient of variation; SD = standard deviation.

falling into zone A, and corresponding to a short/seasonal procurement event (Fig. 2A). On the other hand, *E. hydruntinus* (n = 11) is characterized by high variability and these results are plotted in zone B, which is related to long-term events or a succession of short-term procurement events (Fig. 2A).

3.1.2. *Arbreda Cave*

Most of the levels at Arbreda Cave (levels K, L, M and N) yielded a low number of teeth suitable for analysis (Table 2). Level J was the only one with a sample large enough to present significant results, with the exception of *E. ferus* in levels I (n = 6) and M (n = 6) (Table 2). The data for level J show low variability (CV* and SD) for the three species studied, i.e. *C. elaphus* (n = 14), *E. ferus* (n = 9), and *B. primigenius* (n = 5), all appear within zone A (Table 2; Fig. 2B). *E. ferus* samples from levels I and M show low variability, corresponding to zone A (Fig. 2B). Thus, all the species presenting a relatively large sample size ($n > 5$) indicated short/seasonal procurement events (Fig. 2B). The other samples provide only approximate information. Starting from level I, the *B. primigenius* ($n = 3$) data suggest low variability, as does the *E. ferus* dataset, but the *C. elaphus* data could also indicate high variability (Fig. 2B). Level K was too small sample to be exploitable (Table 2). For level L, the data collected for *E. ferus* ($n = 4$) (Table 2) could indicate short/seasonal procurement event (Fig. 2B). In level M, the *B. primigenius* ($n = 3$) data could be related to low variability, like *E. ferus*, also suggesting short/seasonal procurement events (Fig. 2B). Finally, the same results are observed in Level N for *E. ferus* ($n = 3$) (Fig. 2B).

3.1.3. Abric Romaní

The small sample sizes from all the studied levels from Abric Romani (E, H and I) provide only approximate results (Table 2). In level E, only *E. ferus* ($n = 5$) gives significant results, plotting within zone B (Fig. 2C). The high variability (CV* and SD) shown by the horse data is indicative of long-term events or a succession of short-term procurement events, but the proximity to the zone A boundary calls for caution (Fig. 2C). *C. elaphus* ($n = 3$) clearly plots within zone B, which also suggests long-term events or several short-term events (Fig. 2C). There are no significant results for any species for level H (Table 2). The data for *C. elaphus* ($n = 3$) show a high variability that could be indicative of two non-contiguous short events at different seasons of the year. Conversely, the *E. ferus* ($n = 2$) data show low variability, but the values fall within the boundary between zones A and B. The sample size from level I is large enough to offer meaningful results for the two species studied (Table 2). *C. elaphus* ($n = 6$) shows high variability and appears within zone B, indicating long-term events or a succession of short-term procurement events, whereas the *E. ferus* data are characterised by a low variability, falling within zone A and suggesting short/seasonal procurement events (Fig. 2C).

3.1.4. El Salt

For the two sub-units studied at El Salt (Xa and Xb), only the largest sample from Xa gives sufficient data (Table 2). In this context, *E. ferus* ($n = 22$) displays high variability plotting within zone B, which indicates long-term event or several short-term events throughout the year (Fig. 2D). For *C. pyrenaica* ($n = 7$), the values are not informative since they fall within the boundary between zones A and B (Fig. 2D). However, the small sample of *C. elaphus* ($n = 4$) appears within zone B, suggesting the same pattern attributed to *E. ferus* (Table 2; Fig. 2D).

3.1.5. Dietary traits

The ungulate dietary traits observed at Abric Romaní and El Salt suggest high heterogeneity in the overlap of the two main dietary groups of the ungulates and the mixed feeder group (Table 3). In order to better observe the distribution of the number of scratches of each fossil sample, the raw values were plotted against data extant ungulates for the three main dietary groups (i.e. browser, mixed-feeder and grazer) (Fig. S1).

Abric Romaní is subject to the limitations imposed by small sample size (Table 3). The mesowear (MWS) values of *C. elaphus* suggest high variability within the annual dietary traits, ranging from 0.5 to 2.5 (Table 3). The unique sample large enough to provide representative MWS information belongs to level E ($n = 6$) and indicates dietary patterns typical of browsers (Fig. 3A). The MWS values from level H ($n = 2$) and level I ($n = 2$) suggest higher abrasive properties of the resources consumed by the red deer as they seem to correspond respectively to grass-dominated mixed feeders and mixed feeders (Fig. 3A). The LSR data from level I ($n = 6$) indicate browser-dominated mixed feeders (Fig. 3B). The LSR data from level E ($n = 3$) and level H ($n = 3$) are based on small datasets, but they suggest browser-dominated mixed feeders and grazers respectively (Fig. 3B). The MSW values of *E. ferus* are quite homogeneous since they range from 5 to 5.2 across all levels, although most of the data are from level I ($n = 5$) (Table 3). This range corresponds to a grass dietary pattern (Fig. 3A). The LSR values from level I ($n = 8$) indicate a pure grazer diet, which is also suggested by the small samples from level E ($n = 5$) and H ($n = 2$) (Fig. 3B).

