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Carlos Sánchez-Hernández, Lionel Gourichon, Joaquim Soler, Narcís Soler, Ruth Blasco, et al.. Dietary traits of ungulates in northeastern Iberian Peninsula: Did these Neanderthal preys show adaptive behaviour to local habitats during the Middle Palaeolithic?. *Quaternary International*, 2020, 557, pp.47-62. 10.1016/j.quaint.2020.01.008 . halshs-02975295

HAL Id: halshs-02975295

<https://shs.hal.science/halshs-02975295v1>

Submitted on 23 Nov 2021

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Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Dietary traits of ungulates in northeastern Iberian Peninsula: Did these Neanderthal preys show adaptive behaviour to local habitats during the Middle Palaeolithic?

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ARTICLE INFO

Keywords:

Late pleistocene
Paleodiet
Paleoenvironment
Adaptive behaviour
Dental wear
Dental cementum

ABSTRACT

Diet is closely connected to the habitat exploited by ungulates and is one of the main links between them and the surrounding environment. When climatic fluctuations modified the vegetal cover and habitat, ungulates' dietary behaviours and ecological niches could have been impacted severely. During the Middle Palaeolithic, the Mediterranean peninsulas were known to be climatic refuges because they seemed less susceptible to these changes. However, the altitude or latitude of a given site may have resulted in local particularities that could have influenced the vegetal composition and therefore the feeding behaviour of ungulates as well as the environmental conditions in the surroundings. Dental cementum analysis allows accurately identifying the season of ungulate death and linking an individual's dietary preferences with the seasonal conditions in its last moments of life. As results, red deer at both sites were mixed-feeders in the annual cycle. A slight increase in grass consumption was identified during winter for populations from sub-unit IIIa of Teixoneres Cave. Horse and wild ass based their diet on grasses, but the latter showed seasonal adaptation toward a mixed consumption of grasses and concentrate resources (i.e. leaves, shrubs, forbs, and other woody plants). The seasonal feeding adaptations observed for some of the studied species did not strongly influence their general dietary trends because they kept feeding on the same resources annually.

1. Introduction

Global environmental conditions and the specific ecological features in a given region directly impact the composition and distribution of flora and fauna (Hewitt, 2000; Uriarte, 2003; Rivera Arrizabalaga, 2004; Sánchez-Goñi and D'Errico, 2005; Sánchez-Goñi and Harrison, 2010). The Late Pleistocene displays continuous climatic oscillations, especially

during the Marine Isotopic Stage 3 (MIS 3, ca. 60–30 ka BP). The advance and retreat of glaciers drastically modified the European landscape and, in turn, the adaptive and survival capabilities of flora and fauna (Lowe and Walker, 1984; Dansgaard et al., 1993). The large mammals inhabiting the continent during this period, mostly ungulates, showed a wide range of responses to ecological issues, varying from phenotypically and migratory aspects to disappearance (Graham et al., 1996; Brown and

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<https://doi.org/10.1016/j.quaint.2020.01.008>

Received 14 October 2019; Received in revised form 24 December 2019; Accepted 13 January 2020

Available online 17 January 2020

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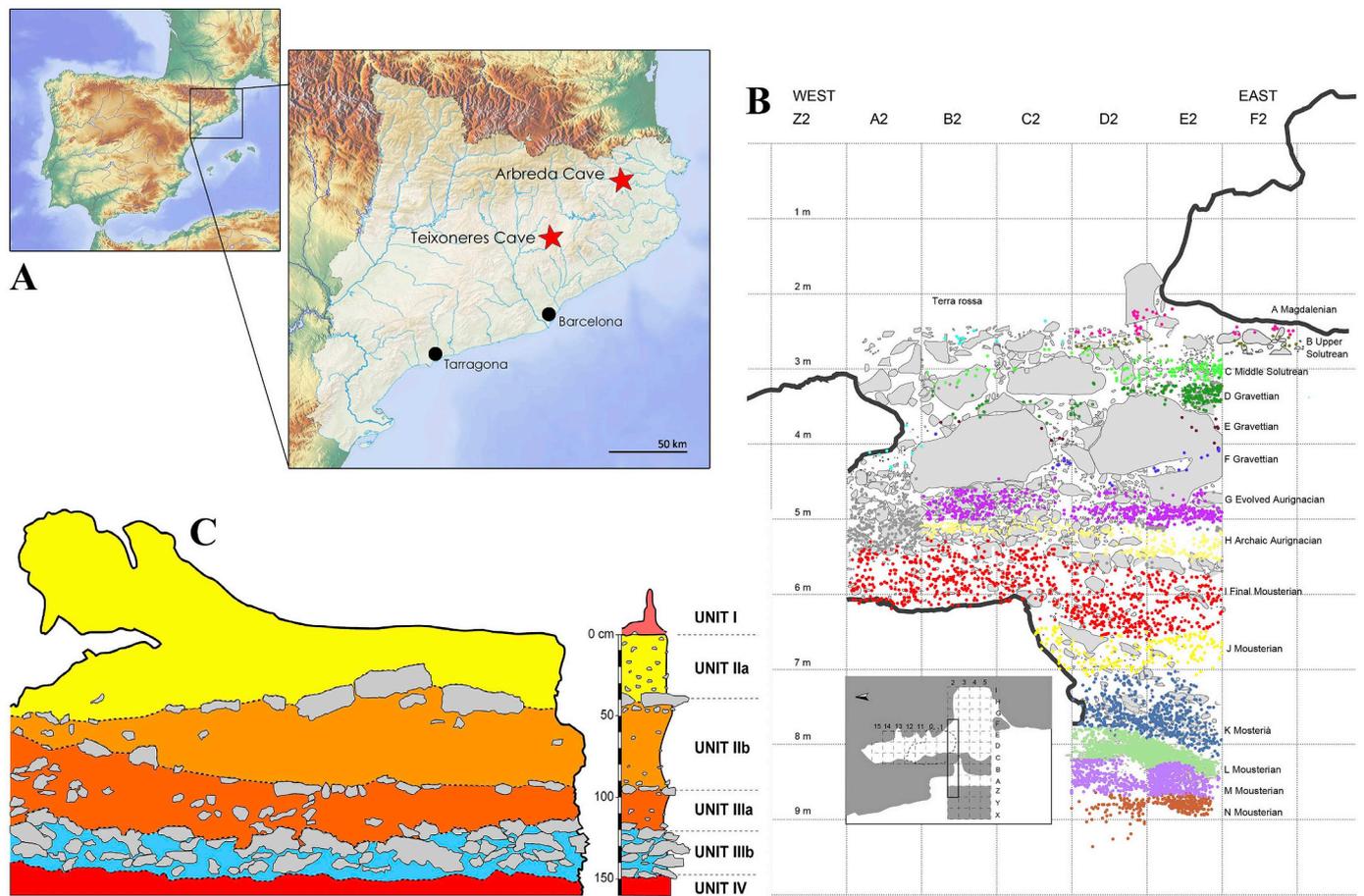


Fig. 1. Location (A) and stratigraphy of Arbreda Cave (B) and Teixoneres Cave (C).

Lomolino, 1998; Forchhammer et al., 2002; Martínez-Meyer et al., 2004). Even on a seasonal and regional basis, environmental features affect the availability and phenology (e.g. nutritional quality) of the plants consumed by ungulates, thereby having implications on their biological and behavioural responses to these changes (Jarman, 1973; Denium, 1984; Helle, 1984; Van Soest, 1994; Weladji et al., 2002; Pettorelli et al., 2005; Arnold et al., 2015). Therefore, ungulates' adaptive success to specific environmental features depends on the habitat tolerance of the communities and the specific dietary limits of each taxa (Graham, 1985; Graham et al., 1996; Williams and Jackson, 2007; Stewart, 2008).

As each taxa shows different degrees of or no dietary plasticity, the current research aims to determine how the main ungulates (*Cervus elaphus*, *Equus ferus*, and *Equus hydruntinus*) hunted by Neanderthals in the northeast of the Iberian Peninsula responded to local environmental features. The study focus on two archaeological sites located above the 40° N parallel and at different altitudes: Arbreda Cave (211 m a.s.l.) and Teixoneres Cave (760 m a.s.l.) (Fig. 1A). Cervids and equids are known for developing differentiated adaptive strategies to cope with environmental variations. Their presence in the same territory during a period of expected environmental fluctuations can provide a much more accurate view of local and regional features through their dietary strategies. *Cervus elaphus* is well known to have great dietary plasticity, feeding in a wide range of resources and being able to adapt to very diverse habitats (Hofmann and Stewart, 1973; Hofmann, 1989; Fonseca, 1998; Azorit et al., 2012; Berlioz et al., 2017). *Equus ferus* is expected to show more restricted dietary plasticity; however, extant and extinct populations demonstrated that they could feed on resources that are not exclusively grasses (Duncan, 1991; Nowak, 1999; Rivals et al., 2009, 2015). *Equus hydruntinus* seems restricted to open areas and

the resources available therein (Orlando et al., 2006; van Asperen et al., 2012; Crees and Turvey, 2014; Boulbes and van Asperen, 2019). Otherwise, some morphological and size aspects (a longer protocone and increased hypsodony) of their teeth suggest wider dietary plasticity (Eisenmann, 1991; Boulbes, 2009).

The aim of the present research is to identify the feeding traits of the above-mentioned ungulates (*Cervus elaphus*, *Equus ferus*, and *Equus hydruntinus*) to test whether they show adaptive dietary behaviour influenced by local environmental features like latitudinal and altitudinal gradients. This knowledge would generate an interesting context to recognise Neanderthals relationship with the environment they inhabit and how these groups respond to the adaptations (whether seasonal or local) of their potential preys. These objectives will be achieved using a combination of two high-resolution techniques, namely, dental wear (meso- and microwear) and dental cementum.