Since the El Salt shelter is also subject to sample size limitations, very little information can be gathered from the mesowear analysis (i.e. MWS). In sub-unit Xa, the MWS ($n = 2$) of *C. elaphus* suggests a browser dietary pattern (Fig. 3A), whereas for the same species the LSR ($n = 4$) could be related to a grass-dominated mixed-feeder diet (Fig. 3B). For *E. ferus* the sample size is relatively large, so the information derived can be considered representative: the MWS ($n = 12$) indicates a grass dietary pattern as does the LSR ($n = 22$) (Fig. 3A–B). Although the samples for *C. pyrenaica* are rather small, the MWS ($n = 4$) suggests a browser diet (Fig. 3A), while the LSR ($n = 7$) is indicative of a mixed-feeder diet (Fig. 3B). In sub-unit Xb, there are no data for *C. elaphus* and only one data point for *C. pyrenaica*, but the LSR of *E. ferus* ($n = 3$) suggests a grass dietary pattern (Table 3; Fig. 3B).

3.2. Cementum

At El Salt, the high degree of fragmentation of the ungulate teeth prevented any dental cementum analysis. For all the other sites, the tooth samples selected for this purpose mostly belonged to *C. elaphus* (Table 4). We also included a unique sample of *Bos primigenius* from Arbreda Cave. The equid (*E. ferus* and *E. hydruntinus*) teeth were not integrated in the analysis pending a better understanding of the seasonal growth of the cementum tissues in such hyper-hypsodont teeth.

3.2.1. Teixoneres Cave

Seven *C. elaphus* teeth from sub-unit IIIb were prepared for study (Table 4). One tooth was sampled from sub-unit IIIa based on its macroscopically good preservation, but we had to remove it once the microscopic observation revealed highly altered cementum. The results for the red deer from sub-unit IIIb suggest a high inter-individual variability as they highlighted distinct procurement events throughout the annual cycle (Fig. 4). Five teeth contain a last cementum band (LCB) corresponding to a translucent band (TB). Of these, three had a minimally developed TB, which indicates that the individual died at the beginning of the good season. The remaining two display an approximately half-complete TB, indicating the death occurred in the middle of the good season. In the last two samples, the LCB is an opaque band (OB), placing these procurement events during the bad season.

3.2.2. Arbreda Cave

Since the poor preservation of the teeth from Arbreda Cave considerably limited the sample size, the results obtained should be considered with caution (Table 4, Fig. 4). Only four teeth from three different levels provide reliable data for *C. elaphus* ($n = 3$) and *B. primigenius* ($n = 1$). In the two *C. elaphus* teeth from level L, the LCB is a partially developed TB, suggesting that these animals were killed during the middle of the good season. In level M, the unique *C. elaphus* tooth sample studied shows a final OB, placing its death during the bad season. For the single *B. primigenius* tooth sample (level N), the microscopic examination of the LCB indicates a minimally developed TB, corresponding to the beginning of the good season.

Table 3
Summary of meso- and microwear data of all the selected sites. Data of Teixoneres and Arbreda caves from Sánchez-Hernández et al., (2020).

Locality	Level	Species	Mesowear		Microwear						
			N	MWS	N	LSR	NS	NP	%LP	%G	SWS
El Salt	Xa	*C. elaphus*	2	**1**	4	**25**	19.5	19.88	100	0	1
		E. ferus	12	**5.1**	22	**0**	23.57	14.8	68.18	0	1
		C. pyrenaica	4	**1**	7	**57.14**	18.07	14.14	71.43	0	1
	Xb	*C. elaphus*	–	**-**	–	**-**	–	–	–	–	–
		E. ferus	3	**-**	3	**0**	23.83	17.67	100	0	1
		C. pyrenaica	1	**-**	–	**-**	–	–	–	–	–
Abric Romaní	E	*C. elaphus*	6	**0.5**	3	**66.66**	17.5	19.33	100	0	1
		E. ferus	–	**-**	5	**0**	25.3	20.1	100	0	1
	H	*C. elaphus*	2	**2.5**	3	**0**	25.5	17.33	100	0	1
		E. ferus	1	**5**	2	**0**	31.25	19.5	100	0	1
	I	*C. elaphus*	2	**1.5**	6	**66.66**	18.42	21.25	100	0	1
		E. ferus	5	**5.2**	8	**0**	25.75	16.5	87.5	0	1
Teixoneres Cave	IIIa	*C. elaphus*	14	**1.8**	15	**44.67**	18.73	19.5	78.95	0	0.26
		E. ferus	17	**4.8**	29	**6.9**	20.31	19.4	38.89	0	0.55
		E. hydruntinus	18	**4.3**	19	**10.5**	19.79	17.59	65	0	0.63
	IIIb	*C. elaphus*	34	**1.4**	42	**38.1**	18.16	19.32	68.52	0	0.44
		E. ferus	10	**5.3**	12	**0**	22.38	18.58	72.22	0	0.75
		E. hydruntinus	8	**4**	11	**27.3**	20.55	16.32	41.67	0	0.64
Arbreda Cave	I	*C. elaphus*	3	**1.7**	3	**33.33**	19	21.83	100	0	0
		E. ferus	4	**4.3**	6	**0**	21.33	20.92	50	0	0.5
	J	*C. elaphus*			14	**42.86**	17.68	19.82	57.14	0	0.29
		E. ferus	2	**6**	10	**10**	19.75	21.3	55.56	0	0.56
	K	*C. elaphus*	1	**1**	1	**100**	13	20	100	0	1
		E. ferus	1	**4**	1	**0**	20	24.5	100	0	1
	L	*C. elaphus*	1	**3**	2	**50**	18.5	19.5	100	0	0.5
		E. ferus	4	**4.8**	4	**0**	19.88	23.63	75	0	0
	M	*C. elaphus*	2	**4.5**	2	**0**	20.5	22.25	50	0	0.5
		E. ferus	4	**5**	6	**0**	19.25	20.83	66.67	0	0
	N	*C. elaphus*									
		E. ferus	2	**5**	3	**0**	19.5	19.17	66.67	0	0.33