The study of ungulates' dental wear gives information about diet because both meso- and microwear are sensitive to dietary changes on different temporal scales (Grine, 1986; Fortelius and Solounias, 2000). Mesowear reveals the average annual diet of the last months/year (> 6 months) before death correlated with the general surrounding environmental features (Fortelius and Solounias, 2000; Ackermans et al., 2018). On the other hand, microwear reflects a very precise moment in an individual diet as it is generated by the diet of the last days/weeks before death (Grine, 1986), thereby highlighting specific environmental conditions at that point and seasonal climatic changes (Merceron et al., 2004; Semperebon et al., 2004; Rivals and Semperebon, 2012). Furthermore, dental cementum analysis—also called cementochronology—provides accurate estimates of the season of death of the animals (Scheffer, 1950; Laws, 1952; Lieberman, 1991; Pike-Tay, 1991a; Gourichon, 2004; Rendu, 2007; Naji et al., 2015), allowing us to correlate the

seasonal feeding patterns with a specific period of the annual cycle (Sánchez-Hernández et al., 2019). In addition, even if the taxa show homogenous feeding traits through the stratigraphic sequences or the archaeological sites, cementum analysis enables assessing whether these patterns are due to seasonal mortality (same season) or stable environmental features allowing them to feed on the same resources. In this study, dental cementum analysis was only applied to red deer because the properties of equid cementum make it difficult to interpret the observations.

2. European and Iberian environmental contexts

The MIS 3 is marked by extreme oscillations characterised by the predominance of notably cold and dry periods (Heinrich events (HE)) interspersed by temperature and humidity recovery events with less extreme environmental conditions (Dansgaard-Oeschger events (DO)) (Dansgaard et al., 1982; Heinrich, 1988; Johnsen et al., 1992; Rasmussen et al., 2014). These cyclical HE and DO alternations affected the European continent in different ways depending on the region because other factors such as latitude and altitude are also deeply involved (Álvarez-Lao and Méndez, 2016; Rivals and Semperebon, 2016). During the HE (also stadial periods), most of the European territory was dominated by tundra and steppe as well as ‘mammoth fauna’ in areas without ice sheets (Guthrie, 1982; Vereshchagin and Baryshnikov, 1982; Kahlke, 2014). On the other hand, mid-climate-adapted vegetation and animals were pushed toward southern areas, considered as climate refugia, such as the Mediterranean peninsulas and the Balkans (Hewitt, 2000; Sommer and Nadachowski, 2006; Álvarez-Lao and Méndez, 2016). These ecologic refugees allowed a rapid recovery of forested areas and animals adapted to temperate conditions in the rest of the continent during DO.

The Iberian Peninsula would not have been strongly affected by the climatic changes occurring during the MIS 3 despite the marginal presence of some cold-adapted taxa like the woolly mammoth (Sánchez-Goñi et al., 2010; Álvarez-Lao and García, 2011; Álvarez-Lao and Méndez, 2016; Rivals and Álvarez-Lao, 2018). The Pyrenees Mountains act as a natural barrier in the north which isolates the Peninsula from the rest of the continent, leaving only two narrow natural paths in the occidental and oriental slopes of these mountains. The Iberian Peninsula is characterised by relatively mild environmental conditions even during the coldest phases (HE) of MIS 3 (Hewitt, 2000; Sommer and Nadachowski, 2006; Álvarez-Lao and Méndez, 2016). The relative stability of the environmental features and the vegetal cover's resilience to global climatic changes are some of the main particularities of this region. These conditions could have guaranteed the constancy of the available resources and the absence of drastic adaptive behaviours resulting in stable faunal ecological niches, especially for ungulates. Nevertheless, the orography and the several oceanic influences observed (i.e. Atlantic and Mediterranean) reflect a wide range of climatic parameters that allow us to consider the Peninsula as a mini-continent in itself. With an average altitude of 600 m a.s.l. and various mountain ranges and river valleys, this territory can be divided into three main areas characterised by distinct ecological features (i.e. latitude, orography, and altitude): the central Iberian area, and the Cantabrian and the Mediterranean basins.

The latitudinal and altitudinal gradients related with climate and vegetation as well as climate instability usually affect ungulate populations (Rivals et al., 2007b, 2010; Rivals and Semperebon, 2016). Along the Iberian Mediterranean basin, several studies indicate a northeast area as cold and dry as the southern area but relatively more humid (Uzquiano-Ollero, 2008; Badal-García et al., 2012; Allué et al., 2017, 2018; Vidal-Matutano, 2018). The north-eastern region was dominated by vegetal cover typical of open forested areas dominated by conifers like *Pinus sylvestris* associated with deciduous and mesophilous taxa (e.g. *Quercus*, *Betula*, and *Corylus*) that suggest warm and humid episodes (Ros-Mora, 1987; Burjachs and Julià, 1994; Rivals et al., 2017;

Allué et al., 2017, 2018). Otherwise, open landscapes and dryer conditions dominated in the southern regions with the occurrence of pine forests (*Pinus nigra-sylvestris* and *Pinus pinea*) along with *Quercus*, *Juniperus*, and *Ephedra* taxa (Ros-Mora, 1987; Uzquiano-Ollero, 2008; Badal et al., 2012; Allué et al., 2017, 2018; Vidal-Matutano, 2017, 2018).

3. Archaeological sites

3.1. Arbreda Cave

The Arbreda Cave is an archaeo-palaeontological site located in the Serinyà locality (42° 9' 38" N, 2° 44' 49" E) (Fig. 1A). Along with other cavities such as Reclau Viver or Mollet I, it forms part of a karstic system belonging to the Banyoles-Besalú basin (Julià, 1980; Roqué et al., 1999). The cave is located in a low area of the pre-Pyrenean region, in an elongated but narrow travertine strip of the river Serinyadell valley. In its surroundings, there is a platform of lacustrine origin called Pla d'Usall to the west and small rivers. The 10 m sedimentary sequence comprises 14 levels from the Middle Pleistocene at the bottom to the Holocene at the top (Fig. 1B) (Soler et al., 1987a, 2014; Bischoff et al., 1989; Kehl et al., 2014). The Mousterian sequence shows an extensive chronological frame: the basal level (i.e. N) was dated by U-series/ESR ca. 120 ka BP (Soler i Subils et al., 2012, 2014), whereas the upper Mousterian level (i.e. I) is dated to 45.840–41.410 cal BP based on AMS radiocarbon dates (Maroto et al., 2005; 2012; Wood et al., 2014). The sequence presents alternating occupations by human groups and carnivores. The faunal assemblage documented for the Late Mousterian levels corresponds to a broad spectrum of both herbivore and carnivore mammals adapted to Euro-siberian and Mediterranean environmental conditions (Soler et al., 1987b, 2014; Galobart et al., 1996; Lloveras et al., 2010, 2018; Ruff et al., 2018). These include a few species from semi-open and wooded areas, like *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, and *Capra pyrenaica*, as well as species typical of open areas, like *Equus ferus* and *Equus hydruntinus*. A calf tooth of *Mammuthus primigenius* represents cold-adapted fauna in level J, whereas a molar of *Castor fiber* indicates running rivers in the vicinity. Carnivores are represented by *Ursus spelaeus*, *Crocota crocuta*, *Canis lupus*, *Vulpes vulpes*, *Felis silvestris*, *Panthera pardus*, and *Lynx cf. spelaea*. Among lagomorphs, *Oryctolagus cuniculus* predominates versus the marginal presence of *Lepus europaeus* (Soler i Masferrer and Maroto, 1987b; Maroto et al., 1996; Lloveras et al., 2010). Level I is the unique Mousterian level where small mammal assemblage has been recovered and studied (Alcalde, 1987; Galobart et al., 1996; Alcalde and Galobart, 2002; López-García et al., 2015). This assemblage, which may be used as a reference for level J on which the present research focuses, is dominated by species with Eurosiberian climatic preferences, such as *Microtus arvalis* or *Talpa europaea*, as well as by generalist taxa such as *Microtus agrestis* or *Apodemus sylvaticus*. There is also an important component of species with Mediterranean requirements, like *Eliomys quercinus*. The climatic and environmental conditions had lower annual temperatures and higher degree of humidity than those seen nowadays (Sans-Fuentes and Ventura, 2000). An alternation between two warm and humid periods and another cold and dry one was identified for level I (López-García et al., 2015). Previous palynological and anthracological studies suggest a landscape of open-wet and forested areas dominated by *Pinus sylvestris* and herbaceous vegetation around the cave (Ros-Mora, 1987; Burjachs and Renault-Miskovsky, 1992; López-García et al., 2015).

3.2. Teixoneres Cave

More than 60 km southwest of the previous site, Teixoneres Cave (41° 48' 25" N, 2° 09' 02" E) (Fig. 1A) belongs to the ‘Coves del Toll’ karstic system (Rosell et al., 2010a, 2017). The cave is located south of the pre-Pyrenean region (Moià, Barcelona, Spain) in a zone of transition between the Mediterranean coast and the hinterland of the North-East

region (Fig. 1A). The surrounding landscape is characterised by highlands with the presence of small hills and rivers of little importance, except for the Llobregat River to the south and the Ter River to the north which delimit the region. The cavity presents ~8 m deep sedimentary sequence where nine stratigraphic units were identified (Fig. 1C) (Serra et al., 1957, 1973; Rosell et al., 2017). The present research focuses on unit III, divided into two sub-units (i.e. IIIa and IIIb) and ranging from > 51 ka ¹⁴C BP to 43.4 ka cal BP (Talamo et al., 2016). Unit III is characterised by an alternation between human occupation at the entrance of the cave and carnivore occupation in the back and darker areas (Rosell et al., 2010b).

In the faunal record, up to 19 different taxa were identified, including carnivores and herbivores. In the unit III, the carnivores correspond to *Ursus spelaeus*, *Crocota crocuta*, *Canis lupus*, *Vulpes vulpes*, *Lynx spelaea*, and *Meles meles*. The broad spectrum of ungulates recovered in this unit indicates a complex environment formed by different habitats such as steppe-like, open forest, and mountains areas (Álvarez-Lao et al., 2017; Rosell et al., 2017). The presence of mixed wooded and semi-open areas is indicated by *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*, and *Bos primigenius*. The open spaces around the cave are suggested by the occurrence of *Equus ferus* and *Equus hydruntinus* and by the cold-adapted taxa *Coelodonta antiquitatis* and *Mammuthus primigenius*. Finally, remains of *Capra pyrenaica* and *Rupicapra rupicapra* were found in the assemblage. The small vertebrate assemblage shows differences in composition and proportion between the sub-units IIIa and IIIb (López-García et al., 2012, 2014). Generalist species like *Apodemus sylvaticus*, *Eliomys quercinus*, or *Bufo calamita* dominate the entire unit III. The Mediterranean species take a significant part, such as *Microtus (Terricola) duodecimcostatus*. The strict Eurosiberian species present in both sub-units include *Rana temporaria*, *Microtus arvalis*, and *Sorex coronatus*. Sub-unit IIIa is characterised by species with a preference for high altitude and rocky terrain, such as *Chionomys nivalis* and *Terricola gerbei* and Mediterranean taxa such as *Anguis fragilis*. This combination suggests a decrease in temperature but still humid conditions, as indicated by the presence of forest. Instead, sub-unit IIIb yielded species of generalist and Mediterranean requirements which are absent in IIIa: *Natrix cf. natrix*, *Coronella austriaca*, *Glis glis*, and *Rhinolophus ferrumequinum*. They show a predominance of forested areas and humid conditions. The pollen and charcoal studies indicate the prevalence of humid and temperate environments in a Mediterranean region characterised by open forest landscape mostly comprising *Pinus sylvestris* and *Quercus* sp., whereas herbaceous taxa (Poaceae, Amaranthaceae, Asteraceae) dominated in open areas (López-García et al., 2012).

4. Material and methods

The material involved in the present research was selected following specific protocols related to each technique (see below) and by taking as a basic premise a good preservation of the morphological integrity and dental tissues. Ideally, it is preferable to perform the whole study on a single type of molar (e.g. the second upper molar). Nevertheless, owing to the relatively high degree of fragmentation in the assemblages (especially those from Arbrede Cave) and to the low amount of cheek teeth, the upper and lower molars as well as the fourth premolar were chosen for all the analyses, in particular for microwear. Xafis et al. (2017) suggested that differences between the microscopic patterns of premolars and molars are not significant, which was also observed for the Schöningen equids by Rivals et al. (2015). We also tested for differences between tooth positions in our material (see section 5.2). The teeth sampled for dental wear belong to *Cervus elaphus* (n = 132) *Equus ferus* (n = 120) from Arbrede and Teixoneres caves and *Equus hydruntinus* (n = 43) which was only present at Teixoneres Cave (Table 1; see Table S1 and S2 from supplementary data). The teeth sampled for cementum analysis belong exclusively to *Cervus elaphus*: seven teeth from sub-unit IIIb of Teixoneres Cave (n = 7) as well as three from

Arbrede Cave (n = 3) (Table 3; see Table S3 from supplementary data). It should be noted that one tooth from sub-unit IIIa was sampled but excluded as it presented taphonomic alterations hiding/obliterating cementum increments. All the mesowear and microwear analyses performed were ran by a single observer (CSH) to avoid possible inter-observer errors. The complexity of cementum analysis required a combined observation between two observers (i.e. CSH and LG).

The success rate of the analysis varies between techniques and the general state of conservation of the different type of teeth (position and laterality) (Table 1; see Table S4 from supplementary data). We developed an ANOVA (Kruskal-Wallis) and Tukey's test to check whether there are or not statistical differences between the dietary traits of the studied teeth (premolars and molars) (see Table S5 from supplementary data). All the samples studied were recovered at levels with a clear anthropic context, associated with invariable evidences of faunal processing, lithic industry, and hearths (Rosell et al., 2010b, 2017; Soler i Subils et al., 2014). The material from Arbrede Cave is curated at the local museum of Banyoles (Girona, Spain) and at the Universitat de Girona (Girona, Spain). The material belonging to Teixoneres Cave is curated at the Institut Català de Paleocologia Humana i Evolució Social (IPHES) (Tarragona, Spain).

Tooth mesowear. The technique developed by Fortelius and Solounias (2000) macroscopically describes the physical modifications over individual dentition owing to the relative amount of attritive-abrasive dental wear caused by the diet. There are two variables to consider, namely, sharpness (sharp, rounded, or blunt) and relief (high or low) of tooth cuspids, which are directly affected by the intrinsic (plant phytoliths) and extrinsic (dust, sand, and grit) abrasive items present in the resources consumed. Precisely, browsers (i.e. feeding on concentrate resources: leaves, shrubs, forbs, and woody plants) are characterised by diets with relatively low levels of abrasion and high attrition producing sharp apices and high relief, whereas grazers (i.e. eating grass and pasture) feed on items of high abrasion and low attrition producing blunt apices and lower relief than browsers. The mixed feeders occupy the gap between the last two dietary groups and are characterised by rounded cusp sharpness and intermediate relief. We follow the Mesowear Score (MWS) developed by Muhlbacher et al. (2011) on equids, which improve the previous scoring method applied for several taxa and based on a four points scale (i.e. from 0 to 3). It was tested on cervids by Rivals and Takatsuki (2015). The new score consists on seven points referring to different cusps shape and relief, where the highest attrition value is represented by stage 0 and the highest abrasion value by stage 6. The selection protocol for the mesowear study includes adult teeth presenting good integrity of both the crown and the cusps (especially in the buccal facet), and teeth with low or high wear rates from young and senile individuals were discarded (Fortelius and Solounias, 2000; Rivals et al., 2007a).

Tooth microwear. The technique standardised by Solounias and Semprebon (2002) describes the microscopic signals produced by intrinsic and extrinsic particles within the feeding bolus. This microscopic signal over the occlusal surface has a very fast turnover known as the 'Last Super Effect' (Grine, 1986), a process by which the old micro-features are over-written by new ones during each new food intake on the occlusal enamel. Precisely, this allows one to know the diet briefly prior to the moment of death, i.e. daily/weekly feeding behaviour (Solounias and Semprebon, 2002) and seasonal/local environmental conditions in the vicinity (Merceron et al., 2004; Semprebon et al., 2004; Rivals and Semprebon, 2012). The relative proportion of microscopic signals, i.e. scratches (NS) and pits (NP), allows distinguishing the main dietary groups (Fig. 2): browsers display a higher proportion of pits than scratches, whereas grazers typically show a higher number of scratches than pits (Semprebon et al., 2004; Solounias and Semprebon, 2002). Mixed-feeders overlap the two previous groups because they show an intermediate number of scratches and pits. Mixed-feeders can also show some preferences/tendencies for one type of resource (i.e. attritive or abrasive) on a daily or seasonally based

Table 1
Summary of sample size by taxa site and techniques.

Species	Site	Sample Size	Techniques		
			Mesowear	Microwear	Cementochronology
			N	N	N
<i>Cervus elaphus</i>	TX	94	48	57	7
	ARB	38	7	22	3
Total		132	55	79	7
<i>Equus ferus</i>	TX	73	26	41	–
	ARB	47	10	30	–
Total		120	36	71	0
<i>Equus hydruntinus</i>	TX	43	25	30	–
	ARB	–	–	–	–
Total		43	25	30	10

Abbreviations: TX = Teixoneres Cave; ARB = Arbreda Cave; N = number of specimens with interpretable data per technique.

Table 2
Summary of meso- and microwear data of Arbreda and Teixoneres caves.

Locality	Level	Species	Mesowear		Microwear						
			N	MWS	N	LSR	NS	NP	%LP	%G	SWS
Arbreda Cave	I	<i>Cervus elaphus</i>	3	1.7	3	33.33	19	21.83	100	0	0
		<i>Equus ferus</i>	4	4.3	6	0	21.33	20.92	50	0	0.5
	J	<i>Cervus elaphus</i>			14	42.86	17.68	19.82	57.14	0	0.26
		<i>Equus ferus</i>	2	6	10	10	19.75	21.3	55.56	0	0.56
	K	<i>Cervus elaphus</i>	1	1	1	100	13	20	100	0	1
		<i>Equus ferus</i>	1	4	1	0	20	24.5	100	0	1
	L	<i>Cervus elaphus</i>	1	3	2	50	18.5	19.5	100	0	0.5
		<i>Equus ferus</i>	4	4.8	4	0	19.88	23.63	75	0	0
	M	<i>Cervus elaphus</i>	2	4.5	2	0	20.5	22.25	50	0	0.5
		<i>Equus ferus</i>	4	5	6	0	19.25	20.83	66.67	0	0
	N	<i>Cervus elaphus</i>									
		<i>Equus ferus</i>	2	5	3	0	19.5	19.17	66.67	0	0.33
Teixoneres Cave	IIIa	<i>Cervus elaphus</i>	14	1.8	15	44.67	18.73	19.5	78.95	0	0.26
		<i>Equus ferus</i>	17	4.8	29	6.9	20.31	19.4	38.89	0	0.55
		<i>Equus hydruntinus</i>	18	4.3	19	10.5	19.79	17.59	65	0	0.63
		<i>Cervus elaphus</i>	34	1.4	42	38.1	18.16	19.32	68.52	0	0.45
	IIIb	<i>Equus ferus</i>	10	5.3	12	0	22.38	18.58	72.22	0	0.75
		<i>Equus hydruntinus</i>	8	4	11	27.3	20.55	16.32	41.67	0	0.64

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; and SWS = scratch texture analysis.

Table 3
Summary of cementum data for *Cervus elaphus* from levels L and M of Arbreda Cave and sub-unit IIIb of Teixoneres Cave.