Abbreviations: N = number of specimens; MWS = mesowear score; LSR = microwear score; NS = average number of scratches; NP = average number of pits; %LP = percentage of individuals with large pits; %G = percentage of individuals with gouges; SWS = scratch width score.

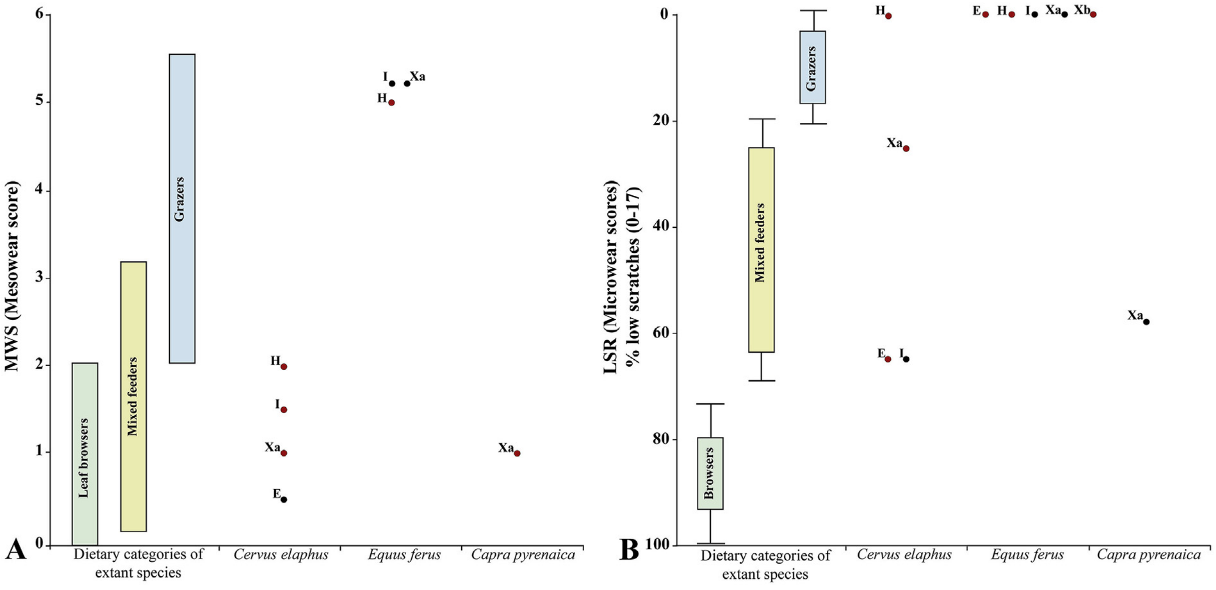

Fig. 3. Mesowear (A) and microwear (B) results of *Cervus elaphus*, *Equus ferus* and *Capra pyrenaica* from the Abric Romaní (levels E, H and I) and El Salt (sub-units Xa and Xb) archaeological sites. Dietary bars correspond to extant ungulates (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). Red dots: n < 4 and n < 5 specimens for MWS and LSR respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.3. *Abric Romaní*

The generally poor preservation of the dental cementum tissues in the studied levels of Abric Romaní, both macroscopically and microscopically, considerably reduced the number of our samples (Table 4). Due to these taphonomical issues, levels E and H were excluded from the analysis. The unique sample of *C. elaphus* from level I yielded some results that must be considered cautiously. It displays an LCB corresponding to an early TB, placing the death at the beginning of the good season (Fig. 4).

Table 4
Summary of cementum data of *Cervus elaphus* and *Bos primigenius* hunting events in Abric Romaní, Teixoneres and Arbreda archaeological sites.

Site	Taxa	Level	Ref	Tooth	Nº CB	LCB	% Dev.	Season of Death
Teixoneres	*Cervus elaphus*	IIIb	TX 2	M1 L	6 (+TB)	TB	**43.53**	Middle Good Season
			TX 13	M2 R	3 (+TB)	TB	**21.68**	Beginning Good Season
			TX 19	m3 L	6 (at least)	OB	**OB**	Bad Season
			TX 20	M1 L	7 (+TB)	TB	**20.47**	Beginning Good Season
			TX 51	m2 L	5 (+TB)	TB	**18.99**	Beginning Good Season
			TX 344	m3 R	5	OB	**OB**	Bad Season
			TX 391	m2 R	2 (at least)	TB	**48.48**	Middle Good Season
Arbreda	*Cervus elaphus*	L	ARB 86	m2 R	5 (+TB)	TB	**62.24**	Middle Good Season
			ARB 102	m3 L	3 (at least) (+TB)	TB	**46.75**	Middle Good Season
		M	ARB 101	m3 R	4	OB	**OB**	Bad Season
	Bos primigenius	N	ARB 92	m1 R	9 (+TB)	TB	**27.85**	Beginning Good Season
Abric Romaní	*Cervus elaphus*	I	AR 7	M1 R	4 (+TB)	TB	**23.69**	Beginning Good Season