Site	Unit	Ref.	Tooth	N° CB	LCB	% Dev.	Season of Death
Arbreda	L	ARB 86	M2 R	5	TB	62.24	Middle Good Season
		ARB 102	m3 L	3 (at least)	TB	46.75	Middle Good Season
		ARB 101	M3 R	4	OB	100	Bad Season
Teixoneres	Sub-unit IIIb	TX 2	M1 L	6	TB	43.53	Middle Good Season
		TX 13	M2 R	3	TB	21.68	Beginning Good Season
		TX 19	m3 L	6 (at least)	OB	100	Bad Season
		TX 20	M1 L	7	TB	20.47	Beginning Good Season
		TX 51	m2 L	5	TB	18.99	Beginning Good Season
		TX 344	m3 R	5	OB	100	Bad Season
		TX 391	m2 R	2 (at least)	TB	48.48	Middle Good Season

Abbreviations: Ref = reference number attributed by the authors; N° 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 at the individual's death; OP = dark and hyper-mineralised cementum band; TB = clear and hypo-mineralised cementum band; M = upper molar; and m = lower molar.

pattern, including a slightly higher proportion of attritive or abrasive items. They are referred to as browse- or grass-dominated mixed-feeders, respectively (Solounias and Semprebon, 2002). The average NS and NP obtained from the archaeological record are represented in a bivariate plot. Similarly, calculating the low range of scratches (LSR) of individuals per taxon (i.e. individuals with NS between 0 and 17) allows recognising the dietary particularities of a given population

(Solounias and Semprebon, 2002; Semprebon and Rivals, 2007). Browsers show a LSR between 72.73% and 100%, whereas grazers show a LSR between 22.2% and 0%. Mixed-feeders show an intermediate LSR between 20.93% and 70%. Other qualitative variables are recorded, such as the scratch width score (SWS) (0 = fine; 1 = mixture of fine and coarse; 2 = coarse; 3 = hyper-coarse, 4 = mixture of coarse and hyper-coarse), the presence of large pits (LP), and gouges (G)



Fig. 2. Microscopic images ($\times 35$) of molar enamel surfaces with observable microwear features (i.e. scratches and pits). From left to right: (A) *Cervus elaphus* from Arbrede Cave; (B) *Equus ferus* and (C) *Equus hydruntinus* from Teixoneres Cave.

(Solounias and Semprebon, 2002; Semprebon et al., 2011). The sampling protocol includes adult teeth presenting occlusal wear facets without strong damage (Solounias and Semprebon, 2002). Initially, the occlusal surfaces are washed using acetone and 96% ethanol. Then, for each tooth, a mould of the occlusal surface is created using a high-resolution silicone (vinylpolysiloxane Heraeus Provil Novo Light Regular Set). Finally, positive casts are made with transparent and high-resolution epoxy resin (C.T.S.[®] EPO 150) and catalyst (K 151). Teeth presenting post-depositional damages are excluded (King et al., 1999; Martínez and Pérez-Pérez, 2004). For quantifying the microscopic features, we use a Zeiss-Stemi 2000C stereomicroscope of transmitted light at $\times 35$ magnification with an ocular reticule delimiting a 0.16 mm^2 square area. The counting process took place in two independent enamel areas, which were also separately analysed in duplicate to obtain the average of microwear features per tooth (Solounias and Semprebon, 2002; Semprebon et al., 2004). This system allows minimizing intra-observer errors (Semprebon et al., 2004). The analysis in those teeth with an integral structure conservation were focused on the protocone (upper molars) and the protoconid (lower molars) (Solounias and Semprebon, 2002; Semprebon et al., 2004). Otherwise, we also analysed small good preserved enamel zones in tooth partially broken or taphonomically affected to increase the sample size.

Dental cementum. The technique is based on the study of the growth marks registered seasonally within the dental cementum which covers the root surface (Scheffer, 1950; Laws, 1952; Sergeant and Pimlott, 1959; Klevezal and Kleinenberg, 1969; Grue and Jensen, 1979; Stott et al., 1982). The analysis is primarily focused on the acellular cementum (specifically, the Acellular Extrinsic Fibre Cementum (AEFC)) owing to its regular and predictable growing pattern throughout the annual cycle (Schroeder, 1986; Sequeira et al., 1992; Naji et al., 2015). The acellular cementum growth is characterised by two types of increment layers which differ by the collagen deposition rate and the mineralisation degree (Klevezal and Kleinenberg, 1969; Jones, 1987; Burke, 1993; Gordon, 1993; Gourichon, 2004). Viewed in transmitted light, these increments appear respectively as translucent (TB) and opaque bands (OB) (Fig. 3) (Scheffer, 1950; Lieberman, 1991, 1993, 1994; Lieberman and Meadow, 1992; Burke and Castanet, 1995; Pike-Tay, 1995; Gourichon, 2004). The hypo-mineralised TB, also called ‘growth zones’, result from a fast growth pattern and are generally thicker than the OB. The hyper-mineralised OB, also called ‘annuli’ or ‘rest line’, result from a slow growth pattern and may sometimes appear as thin lines of arrested growth (Fig. 3) (LAG; e.g. Burke and Castanet, 1995). A wide range of mammals from temperate regions is characterised by presenting seasonality within the increment growing patterns (e.g. Cervidae, Bovidae, Caprinae). The causes of seasonal increment depositions cannot be strictly defined although multiple factors (exogenous and endogenous) could be involved in the process; however, latitude seems to play an important role (i.e. arctic, temperate, or tropical regions). It is also suggested that not all mammals cohabiting the same region (e.g. some carnivores from Denmark) necessary follow the same increment deposition schedule (Grue and Jensen, 1979). In other words, for the ungulates studied here, the TB are generally

deposited during seasons of greater amount of daily light, also called ‘good seasons’ (i.e. spring to fall) (Pike-Tay, 1991a, 1991b, 1995), whereas the OB are seen during the ‘bad season’ (i.e. winter) (Pike-Tay, 1991b, 1995; Lieberman, 1994). One pair of bands (TB + OB) is therefore expected to correspond to a whole annual cycle. The age at death of an individual can be estimated by adding the total number of pairs of bands observed to the time of tooth eruption, whereas the season at death is deduced from the nature and growth rate of the last cementum increment. When it corresponds to a TB, a more accurate estimation can be reached by assessing its development ratio in comparison with the mean thickness of the preceding and fully formed TB: beginning of the ‘good season’ (up to one-third of the mean thickness; 1%–33.3%), middle (from one-to two-thirds; 33.4%–66.6%), or late (more than two-thirds; 66.7%–100%) (Gourichon, 2004). Because of its small thickness, the OB can hardly be measured and provides only a general estimation (‘bad season’). According to the available literature, the period of OB formation in the dental cementum of *Cervus elaphus* appears to be partly related to latitudinal gradients: November–January in southern Iberia and January–April in Scotland (Mitchell, 1967; Azorit et al., 2002, 2004; Azorit, 2011). Because the formation of rest lines is delayed as the latitude decreases, we propose that the bad season in northern Iberia would correspond to December–February, whereas the good season would correspond to March–November (see Supplementary Fig. S1). Furthermore, we performed a comparison between the growth percentage of the last cementum band and the NS/NP ratio obtained for each individual to assess whether a specific dietary trend corresponds to a particular season within the annual cycle.

The tooth samples were prepared following the standard techniques used for ground thin-sections (Lieberman et al., 1990; Pike-Tay, 1991a; Stutz, 2002; Gourichon, 2004; Rendu, 2007; Naji et al., 2015). As recommended by one of us (LG), only one root was extracted to keep the maximum tooth integrity. Upper and lower molar with apparent good preservation state (no or only few fractures on the cementum surfaces) were chosen for the analysis. Primarily, the root was embedded within a transparent epoxy resin and, after drying, was separated from the crown. Next, 2–4 sections with thickness of 0.5–1 mm were cut from the root using a slow-speed rotating saw (Buehler Isomet 1000 or 5000), glued separately on a glass support, and then abraded to the required thickness using a semi-automatic grinding device (Buehler PetroThin) (Gourichon, 2004; Rendu, 2007; Naji et al., 2015). The analysis was performed using a polarising light microscope Leica 2500P with $\times 100$, $\times 200$, $\times 400$, and $\times 500$ magnifications and connected to a computer via a high-resolution digital camera (full-screen video) using three distinct light filters: plane-polarised light, cross-polarised light, and full-wave retardation plate (λ plate) (Stutz, 2002).

5. Results

5.1. Mesowear analysis

The tooth mesowear values (MWS) observed for *Cervus elaphus* from both sites present a remarkable heterogeneity ranging from 1 to 4.5

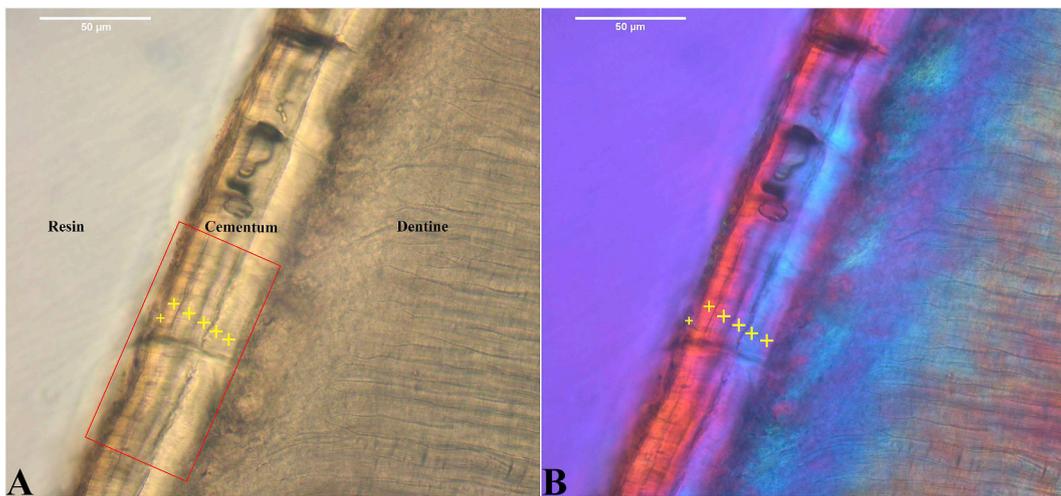


Fig. 3. Microscopic view with natural (A) and polarized light plus λ lame (B) of translucent and opaque cementum bands (TB & OB). Crosses point out the observed translucent bands (TB); Red square represents a small zone of cementum, which extends on a northeast/southwest axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