Abbreviations: Ref. = reference number attributed by the authors; Nº CB = number of pairs of bands observed in the acellular cementum; LCB = last cementum band observed; %Dev. = % growth ratio of the last cementum increment; Seasonality = season of the individual's death; OB = dark and high mineralized (opaque) cementum band; TB = clear and low mineralized (translucid) cementum band; M = upper molar; m = lower molar; L/R: left or right.

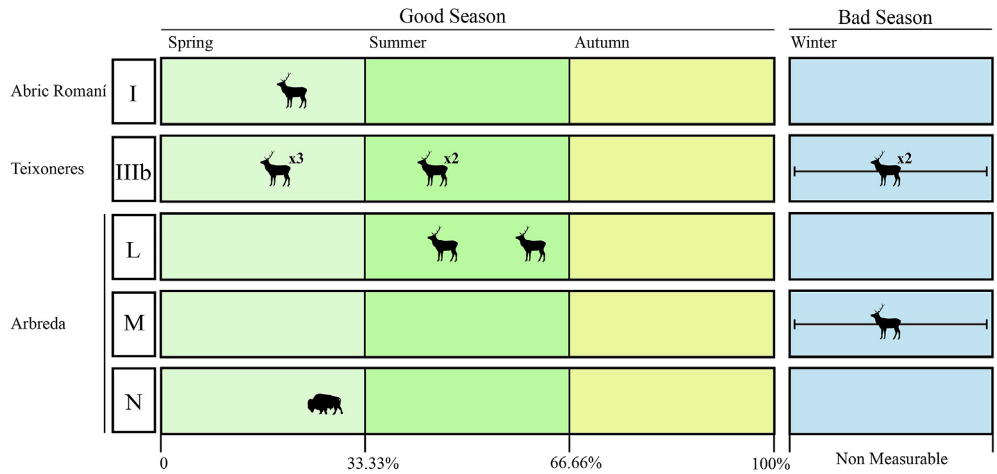

Fig. 4. Schematic representation of *Cervus elaphus* and *Bos primigenius* hunting events in the Abric Romaní, Teixoneres and Arbreda archaeological sites. Percentages correspond to the degree of development of the last translucent cementum band (TB). Silhouettes were freely downloaded from PhyloPic database (www.phylopic.org), under the Public Domain Dedication 1.0 license (*Bos bison*).

4. Discussion

Characterizing the settlement patterns is key to a better understanding of the relationship between human groups and their surrounding habitat. Determining the duration as well as the season(s) of the year in which the settlements took place provides information about how humans groups faced environmental and resource constraints. The settlement features would indirectly help in the recognition of territorial context and the potential resources available to sustain group survival (Binford, 1978, 1980; Kelly, 1983, 1992; Grove, 2009; Rivals et al., 2009b; Moncel and Rivals, 2011; Blasco et al., 2013b; Sánchez-Hernández et al., 2019), as well as the mobility throughout the territory. Considering the environmental influence over the Neanderthal prey's behaviour in the Iberian Mediterranean zone, some regions could have guaranteed the occurrence and availability of biotic resources for the Neanderthals throughout the annual cycle (Sánchez-Hernández et al., 2020). Additionally, bearing in mind the small size of the Neanderthal groups, the impact of their hunting activities was not expected to be large enough to deplete these resources in the short-term, which could have allowed a long-term presence of these groups in this region. In this context, we assume that in addition to environmental characteristics, other factors might also have played a role in the dynamics of settlement patterns.

Indeed, as suggested by the microwear data from this study, the procurement events of the ungulates hunted by Neanderthals reflect different durations from short to long-term. In archaeological terms, this implies a large variability in the settlement patterns performed by Neanderthals, who alternated between short/seasonal and long-term settlement events. However, various possible alternative biases could alter/hide this kind of information, such as the persistence of vegetation with similar properties and the absence of substantial changes in the diet of the ungulates hunted by Neanderthals, or the existence of palimpsests in the settlement layer considered. The data from cementum analysis would help to overcome the first bias factor; however, the second requires specific microstratigraphic analyses that are still pending. The great complexity and characteristics of each site require a combined approach to address this issue.

The majority of the microwear data obtained at both sub-units for Teixoneres Cave (IIIa and IIIb) highlights a low variability in the prey procurement duration, suggesting a unique short-term procurement event or a succession of short/seasonal procurement events under similar environmental conditions throughout the years. This result seems in partial disagreement with findings from previous works about the settlement patterns at the cave, which suggested a recurrent presence of Neanderthals at different times of the year: successive and seasonal short-term events during the annual cycle in sub-unit IIIa and at least two different short-term events in sub-unit IIIb (Sánchez-Hernández et al., 2014, 2016). Indeed, the tooth eruption pattern observed for horse at sub-unit IIIa seems to agree with this hypothesis of short/seasonal Neanderthal settlement since it indicates their summer presence in the area. However, these short acquisitions would be related to seasonal animal movements from the Moianès highlands (summer) to the lower and coastal areas of Catalonia (i.e. winter) (Rosell et al., 2017), because red der showed longer procurement events (Sánchez-Hernández et al., 2014). Therefore, we are faced with a microwear bias based on the absence of seasonal dietary changes within the Neanderthal prey brought to Teixoneres Cave, especially for sub-unit IIIa. The case of sub-unit IIIb is similar to IIIa since the red deer and horse data also suggest a short/seasonal procurement event, with the exception of *E. hydruntinus*. The wild ass data break the general trend, suggesting longer hunting periods and, therefore, a more persistent Neanderthal presence during the year for sub-unit IIIb, in accordance with previous studies (Sánchez-Hernández et al., 2014, 2016). This is also in agreement with the red deer tooth eruption pattern from the same sub-unit (Sánchez-Hernández et al., 2014), and cementum analysis performed for the same species in this research study, indicating successive short/seasonal settlement events during the annual cycle (except autumn).

This raises the question as to why wild ass from sub-unit IIIb, whose territorial behaviour was assumed to be as similarly restricted as the red deer (Burke et al., 2003; Burke, 2006b) indicates longer procurement events (i.e. instead a short one) within the context of relatively stable vegetal resources. The answer could be found in a seasonal ecological competition between equids (i.e. horse and wild ass) in a landscape characterized as relatively humid and dominated by forested areas for sub-unit IIIb (López-García et al., 2012, 2015; Fernández-García, 2019; Ochando et al., 2020; Sánchez-Hernández et al., 2020). Therefore, the altitudinal movements suggested for horse in the Moianès area could have occasionally pushed the wild ass to vary their dietary behaviour during the summer, which was recorded in the microwear data. The seasonal variation in the wild ass diet from sub-unit IIIb could then be related to the altitudinal displacement of horses into highlands during summer, as was observed for sub-unit IIIa. It also suggests seasonal horse procurement in sub-unit IIIb, while red deer and wild ass could have been targeted along the entire annual cycle. However, the autumn absence of red deer capture highlighted by the tooth eruption pattern and cementum analysis could be related to their mating period, when herds moved to places more suitable to withstanding their pressure over resources (Carranza et al., 1991; Carranza, 1995, 2011). Indeed, in Mediterranean areas mating of extant red deer occurs in late summer and early autumn, precisely during the period of highest resource stress (Carranza, 2011; Azorit et al., 2012). Thus, Neanderthal groups from sub-unit IIIb could seasonally have left the cave, possibly in autumn (a fact compatible with the carnivore activity evidence in the same sub-unit), or possibly would be focus to procure other biotic and abiotic resources than red deer and that are not reflected in the archaeological record. However, the combined use of microwear and cementum data reveal a seasonal but recurrent Neanderthal presence during the entire year at sub-unit IIIb.

There is no reason to suppose that sub-unit IIIa was not equally affected by the dietary stability of the Neanderthal prey, which biased the microwear data and modified the interpretations of their settlement patterns. Given the absence of cementum data for sub-unit IIIa and in accordance with the findings from previous studies (Sánchez-Hernández et al., 2014, 2016), we also propose a continuous presence of Neanderthal groups throughout the annual cycle for this stratigraphic context.

If all levels with sufficient sample size to provide reliable information are used (i.e. levels I, J and M), the settlement patterns at Arbreda Cave indicate that the duration of the prey procurement events took place in a short time or as a sequence of short periods with similar environmental conditions through years. Previous studies on faunal and lithic remains along with carnivores evidence (e.g. ursids) agree with the short/seasonal duration indicated within levels I, J and M (Kehl et al., 2014; Soler i Subils et al., 2014). Nevertheless, as it was suggested for Teixoneres Cave, the relatively stable vegetal resources observed at Arbreda Cave had a low impact on the dietary traits of the ungulates, allowing the occurrence of these animal populations in the surroundings throughout most of the annual cycle (Sánchez-Hernández et al., 2020). The permanence of a diversified landscape during the Mousterian sequence could have guaranteed the absence of dietary competition even seasonally (Sánchez-Hernández et al., 2020). In this sense, the cementum analysis performed on levels L, M and N identified short procurement events at different seasons for each level. In the case of level M, where both combined microwear and cementum data are available, the unique procurement event identified (i.e. *C. elaphus*) corresponds to winter. Taking into account the lower altitude of Arbreda Cave relative to Teixoneres Cave and the seasonal and altitudinal movement of horses proposed by Rosell et al. (2017) for the latter cave (i.e. higher altitudes during summer and lower at winter), we argue that level M could present one or more winter Neanderthals settlements related to horse and large bovid acquisition. Although the samples from levels L and N are too small to offer representative microwear information, they suggest different seasonal occupations during the annual cycle. However, given the environmental similarities with Teixoneres Cave and the absence of cementum information for levels I and J (López-García et al., 2012; Fernández-García, 2019; Sánchez-Hernández et al., 2020), we cannot exclude repeated Neanderthal visits throughout the annual cycle. These visits could be hidden by the persistence of vegetal taxa with similar properties within the ungulates diet (no matter the season). They would result in a palaeodietary bias indicating a short-term procurement event and therefore, a short-term settlement, or even a succession of non-related but repeated short-term procurement events within seasons of similar environmental conditions. In addition, in the levels that provide cementum data autumn hunting was not evidenced for red deer.