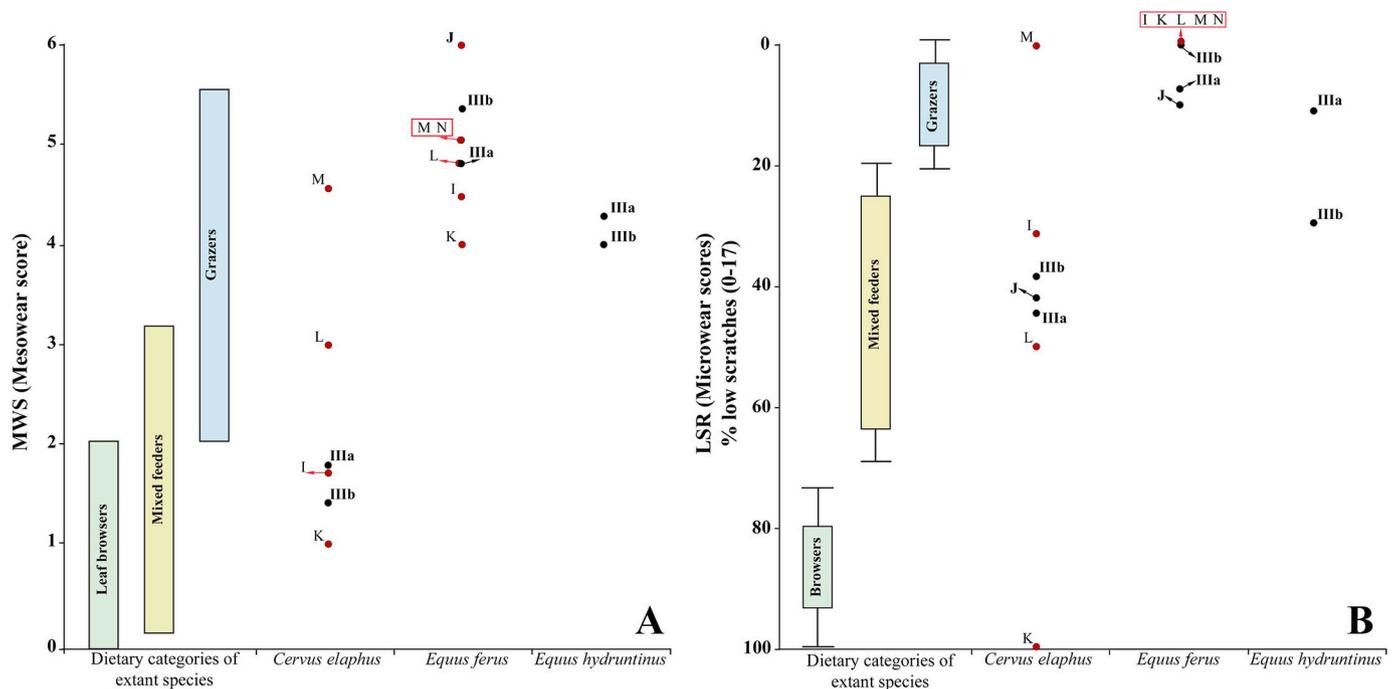


Fig. 4. Mesowear (A) and microwear (B) results of the three selected ungulates from Arbreda (level J) and Teixoneres caves (sub-units IIIa and IIIb) and dietary bars of extant ungulates (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002).

(Table 2), that is, from browsers (concentrated resource feeders) to grazers (grass and other herbaceous plant feeders). Red deer from sub-units IIIa (n = 14) and IIIb (n = 34) of Teixoneres Cave have values corresponding to animals with a typical annual diet pattern of mixed feeders (Table 2, Fig. 4A). Although the *Cervus elaphus* sample from Arbreda Cave is too small to obtain reliable results (Table 2), we got approximate information from all levels where the red deer is present except for levels J and N. Data from level I (n = 3) suggest mixed feeders, whereas that from level K (n = 1) suggested a browser diet. Levels L (n = 1) and M (n = 2) show the highest values (MWS = 3 and 4.5, respectively) (Table 2, Fig. 4A). These results suggest grass-dominated mixed-feeding for level L, whereas higher levels of abrasion characterised the pure grazer, namely, red deer, for level M (Fig. 4A).

Equus ferus teeth display similar MWS values ranging from 4 to 6 from an intra- and inter-site perspective at both Mediterranean sites

(Table 2). Horse are well-represented at Teixoneres Cave, where sub-units IIIa (n = 17) and IIIb (n = 10) are representative of annual dietary traits typical of pure grazers (Table 2, Fig. 4A). Regarding the horse from Arbreda Cave, the small sample size limits the interpretation of the results (Table 2). However, the MWS values from all levels suggest dietary patterns based on very abrasive items such as grass (Table 2, Fig. 4A). It is therefore possible to observe small intra- and inter-site variations but always within the same dietary group, namely, the grazers.

At Teixoneres Cave, the dietary pattern of *Equus hydruntinus* is comparable to that shown by the horse. Wild asses from sub-unit IIIa (n = 18) and sub-unit IIIb (n = 8) are characterised by an annual dietary pattern typical of grazers (Table 2, Fig. 4A).

5.2. Microwear analysis

The ANOVA (Kruskal-Wallis) and Tukey's test indicate non-

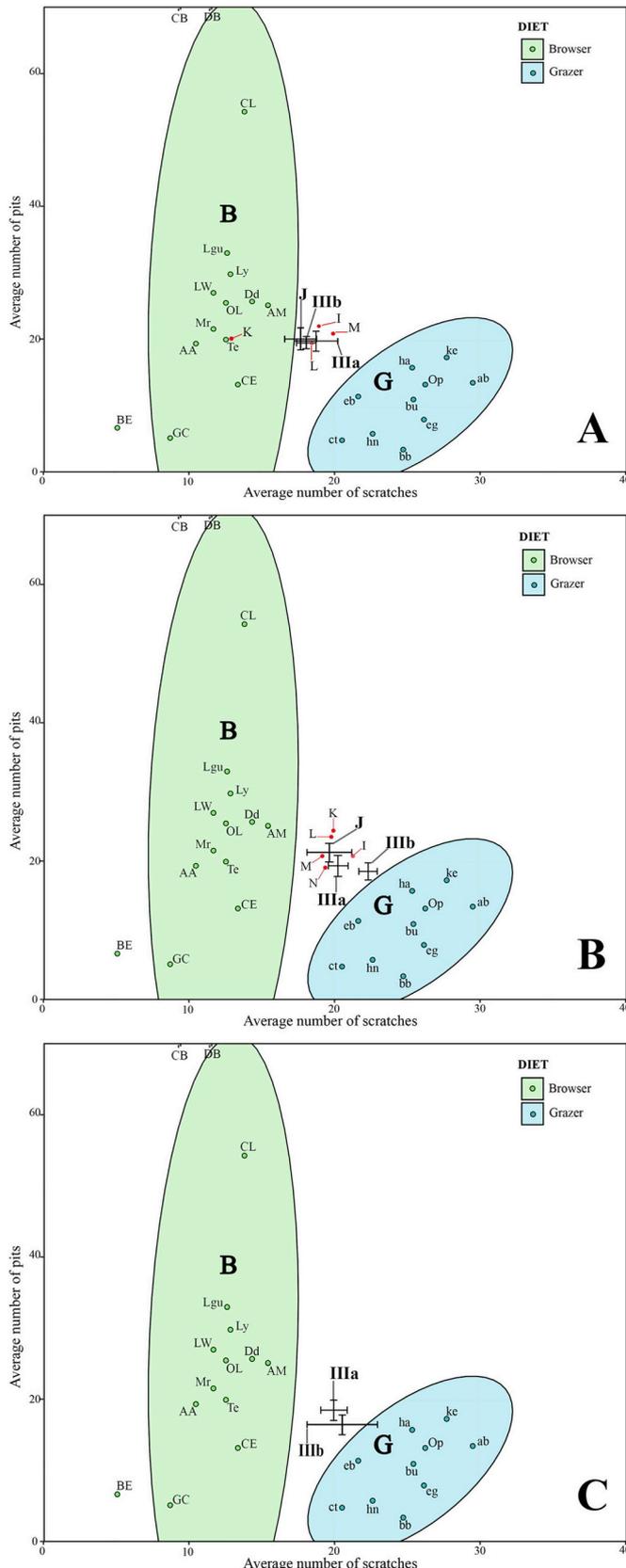


Fig. 5. Bivariate plot of the average number of pits and scratches from the three selected ungulate taxa from Arbreda and Teixoneres caves: *Cervus elaphus* (A), *Equus ferus* (B), and *Equus hydruntinus* (C). Errors bar correspond to standard deviation (± 1 S.D.) for the fossil samples. Plain ellipses correspond to Gaussian ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Sempredon (2002) and Rivals et al. (2010). Abbreviations: ab (*Alcelaphus buselaphus*), AA (*Alces alces*), AM (*Antilocapra americana*), BE (*Boocercus eurycerus*), bu (*Bubalus mindorensis*), CB (*Camelus bactrianus*), CL (*Camelus dromedarius*), CE (*Cervus elaphus*), ct (*Connochaetes taurinus*), Dd (*Dama dama*), DB (*Diceros bicornis*), eg (*Equus grevi*), GC (*Giraffa camelopardalis*), ha (*Hippopotamus amphibius*), hn (*Hippotragus niger*), kc (*Kobus ellipsiprymnus*), Lgu (*Lama guanicoe*), LW (*Litocranius walleri*), Ly (*Loxodonta cyclotis*), and Mr (*Muntiacus reevesi*).

significant differences between the 6 M dental positions (upper and lower M1 to M3) both in *Cervus elaphus* ($F = 0.782$; $p = 0.568$) and *Equus ferus* ($F = 2.631$; $p = 0.083$). The comparison of the different dental position in the red deer from Teixoneres sub-units IIIa and IIIb did not show any significant difference ($F = 1.189$; $p = 0.334$). Similarly, the statistical analysis between the samples from sites do not show significant differences: *Cervus elaphus* ($F = 0.104$; $p = 0.748$) and *Equus ferus* ($F = 0.191$; $p = 0.670$) (see Table S5 from supplementary dataset). Premolars were excluded from the analysis due to the extremely low sample size. We can conclude that there are no significant differences in microwear patterns among the different dental positions in red deer and horse, and that all molars can be lumped together to increase sample size.