The microwear results are in agreement with the previous studies performed for level I of Abric Romaní and recognize short but repeated settlement events by Neanderthal groups (Carbonell, 2002; Vallverdú et al., 2005; Marín et al., 2017). Indeed, the data for the red deer indicate long-term procurement events lasting more than one season and are supported by the absence of dietary variability in their feeding behaviour (i.e. mixed-feeders). According to Marín et al. (2017), the age profile of this species in level I shows a high proportion of juvenile specimens that suggest their acquisition during red deer birth periods (i.e. spring and/or summer). The unique tooth that yielded cementum information for this level belongs to a juvenile/sub-adult individual and supports this hypothesis, since this animal died during the beginning of the good season (i.e. spring). Furthermore, we identified some dietary discrepancies between the red deer age groups as prime adults fed on concentrated resources (such as leaves and shrubs) whereas older adults fed on grasses. In this context, although an age-territorial distribution could also condition access to resources, these dietary differences are probably related to hunting events in different seasons of the annual cycle. The Mediterranean influences in this area would affect the seasonal quality/distribution of resources as concentrated ones would be preferred during spring-summer and grasses would be consumed at the end of autumn/winter (Weladji et al., 2002; Bugalho and Milne, 2003; Carranza, 2011; Azorit et al., 2012).

On the other hand, the horse acquisition seems to have taken place in a unique short-term event or perhaps as a succession of non-related short-term events with similar environmental features – probably winter. We suggest a winter hunting event based on the strictly grass diet that characterizes these horses and the fact that winter is the period that would provide higher-quality pastures in the Iberian Mediterranean area (Weladji et al., 2002; Bugalho and Milne, 2003; Carranza, 2011; Azorit et al., 2012; Sánchez-Hernández et al., 2020). The similarities observed between the horse hunting events identified in level M of Arbreda Cave and those from level I of Abric Romaní, could be related to the similar altitudes, which are lower than Teixoneres Cave. The possible seasonal changes in the resource availability would support the assumption of a seasonal altitudinal movement made by Rosell et al. (2017) for the horses in this region and, consequently the hypothesis of winter equid hunting.

For the sub-unit Xa of the El Salt shelter the microwear study also suggests a long-term or several short-term but repeated Neanderthal visits during the annual cycle. This is in agreement with the lithic and faunal studies that indicate a recurrence of several and non-related short-term Neanderthal occupations (Fagoaga et al., 2015, 2019; Fagoaga-Moreno et al., 2015; Machado and Pérez, 2016; Machado et al., 2017; Leierer et al., 2019; Pérez, 2019). Indeed, there is evidence of abandonment (e.g. a sterile layer) and carnivore activities (e.g. digestion, tooth marks, coprolites) in the unit X supporting the hypothesis of intermittent use of the shelter by Neanderthal groups (Pérez et al., 2015, 2017; Machado and Pérez, 2016; Leierer et al., 2019). The approximate data obtained by the microwear study for red deer could be in accordance with this interpretation because they also suggest short-term and seasonal prey acquisition during the annual cycle. Although the microwear results for the Iberian ibex are not informative of the hunting event duration, the differences between the annual and the specific dietary traits at their time of death suggests seasonal mortality and therefore, seasonal prey acquisition (Sánchez-Hernández et al., 2016). Therefore, the apparent long-term acquisition of horses should be understood as a succession of seasonal/short-term procurement events aggregated by a palimpsest effect, and not as a stable and continuous Neanderthal settlement throughout the year.

Considering the altitude of El Salt (i.e. 680 m a.s.l.) and the supposed horse movement pattern at Teixoneres, Arbreda and Abric Romaní, it must be expected that a seasonal acquisition (e.g. summer) and a possible discrepancy between the annual and seasonal dietary traits of horses would be identified. Nevertheless, the microwear data are consistent with the tooth eruption pattern in the sense that both suggest continuous acquisition during the annual cycle (Pérez, 2019). So, the absence of a marked and seasonal horse hunting events in sub-unit Xa could have resulted from particular environmental and orographic features (Pérez et al., 2020). The supra-Mediterranean climatic data inferred from the study of unit X (both sub-units Xa and Xb) indicate cold but humid conditions allowing the development of various habitats, mainly dominated by forests, but with important open areas. These environmental features, as well as the proximity of the Serpis river valley, allowed a wide range of potential prey in the surrounding areas of the shelter during the annual cycle (Fagoaga-Moreno et al., 2015; Vidal-Matutano, 2017; Fagoaga et al., 2018; Pérez, 2019). The proximity of hydric resources could also have played a role in the maintenance of horse populations in the area due to their water dependence as pointed out by Marín et al. (2019) for the level P of Abric Romaní (Berger, 1986; Burke, 2006a), which could have been a strategic point in the hunting of this taxon and other species.

However, we identified variations in the abrasiveness of the grazer diet of the horse which could be related to the average number of scratches for two distinct groups: highly abrasive and less abrasive. These could be a result of the horse feeding in pastures nearby the shelter and would, therefore, be affected by the phenology of the vegetation (i.e. quality changes). If so, one could expect that horse carcasses were processed at killing sites close to the settlement and, therefore, to find a relatively even representation of all the horse skeletal parts at El Salt. However, it could also be a consequence of horse seasonal movements between different feeding areas. Actually, the horse's anatomical profile found in unit X is dominated by the presence of appendicular elements, showing a preference for high nutritive anatomical parts which can be transported to the campsite (Pérez, 2019). In addition, the lower but persistent occurrence of axial elements could reflect the distance variation between the killing sites and the shelter in relation to the seasonal horse mobility within the surrounding areas and the Alcoy valleys (Pérez et al., 2020). Therefore, all the presented data and the previous studies support a constant acquisition of horse by Neanderthal groups over the year (Pérez, 2019; Pérez et al., 2020).

The observed hunting strategies developed by Neanderthal groups at these Mediterranean sites demonstrate a wide knowledge about their prey behaviour and territorial distribution during the annual cycle. The studied contexts also show similar settlement patterns, where short/seasonal visits seem to have been the rule for these Neanderthal groups. Furthermore, the concentration of human settlements in relatively small spaces (the outer area at Teixoneres Cave and close to the wall at the El Salt shelter), along with the intermittent presence of carnivore activity, excludes the residential character of these sites (Carbonell, 2002; Vallverdú et al., 2005; Rosell et al., 2010, 2017; Soler i Subils et al., 2014; Rufí et al., 2018; Pérez, 2019). Actually, the settlement and mobility model developed by these groups seems to be related to non-residential settlements and to predation interests. One of the questions derived from the non-residential settlements concerns the intentionality of the hunting events, i.e. whether they were specialized or opportunistic strategies within logistical or circulating mobility models.

The duration of human settlements (i.e., short-term but recurrent during the annual cycle) does not support the supposition that opportunistic and random predation strategies were the main survival system developed by Neanderthal groups. On the contrary, intentionality can be deduced from the mobility pattern throughout the territory to acquire certain prey, in the form of seasonal hunting specializations as shown in level I of Abric Romaní (i.e. red deer and horse) and levels I, J and M of Arbreda Cave (i.e. aurochs and horse). The marked seasonality of these acquisitions suggests logistical movements to obtain specific resources at different times of the year. On the other hand, the prey acquisition patterns observed both at Teixoneres Cave and El Salt seem to be the result of more recurrent hunting events during various seasons. Indeed, the results obtained for the different taxa complement and overlap one other within this temporal frame (Sánchez-Hernández et al., 2014, 2016; Rosell et al., 2017; Fagoaga et al., 2019; Leierer et al., 2019; Pérez, 2019). Although there are seasonal data for other species (i.e. Iberian ibex from sub-unit Xa at El Salt, and horse from sub-unit IIIa at Teixoneres), the hunting of red deer at both sites does not correspond to a marked seasonal pattern, but rather long term events during the annual cycle. The wild ass data also show a similar pattern at Teixoneres, since its strong territorial behaviour could make it an ubiquitous taxon like the deer and allow its capture at any time of the year in the same area (Burke et al., 2003; Burke, 2006b).

These observations seem to point to a residential model for the Neanderthal groups at Teixoneres and El Salt. However, as mentioned above, the reduced and concentrate spatial settlements at the entrance of Teixoneres and close to the wall at El Salt, along with the occurrence of carnivore activities, rule out this possibility, as does the evidence of palimpsest effects within these stratigraphic contexts. Conversely, it seems that these relatively high-altitude sites would have been part of a circular model, which allowed radial logistic movements to obtain both biotic and abiotic resources within a specific territory (Binford, 1980, 1982; Kelly, 1983, 1992; Müller et al., 2003). Indeed, the high mobility attributed to Neanderthal groups and the seasonal availability of certain taxa would have allowed frequent returns to these places based on the specific needs of the group such as for the acquisition of a wide range of meat resources. Specifically, the radial logistic procurement model can explain the absence of autumn hunting episodes in sub-units IIIb of Teixoneres and Xb of El Salt. This seasonal gap might be due to the red deer and horse ethology (i.e. mating period and seasonal or altitudinal movements, respectively), since their behavioural requirements suggest a minimal presence or even their absence in the surroundings in autumn. It is reasonable to think that, in regions dominated by wooded areas, the horse moved towards lower altitudes in search of pastures, since the red deer would move to more open spaces with greater availability of resources during the mating season (Carranza et al., 1991; Carranza, 1995, 2011; Rosell et al., 2017). Autumnal settlement abandonment seems to be a repeated pattern in other relatively high-altitude sites as evidenced by levels III-b/d and III-i/j of Cueva Antón (Murcia, Spain) (Sanz et al., 2019), and even at others sites of lower altitude, such as the level M of Arbreda presented in this research. However, because the mortality pattern suggested for *C. pyrenaica* in sub-unit Xa of the El Salt shelter (Pérez, 2019) places the hunting during autumn, we cannot affirm that the autumnal absence of red deer hunting in sub-unit IIIb of Teixoneres is due to an abandonment of the site by Neanderthal groups. They could have remained in the general vicinity, focusing their activities on other resources, whether vegetal or animal.