Cervus elaphus do not show strong variations in dental microwear at the two sites, as evidenced by the average NS and NP (Fig. 5A) as well as by LSR (Fig. 4B) (Table 2). Red deer from sub-units IIIa ($n = 15$) and IIIb ($n = 42$) of Teixoneres Cave and level J ($n = 14$) of Arbreda Cave were mixed-feeders (Table 2, Figs. 4A and 5A). Nevertheless, the sample from level I of Arbreda Cave ($n = 3$) suggests grass-dominated mixed-feeders and that from level L ($n = 2$) suggests a mixed-feeder diet (Table 2, Figs. 4B and 5A); however, they do not allow obtaining statistically reliable results because the number of teeth is very low. Instead, the approximate results from level K ($n = 1$) appear to be shifted toward the browser zone of the confidence ellipse and differ from the general dietary features evidenced for the other levels (Fig. 5A). Level M ($n = 2$) show NS and NP values that suggest mixed-feeder traits (Fig. 5A).

Looking at the results individually, the red deer population from level J of Arbreda Cave is characterised by a scratch width score (SWS) predominated by fine scratches that reflect the consumption of more attritive resources than abrasive ones. In addition, the intermediate value of large pits (LP) suggests the occasional consumption of hard items like twigs, whereas the absence of gouges and puncture pits suggests no regular consumption of fruits (Table 2). Red deer from Teixoneres Cave present a similar pattern at both sub-units, where the slightly higher SWS at sub-unit IIIb agrees with the results observed at level J of Arbreda Cave (Table 2), suggesting the ingestion of hard items. In addition, they present an increase in LP values with respect to level J (Table 2), suggesting greater ingestion of hard elements such as twigs. Similarly, the absence of gouges suggests no fruit/seed consumption (Table 2).

Equus ferus shows similar grazer dietary traits at an intra- and inter-site level (Table 2). The horse tooth samples from sub-units IIIa ($n = 29$) and IIIb ($n = 12$) of Teixoneres Cave and from level J ($n = 10$) of Arbreda Cave (with slightly higher NP) lie outside the grazer confidence ellipse despite their NS values being representative of grazers (Fig. 5B). Otherwise, the LSR values indicate grazer dietary patterns (Table 2, Fig. 4B) and agree with the NS values (Fig. 5B). Therefore, although the high NP values are placed three levels above the grazer confidence ellipse, the NS range still corresponds to typical grazers, highlighting a very abrasive diet for horse (Table 2, Fig. 5B). Regarding the levels of Arbreda Cave with small sample size (i.e. I, K, L,

M, and N) (Table 2), all showed NS and NP values as well as LSR values close to the three levels described previously, which are typical of a grazer dietary pattern (Table 2, Figs. 4B and 5B).

The SWS values observed at both sites correspond to a mixture of fine and coarse scratches, which indicate the ingestion of resources with abrasive properties (Table 2). The high XS and low LP values observed for sub-unit IIIa and level J correlate with typical grazers, whereas data from sub-unit IIIb show an XS intermediate value and an elevated LP proportion, which are atypical for grazers (Table 2). The absence of gouges (G) and puncture pits indicates that seeds and fruits were not regularly consumed (Table 2).

Regarding the *Equus hydruntinus* sample from Teixoneres Cave, both sub-units (IIIa and IIIb) show a high NP and lie outside the modern grazer confidence ellipse; however, the NS corresponds to grazer dietary patterns (Table 2, Fig. 5C). The LSR data from sub-unit IIIa agree with the NS values because they indicate a grazer diet, whereas those from sub-unit IIIb indicate a grass-dominated mixed-feeder diet (Table 2, Fig. 4B). The SWS values observed at both sub-units (IIIa and IIIb) show a mixture of fine and coarse scratches typical of animals consuming abrasive resources (Table 2). However, sub-unit IIIa shows a higher proportion of XS and lower values of LP, representing grazer features, whereas at sub-unit IIIb, the XS and LP values show increased attritive resource consumption as mixed-feeders (Table 2).

5.3. Cementum analysis

The cementum analysis was performed on *Cervus elaphus* from both Teixoneres and Arbrede caves. The study of the samples from Teixoneres Cave produced data for sub-unit IIIb (n = 7) but not for sub-unit IIIa (n = 1) (Table 3) owing to the bad preservation of cementum tissue. The seven teeth from IIIb provide a large variety of estimates regarding the season of death (Table 3). For five of them, the last increment identified is a translucent band (TB) either at the first growth stage (n = 3) or at an intermediate stage (n = 2) (Fig. 6). The two remaining teeth show a final opaque band whose degree of growth cannot be measured (Table 3, Fig. 6).

Concerning Arbrede Cave, data from only three *Cervus elaphus* teeth

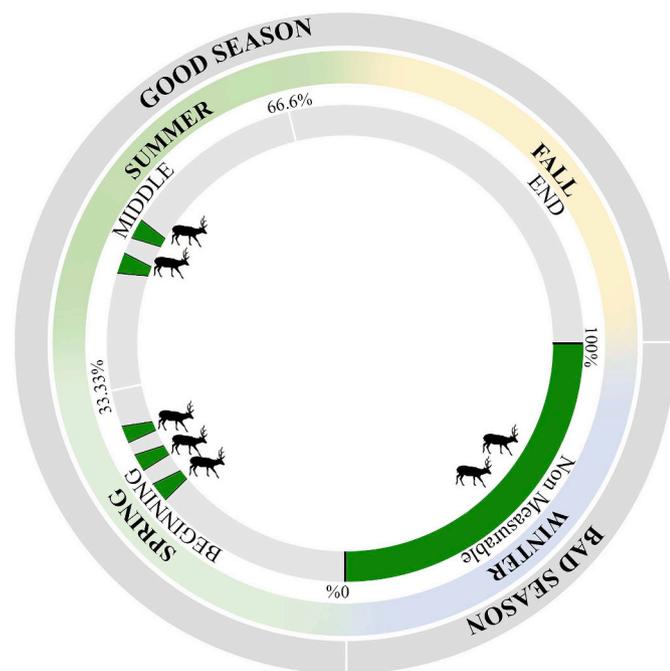


Fig. 6. Schematic representation of *Cervus elaphus* death events in sub-unit IIIb of Teixoneres Cave. Percentages correspond to the degree of development of the last TB.

are available owing to the extreme fragmentation and bad preservation of the dental assemblage. In the two samples from level L, the cementum sequence ends with a TB in its intermediate growth stage, whereas the single tooth from level M shows a final OB (Table 3 and Table S3 from supplementary data). However, the samples from these levels (i.e. L and M) is not large enough to provide interpretable data, neither to be integrated into the discussion.

Finally, we compared the microwear dietary results with the estimated season of death for each individual (Table 4, Fig. 7). Considering the complex histological processes involved in the formation and deposition of dental cementum in the equid teeth as well as the poor state of preservation of red deer teeth at Arbrede level J and Teixoneres sub-unit IIIa, we only have interpretable data for sub-unit IIIb. Although red deer from sub-unit IIIb comprise a wide range of death times throughout the annual cycle (Table 3; Fig. 6), we cannot identify any distinct feeding pattern related to the natural seasons (i.e. spring, summer, autumn, winter). However, by dividing the annual cycle between good season (i.e. spring to fall) and bad season (winter), the data reveal a slight increase in the intake of attritive items during the bad season (Table 4; Fig. 7).

6. Discussion

6.1. Ungulates' dietary traits

The vegetation composition and distribution in the Iberian Peninsula have been affected by the climatic fluctuations of the MIS 3 (Roucoux et al., 2005; Sánchez-Goñi and D'Errico, 2005; Uzquiano-Ollero, 2008; Sánchez-Goñi et al., 2010; Uzquiano-Ollero et al., 2016; Allué et al., 2017). In addition, the latitudinal location of the Peninsula along with the complex orography favours a broad diversity of faunal and vegetal resources. Consequently, substantial changes can be expected in the quality and type of vegetal cover along with the environmental conditions within a small area and over short distances. While located in a relatively stable climatic Mediterranean zone characterized by patchy landscapes as attested in several stratigraphic sequences of the MIS 5 to 3, e.g. Abric Romani, Cova Gran, Coll Verdader, Riera de les Terrasses dels Canyars, or Cova del Rinoceront (Allué et al., 2018, 2017; Daura et al., 2017, 2015; Fernández-García, 2019; Fernández-García et al., 2016; López-García et al., 2015), the latitude and altitude characteristics of Arbrede and Teixoneres caves could have influenced the feeding strategies of the fauna living around. However, the dietary behaviour observed for the two most common ungulates, *Cervus elaphus* and *Equus ferus*, do not show adaptive changes irrespective of the site and stratigraphic level (Ramírez-Pedraza et al., 2019). The same was not true of *Equus hydruntinus*, which showed seasonal variations in its dietary behaviour.

The feeding plasticity observed in the extant red deer refers to an alternation of browsing (i.e. concentrate resources) and grazing (i.e. grasses and other herbaceous plants) as mixed-feeders (i.e. attritive-abrasive items) (Staines and Crisp, 1978; Hofmann, 1989; Gebert and Verheyden-Tixier, 2001; Solounias and Semprebon, 2002; Berlioz et al., 2017). Specifically, this selective alternation between different types of resources is indicative of seasonal patterns shifting along the annual cycle as a consequence of their availability and nutritional quality (Mátrai and Kabai, 1989; Bugalho et al., 2001; Carranza, 2011; Azorit et al., 2012; Ismaili et al., 2018). Indeed, annual (mesowear) and daily/weekly (microwear) dietary trends observed for the red deer from Teixoneres Cave correspond to the pattern observed for some extant populations as typical mixed-feeders. However, we are not able to identify adaptive behaviours related to seasonal preferences, probably owing to a continuous input throughout the year by Neanderthals within the cave (Sánchez-Hernández et al., 2014, 2016). A slight predominance of concentrate items over grasses could be argued for because of the predominance of fine scratches (low SWS) at both sub-units (IIIa and IIIb), suggesting browse-dominated mixed-feeders. However,

Table 4
Summary of cementum and NS/NP data for the *Cervus elaphus* from sub-unit IIIb of Teixoneres Cave.