The logistic nature of Neanderthal settlements is observed at all the sites analysed here, with small variations related to the altitude of the sites themselves. The lower altitude sites (i.e. Abric Romaní and Arbreda Cave) present a more selective and seasonal resource acquisition pattern than those of higher altitude, contrary to what one might expect. This is reflected in a seasonal interest to obtain certain resources (i.e. horse and large bovids in winter vs. red deer mainly in spring). However, these sites do not achieve the high degree of specialization observed, for example, in southern France where hunting focused on reindeer (Jonzac, Les Pradelles or Pech de l'Aze IV) or bison (Mauran, La Rouquette, La Quina 6c level) (Farizy et al., 1994; Chase, 1999; Costamagno et al., 2006; Rendu, 2007; Rendu and Armand, 2009; Niven et al., 2012; Niven, 2013). This leads us to characterize Abric Romaní (level I) and Arbreda (levels I, J, M) as seasonal camps dedicated to the acquisition and processing of meat resources (intermediate butchery sites). Actually, the lithic technological data for level I of the Abric Romaní shelter indicate ephemeral and punctual visits (Carbonell, 2002; Vallverdú et al., 2005; Marín et al., 2017). Whereas the lithic studies of Arbreda Cave indicate a broad knowledge of the distribution of abiotic resources surrounding the cave, prioritization of the use of local raw material and preservation of the non-local tool kit (for distances greater than 100 km) (Maroto et al., 1996; Duran and Soler i Masferrer, 2006; Lloveras et al., 2018; Rufí et al., 2018). Therefore, the repetitive use of low altitude sites based on seasonal taxa availability suggests task-specific camps specialized in temporary hunting within a clearly logistic mobility framework.

On the other hand, the greater recurrence of Neanderthal visits identified at the higher altitude sites (i.e. in sub-unit IIIa of Teixoneres Cave and sub-unit Xa of El Salt) and the temporary overlapping of the seasonal prey acquisitions could suggest a lower selective pattern which could be determined by the chance of encountering prey in the surroundings of more residential settlements. However, lithic and raw material supply evidenced at both sites are characterized by fragmented reduction sequences and the use of mixed knapping strategies (among hierarchized and expedient) according to the origin of the raw material (i.e. local vs. non-local). These suggest high group mobility combined with a high plasticity based on immediate requirements (Rosell et al., 2010, 2017; Machado-Gutiérrez et al., 2011; Machado and Pérez, 2016; Bustos-Pérez et al., 2017; Machado et al., 2017; Picin et al., 2020). Likewise, the pattern of acquisition of horse at Teixoneres Cave (sub-unit IIIa), and that of Iberian ibex and red deer at El Salt (sub-unit Xa) do not fit with a residential camp, but suggest seasonal inputs of preys within these two sub-units. The semi-mountainous nature of these areas and the altitudes of these sites could have propitiated microclimate features guaranteeing territorial stability and the availability of a wide variety of resources throughout the year (Bennet and Mathias, 1984; Carrión, 2012; Domingo et al., 2017). A greater survival interest could have persisted in these areas, allowing a highly intensive logistic model as the recurrence of the Neanderthal visits suggest. Furthermore, these settlement patterns seem to have resulted from a high territorial control as suggested by other Mediterranean sites, such as levels IV of Bolomor and at Abrigo de la Quebrada (Fernández Peris, 2007; Sañudo and Fernández Peris, 2007; Blasco et al., 2013b; Villaverde et al., 2017).

5. Conclusion

The combined application of tooth microwear and dental cementum should not be understood as a closed and definitive approach, but as a general method for resolving various information biases (i.e. relatively stable vegetal persistence and low/absent dietary variability, palimpsests) and thereby increasing the accuracy of the interpretations of human settlement patterns. Thus, this methodological approach benefits from its complementarity with the classical approaches (i.e. zooarchaeology, lithic technology, taphonomical studies, etc.) and other high-resolution techniques, such as oxygen and carbon isotopes studies.

The results obtained suggest that a comprehensive knowledge of the territory and potential prey behaviour allowed Neanderthals to fully or partially follow logistic models in the Mediterranean region. According to these models, the possible oscillations of the environmental conditions around the sites did not affect the settlement model since the Neanderthals would visit these sites continuously. It follows that the recurrence of short and seasonal settlements throughout the year within a logistic mobility model seems to have been the norm in this domain. Moreover, the altitudinal factor likely had a great influence on their prey ethology, conditioning the interest of certain places at specific times of the year. The more recurrent and less seasonally-dependent settlement patterns, along with the less selective prey acquisition patterns observed at the higher altitude sites, seem to contradict the expected pattern, where low altitudinal sites would have offered wider prey availability and territorial stability throughout the annual cycle. In this sense, extending such studies to other elevated sites in the Mediterranean region is required in order to contrast the Neanderthal settlement models and the ethology of the surrounding prey hunted by the human groups.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106523.

Author contributions

CSH conceived/designed the study in collaboration with FR and LG. RB, EC, GC, BG, CHG, FR, JR, PS, JS, NS, and JV provided materials for the research. CSH performed the dental wear and cementum sampling processes. CSH analysed the materials and the results with contributions from LG and FR. CSH wrote the original draft with input from FR and LG. All authors have read and approved the manuscript.

Data availability

All data generated during this study are included here and in the Supplementary Information file.

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