Ref.	Square	Tooth	Cementum			Microwear			
			N° CB	LCB	% Dev.	NS	NP	NS/NP	NP/NS
TX 2	J23	M1 L	6	TB	43.53	18.50	20.00	1.08	0.93
TX 13	L11	m2 R	3	TB	21.68	17.00	19.50	1.15	0.87
TX 19	M15	m3 L	6 (at least)	OB	100	15.50	20.00	1.29	0.78
TX 20	L12	M2 L	7	TB	20.47	17.00	19.00	1.12	0.89
TX 51	K11	m2 L	5	TB	18.99	21.00	19.50	0.93	1.08
TX 344	L11	m3 R	5	OB	100	17.50	19.50	1.11	0.90
TX 391	L11	m2 R	2 (at least)	TB	48.48	21.00	25.00	1.19	0.84

Abbreviations: Ref = reference number attributed by the authors; N° CB = number of pairs of bands observed in the acellular cementum; LCB = last cementum band observed; % Dev = % growth ratio of the last cementum increment; OB = dark and high mineralised (opaque) cementum band; TB = clear and low mineralised (translucent) cementum band; NS = number of scratches; NP = number of pits; NS/NP = ratio of number of scratches and pits; NP/NS = ratio of number of pits and scratches; M = upper molar; and m = lower molar.

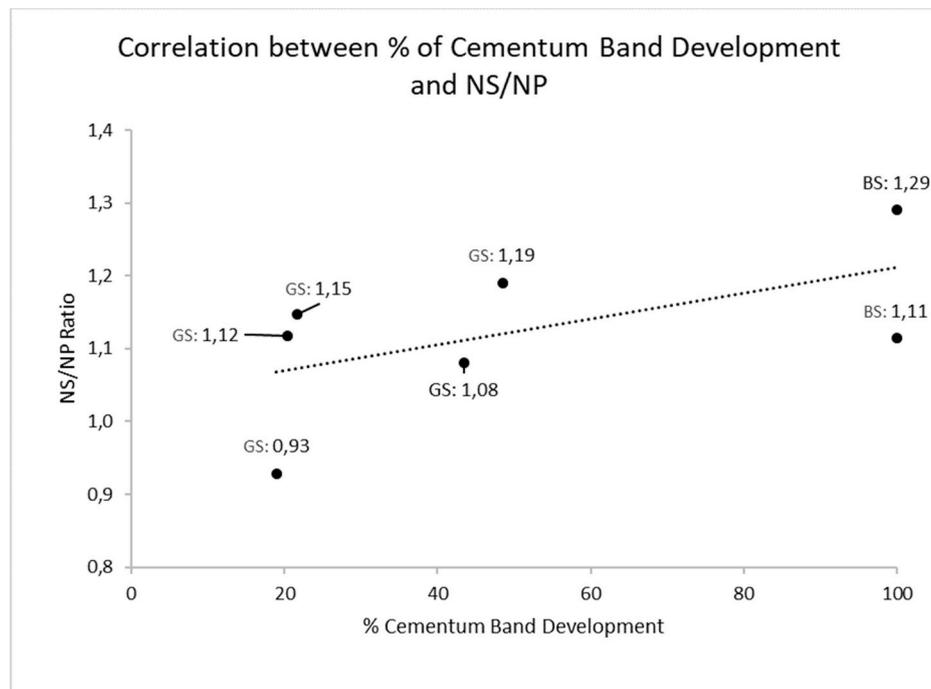


Fig. 7. Dispersion graph between the percentage of cementum band development and the ratio of number of scratches (NS) and number of pits (NP) of *Cervus elaphus* at death from sub-unit IIIb of Teixoneres Cave. Abbreviators: GS = Good Season; BS = Bad Season.

the absence of other features related to strict hard element consumption (e.g. lignified forage plants, bark, seeds, or fruits) like coarse or mixed scratches type and gouges suggest that the high percentage of large pits could not be exclusively attributed to browsing episodes during the mixed diet. Indeed, in mixed-feeders, grass consumption close to the ground may also increase the number of large pits owing to the abundance of extrinsic particles in the bolus (i.e. dust, grit) (Solounias and Sempredon, 2002; Sempredon and Rivals, 2007).

The level J of Arbreda Cave lacks annual dietary data (mesowear); however, this interpretation could be approached by combining the microwear results of this level and the extant reference database. Both suggest a typical mixed-feeder diet without concentrate or grass preferences (browser or grazer, respectively). The lower percentage of large pits observed at level J of Arbreda Cave may indicate minor consumption of both hard items and extrinsic particles in comparison to that at Teixoneres Cave.

Cervus elaphus seems to alternate between concentrate resources and grasses (i.e. attritive and abrasive) as long as they are available in the surroundings of both sites and their quality is enough to cover their nutritional demands for survival. This perspective could be reinforced

by the combined results of Arbreda Cave levels M and L, where annual and daily/weekly diets show different results (i.e. grazer and mixed-feeder, respectively). It seems to be a common feeding behaviour within the region because red deer from the Abric Romaní (Capellades, Barcelona, Spain) shelter also show a wide dietary pattern (i.e. from browser to grass-dominated mixed-feeders) (Fernández-Laso et al., 2011b; Allué et al., 2012; Burjachs et al., 2012).

Similarly, *Equus ferus* shows a stable average annual and daily/weekly dietary pattern at both sites that is focused exclusively on grass consumption (abrasive items). These dietary traits are indicative of strict grazer behaviour and are supported by the high proportion of coarse scratches on the enamel surface. Nevertheless, an unexpectedly high number of pits is seen for typical grazers, which could initially suggest concentrate resource ingestion (attritive wear). This may be conceivable because it has been suggested that modern (Duncan, 1991; Nowak, 1999; Baskin and Banell, 2003; Ungar, 2010) and ancient horse populations (Rivals et al., 2009, 2015; Ecker et al., 2013) occasionally browsed. However, MWS and LSR values unequivocally indicate a grazing diet at both sites, with no suggestion of concentrate item consumption and opening new alternatives to explain the high number of

pits. The grazing behaviour combined with the high number of pits have already been seen in the archaeological record of Payre level D (Rhône Valley, France), Wallertheim level F (Mainz, Germany), and Covalejos levels 8 and 7 (Cantabria, Spain) (Rivals et al., 2009; Sánchez-Hernández et al., 2019). Specifically, Wallertheim (level F) and Covalejos (levels 8 and 7) caves are related to the appearance of colder and dryer pulsations that increase dust particles in the ingested resources. We suggest that this explanation is also relevant for Arbrede and Teixoneres caves, where both concentrate resources and grasses would contain elevated amounts of extrinsic particles.

According to the dental wear results, the dietary traits of *Equus hydruntinus* show an annual grazing pattern at both Teixoneres sub-units, indicating strict grass consumption. However, these annual dietary traits, always as a grazer, present lower values than those for horse (less abrasiveness). This could be related to the phenotypic variation of plants (Dziedziolowski, 1970; Janis, 1976; Albon and Langvatn, 1992; Walker et al., 1995; Langvatn et al., 1996; Walsh et al., 1997; Post and Stenseth, 1999; Pettorelli et al., 2005), pushing equids to feed on diverse sections of the same plants or even on different herbaceous species. In fact, the annual and daily/weekly diets at sub-unit IIIa reflect strict grass consumption. On the other hand, the sub-unit IIIb daily/weekly diet indicates seasonal intake of concentrate items shifting toward a mixed-feeder diet. The fact that this dietary shift does not have a significant influence on the annual feeding pattern suggests that it could correspond to short event(s) within similar environmental conditions through time.

Therefore, these equids seem to adopt similar dietary strategies at Teixoneres Cave because both annually feed on grasses despite different abrasiveness values. It could be considered that they do not simultaneously inhabit the area, which would allow them to feed on the same resources without interspecific competition. Although the wild ass is proposed to be a seasonal migrator within limited and small areas as a taxa with a strong territorial habit (Burke et al., 2003; Burke, 2006), some authors questioned these seasonal movements as well as the long-distance migratory character of Palaeolithic horse (Britton et al., 2012). On the assumption that both equid species cohabited in the same area throughout the year, we consider other ways to explain the absence of interspecific competition and different adaptive strategies at sub-unit IIIa. Actually, there are similarities with the Serengeti ungulates that have shown a dietary succession within ungulate species in the same space (Vesey-Fitzgerald, 1960; Gwynne and Bell, 1968). Specifically, ungulates feeding on grasses could get partitioned access to food both qualitatively (i.e. fed on different parts of the same plants) as well as seasonally. Furthermore, Fortelius and Solounias (2000) later confirmed these feeding behaviours in the same region through dental mesowear. In this perspective, for sub-unit IIIa, the lower annual abrasive values observed for the wild ass, along with the territorial behaviour of this taxa, suggest differential access to the same grasses compared to contemporary horse. On the contrary, at sub-unit IIIb, we identified different adaptive behaviours of the wild ass, which complemented grass intake with concentrate resources. Here, wetter environmental conditions appear to have seasonally influenced the quality or/and availability of grasses on which both equids fed (López-García et al., 2012). This periodically pushed wild asses to adapt their feeding strategies and to perform a seasonal partitioning of the resources to survive.

Indeed, neither the latitude nor the almost 600 m difference in altitude between the two sites seem to have strongly modified the surrounding resources because the red deer and horse were not forced to adapt their annual feeding strategies. The natural course of the annual cycle seems to have a low impact on available resources except for sub-unit IIIb, where grasses are temporarily reduced, thus modifying the diet of the wild ass. Therefore, although we could consider that the annual dietary homogeneity of these taxa was due to the low mesowear sensitivity in detecting seasonal variations (i.e. suitable for long-term measurements), the microwear results are conclusive with the annual

dietary pattern. Thereby, no long-term shifts and interspecific competition between cervids and equids related to latitude or altitude can be detected for these contexts; they are seen only at the intraspecific level for equids.

6.2. Seasonality of diet

The feeding behaviour of red deer at sub-unit IIIb shows a slight seasonal pattern with increased consumption of grasses and other herbaceous plants during winter, as evidenced by the correlation of daily/weekly feeding traits and the season of death. This trend contradicts the expected seasonal variation observed for the extant European red deer, which usually tend to increase browsing during winter as a result of nutritional constraints (Staines and Crisp, 1978; Gebert and Verheyden-Tixier, 2001). However, Mediterranean environments reach the richest nutritional period at the end of autumn and during winter. During this period, the extant red deer prioritises grasses and other herbaceous items because the tissue of concentrate resources would lignify, thus hindering the digestive process (Gutman and Seligman, 1979; Seligman, 1996; Bugalho et al., 2001; Weladji et al., 2002; Bugalho and Milne, 2003; Azorit et al., 2012). This could explain the increased NP and NS. In addition, this case is not isolated; the same trend has also been observed in the level M of Abric Romaní, whose individuals were hunted from October to December and showed a predominance of grass consumption within the mixed diet (Fernández-Laso et al., 2011a).

However, this dietary particularity in sub-unit IIIb cannot be considered a drastic adaptive response to seasonal environmental oscillations because it occurs within the same dietary group: mixed-feeder. Instead, it could suggest that the dietary behaviour of Palaeolithic red deer at these sites was closer to that of current Iberian cervids than in the rest of the European continent. This implies that their current dietary behaviour in this area could have begun to generalise during the Middle Palaeolithic. The previous interpretation also reinforces the idea of the Iberian Peninsula as a climatic refuge during the Palaeolithic climatic oscillations and supports the important role of the Mediterranean as a determining factor for the environmental, vegetal, and faunal development of this area in this period. With regard to vegetal issues, the Mediterranean winter would favour an increase in grass quality and a decrease in concentrate resources and their availability. Therefore, the seasonal increase in the consumption of concentrate resources by the wild ass could be indirectly placed during the summer because the expected lower quality or availability of grasses in this season could push them to complement their diet with leaves or shrubs (Rodríguez-Berrocal, 1978; Gutman and Seligman, 1979; Bugalho et al., 1998; Seligman, 1996).

Given these results, questions arise about the type of mixed-feeding behaviour of the red deer, that is, seasonal or meal-by-meal (Solounias and Semprebon, 2002). Although the regression line indicates a slight increase in grasses in winter suggesting seasonal influences, the variation is minimal and remains within the same dietary group. Therefore, in the absence of a larger study, the regular alternation between concentrate items and grass consumption could correspond to a meal-by-meal mixed-feeding pattern.

6.3. Palaeoenvironmental conditions

The dietary reconstruction of ungulates through dental wear and cementum analysis may be used as an indirect proxy to reconstruct the palaeoenvironmental conditions and the landscape features in which they inhabited. The homogenous dietary pattern of *Cervus elaphus* at both sites is characterised by undifferentiated feeding on concentrate items and grasses, suggesting immediate access to both open and wooded habitats. The feeding behaviour of *Equus ferus* indicates the permanent presence of open areas in the surroundings of both sites, whereas that of *Equus hydruntinus* indicates some seasonal fluctuations

within a relatively stable environment for Teixoneres Cave during the year. Therefore, ungulates' dietary patterns as observed at Arbreda and Teixoneres caves suggest similar landscapes mainly comprising patched areas with comparable proportions of open and wooded areas. This landscape reconstruction is in accordance with the temperate environmental requirements of large and small vertebrates and the vegetal assemblages identified at these sites (López-García et al., 2012, 2015; Álvarez-Lao et al., 2017; Luzi et al., 2017; Rosell et al., 2017; Ruff et al., 2018). The dietary features observed for ungulates correlate well with the relative temperate and humid conditions for the three studied assemblages.

Regarding Arbreda Cave, such conditions as described above for level J could have been similar to those proposed for level I through the study of micro-vertebrates (as data are not available yet for level J), where the relative degree of humidity could occasionally decrease (López-García et al., 2015). For Teixoneres Cave, temperate and humid conditions were also recognised for the whole unit III by other micro-vertebrate studies (López-García et al., 2012; Luzi et al., 2017). However, our data allow identifying small variations for sub-units IIIa and IIIb. Specifically, the seasonal increase in the consumption of concentrate items by the wild ass indicates a major pressure over grasses, probably because of the seasonal intensification of humidity around the cave. On the contrary, sub-unit IIIa is characterised by an increase in grass consumption by both the red deer and the wild ass along with the strict grazer diet of the horse, suggesting the presence of open areas around the cave. It could also evidence the worsening of environmental features toward colder and dryer conditions with respect to sub-unit IIIb, as identified previously, which eventually culminate in unit II (López-García et al., 2015; Fernández-García, 2019).

Deriving out from a regional perspective, the unexpectedly high number of pits for horse at both sites could be a consequence of the occurrence of dry pulsations, especially for level J and sub-unit IIIa. This was previously observed at Covalejos Cave (Cantabria, Spain) and was attributed to an aridity increase (Sánchez-Hernández et al., 2019). At the two caves, the marginal and occasional presence of cold-adapted taxa such as *Mammuthus primigenius* (level J and sub-unit IIIa) and *Coelodonta antiquitatis* (sub-unit IIIb) support the hypothesis about the persistence of open areas (i.e. steppes) and the effects of cold and dry pulsations (Álvarez-Lao et al., 2017; Ruff et al., 2018).

Due to the rapid and extreme climatic fluctuations during the MIS 3, strong fluctuations should be expected in the habitats at each site. Indeed, the paleoenvironmental reconstruction based on ungulates' palaeodiets at both sites agree well with the cyclical HE and DO oscillations (Dansgaard et al., 1982; Heinrich, 1988; Johnsen et al., 1992; Rasmussen et al., 2014), as evidenced by the alternation of temperate-humid and cold-dry phases. However, we suggest softer consequences than expected for the northeast Iberian because neither the dietary patterns nor the ecological features corresponding to these levels seem to have been strongly affected; only seasonal variations were seen. Previous anthracological and pollen studies support our hypothesis because they show a transitional vegetal cover where the patched landscape was dominated by *Pinus sylvestris* along with steppe taxa during cold pulsations and tree taxa with temperate requirements (Allué, 2002; Burjachs et al., 2012b; Carrión et al., 2010; Rubiales et al., 2010; Daura et al., 2013; Allué et al., 2017, 2018). Furthermore, available data from other archaeological sites in the same region and dated to similar periods agree with the environmental features exposed herein. Indeed, level J from Abric Romani (50.4 ± 1.6 to 49.3 ± 1.6 ka BP) (Bischoff, 1988; Vallverdu, 2012; Vaquero, 2013) and the Mousterian sequence from Cova Coll de Verdager (Barcelona, Spain) (56–34 ka BP) (Daura et al., 2017) show the predominance of temperate conditions. Besides the significant presence of wooded areas similarly to that observed in sub-unit IIIb of Teixoneres Cave (Allué et al., 2012; Daura et al., 2015). By contrast, level J (Arbreda Cave) and sub-unit IIIa (Teixoneres Cave) are consistent with the spread of open areas and maintenance of forests during the colder-dryer environmental

pulsations. This trend will culminate in the worsened environmental features identified at unit II of Teixoneres Cave and Terrasses de la Riera dels Canyars (López-García et al., 2012; Daura et al., 2013; Allué et al., 2017; Fernández-García, 2019). The contextualisation of our results highlighted that even during pulsations of severe climate deterioration, the region remained an environmental refuge with relatively temperate and humid conditions and without complete disappearance of woodland areas. The features of these landscapes could generate an environmental context conducive to the survival of Neanderthal groups, where the availability of different preys would guarantee their acquisition at any time of the year (Sánchez-Hernández et al., 2019). The new perspective could suggest as hypothesis that the short but repetitive occupations observed for Teixoneres Cave (Sánchez-Hernández et al., 2016, 2014) would not be determined by factors such as hominin ecological pressure over the resources, but that other factors would be involved in decision-making within the dynamics of settlement and movement of these populations.

7. Conclusion

Starting from a methodological perspective, we can conclude that the combination of dental wear and cementum analyses has provided fundamental information for the dietary behaviour of red deer and equids and for environmental reconstructions. The maintenance of the homogenous dietary behaviour of red deer and horse at both sites revealed similar local environmental features over a long-term scale despite the latitude and altitude. By contrast, the wild ass (without a counterpart at Arbreda Cave) suggested a slight influence of the season and altitude on resource quality and availability during the annual cycle at Teixoneres Cave.

This combination also proved itself useful in identifying and placing the dietary trends of red deer within the annual cycle and in linking them to possible seasonal environmental factors. Nevertheless, a larger sample size for cementum analysis is required to assess whether the dietary trend of the red deer in sub-unit IIIb is due to seasonal influences or the circumstantial behaviour of these seven individuals with a meal-by-meal mixed-feeder diet. The more accurate knowledge of ungulate palaeodiets would help in further research with archaeological perspectives to precise the relevance of the ungulates preys and environmental features within the decision taken by Neanderthal groups for survival within the Mediterranean region of the Iberian Peninsula.

Therefore, further investigations should expand the archaeological cementum sample to corroborate these observations and to extend them to other ungulates like equids at these sites. This will provide a broader view of the dietary behaviours of various species. The present study also highlights the need to work on the extant counterpart of Neanderthal prey like equids to create a more solid reference database and to develop studies of increased deposition schedules of north Iberian red deer.

Author contributions

CSH conceived/designed the study in collaboration with FR and LG. JR, RB, FR, JS, and NS 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 inputs 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.

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.

Acknowledgments

This work was supported by research grants from the Ministerio de Ciencia e Innovación HAR2016-76760-C3-1-P to FR and CSH, AEI/FEDER, EU projects CGL2015-65387-C3-1-P, CGL2016-80000-P and CGL2015-68604-P to JR and RB, the Generalitat de Catalunya projects 2017-SGR-836 and CLT009/18/00055 to CSH, FR, JR and RB, and the French National Research Agency: Project CemeNTAA (ANR-14-CE31-0011) from the French Research Agency and the CEPAM laboratory (UMR 7264, CNRS, UCA) to LG and CSH. CSH was supported by a predoctoral grant (FPI) from the Ministerio de Ciencia e Innovación (BES-C-2014-0034). The research of JR and FR is funded by the CERCA Programme/Generalitat de Catalunya. We would like to thank the local Museum of Banyoles and the Universitat de Girona for providing access to the archaeological material from Arbrede Cave.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2020.01.008>.

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