



**HAL**  
open science

## Dosimetric performance of continuous EPID imaging in stereotactic treatment conditions

Ana Rita Barbeiro, Laure Parent, Laure Vieillevigne, Regis Ferrand, Xavier Franceries

► **To cite this version:**

Ana Rita Barbeiro, Laure Parent, Laure Vieillevigne, Regis Ferrand, Xavier Franceries. Dosimetric performance of continuous EPID imaging in stereotactic treatment conditions. *Physica Medica*, 2020, 78, pp.117 - 122. 10.1016/j.ejmp.2020.09.009 . hal-03492499

**HAL Id: hal-03492499**

**<https://hal.science/hal-03492499>**

Submitted on 26 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 Dietary traits of ungulates in northeastern Iberian Peninsula: Did  
2 these Neanderthal preys show adaptive behaviour to local  
3 habitats during the Middle Palaeolithic?  
4

5 Carlos Sánchez-Hernández<sup>1,2,3,\*</sup>, Lionel Gourichon<sup>3</sup>, Joaquim Soler<sup>4</sup>, Narcís Soler<sup>4</sup>, Ruth Blasco<sup>5</sup>,  
6 Jordi Rosell<sup>1,2</sup>, Florent Rivals<sup>1,2,6</sup>.

7  
8 (1) Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Zona Educativa 4, Campus Sescelades URV  
9 (Edifici W3), 43007 Tarragona, Spain.

10 (2) Universitat Rovira i Virgili (URV), Àrea de Prehistòria, Avinguda de Catalunya 35, 43002 Tarragona, Spain.

11 (3) Université Côte d'Azur, CNRS, CEPAM, 06300 Nice, France.  
12

13 (4) Institut de Recerca Històrica, Universitat de Girona, Plaça Josep Ferrater i Móra, 1, 17004 Girona,  
14 Spain.  
15

16 (5) Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002  
17 Burgos, Spain.  
18

19 (6) ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain.  
20

21 \*Corresponding author: C. Sánchez-Hernández ([carsanher88@gmail.com](mailto:carsanher88@gmail.com))  
22

23 **Abstract.** Diet is closely connected to the habitat exploited by ungulates and is one of the main  
24 links between them and the surrounding environment. When climatic fluctuations modified  
25 the vegetal cover and habitat, ungulates' dietary behaviours and ecological niches could  
26 have been impacted severely. During the Middle Palaeolithic, the Mediterranean peninsulas  
27 were known to be climatic refuges because they seemed less susceptible to these changes.  
28 However, the altitude or latitude of a given site may have resulted in local particularities that  
29 could have influenced the vegetal composition and therefore the feeding behaviour of  
30 ungulates from the same region. In the present research we investigate whether these  
31 variables necessitated adaptive changes in the feeding behaviours of ungulates hunted by  
32 Neanderthals through the study of two archaeological sites, Arbreda Cave (Serinyà, Girona,  
33 Spain) and Teixoneres Cave (Moià, Barcelona, Spain). We use a combined analysis of dental  
34 wear (meso- and microwear) and dental cementum analysis of *Cervus elaphus*, *Equus ferus*,  
35 and *Equus hydruntinus* teeth. Dental wear reflects the immediate and average annual dietary

36 traits of ungulates as well as the environmental conditions in the surroundings. Dental  
37 cementum analysis allows accurately identifying the season of ungulate death and linking an  
38 individual's dietary preferences with the seasonal conditions in its last moments of life. As  
39 results, red deer at both sites were mixed-feeders in the annual cycle. A slight increase in grass  
40 consumption was identified during winter for populations from sub-unit IIIa of Teixoneres  
41 Cave. Horse and wild ass based their diet on grasses, but the latter showed seasonal  
42 adaptation toward a mixed consumption of grasses and concentrate resources (i.e. leaves,  
43 shrubs, forbs, and other woody plants). The seasonal feeding adaptations observed for some  
44 of the studied species did not strongly influence their general dietary trends because they kept  
45 feeding on the same resources annually.

46 **Keywords.**

47 Late Pleistocene, Paleodiet, Paleoenvironment, Adaptive behaviour, Dental wear, Dental  
48 Cementum

## 49 **1. Introduction**

50 Global environmental conditions and the specific ecological features in a given region  
51 directly impact the composition and distribution of flora and fauna (Hewitt, 2000; Uriarte,  
52 2003; Rivera Arrizabalaga, 2004; Sánchez-Goñi and D'Errico, 2005; Sánchez-Goñi and Harrison,  
53 2010). The Late Pleistocene displays continuous climatic oscillations, especially during the  
54 Marine Isotopic Stage 3 (MIS 3, ca. 60-30 ka BP). The advance and retreat of glaciers drastically  
55 modified the European landscape and, in turn, the adaptive and survival capabilities of flora  
56 and fauna (Lowe and Walker, 1984; Dansgaard et al., 1993). The large mammals inhabiting the  
57 continent during this period, mostly ungulates, showed a wide range of responses to ecological  
58 issues, varying from phenotypically and migratory aspects to disappearance (Graham et al.,  
59 1996; Brown and Lomolino, 1998; Forchhammer et al., 2002; Martínez-Meyer et al., 2004).  
60 Even on a seasonal and regional basis, environmental features affect the availability and  
61 phenology (e.g. nutritional quality) of the plants consumed by ungulates, thereby having  
62 implications on their biological and behavioural responses to these changes (Jarman, 1973;  
63 Denium, 1984; Helle, 1984; Van Soest, 1994; Weladji et al., 2002; Pettorelli et al., 2005; Arnold  
64 et al., 2015). Therefore, ungulates' adaptive success to specific environmental features  
65 depends on the habitat tolerance of the communities and the specific dietary limits of each  
66 taxa (Graham, 1985; Graham et al., 1996; Williams and Jackson, 2007; Stewart, 2008).

67 As each taxa shows different degrees of or no dietary plasticity, the current research  
68 aims to determine how the main ungulates (*Cervus elaphus*, *Equus ferus*, and *Equus*  
69 *hydruntinus*) hunted by Neanderthals in the northeast of the Iberian Peninsula responded to  
70 local environmental features. The study focus on two archaeological sites located above the  
71 40° N parallel and at different altitudes: Arbreda Cave (211 m a.s.l.) and Teixoneres Cave (760  
72 m a.s.l.) (Fig. 1. A). Cervids and equids are known for developing differentiated adaptive  
73 strategies to cope with environmental variations. Their presence in the same territory during a

74 period of expected environmental fluctuations can provide a much more accurate view of local  
75 and regional features through their dietary strategies. *Cervus elaphus* is well known to have  
76 great dietary plasticity, feeding in a wide range of resources and being able to adapt to very  
77 diverse habitats (Hofmann and Stewart, 1973; Hofmann, 1989; Fonseca, 1998; Azorit et al.,  
78 2012; Berlioz et al., 2017). *Equus ferus* is expected to show more restricted dietary plasticity;  
79 however, extant and extinct populations demonstrated that they could feed on resources that  
80 are not exclusively grasses (Duncan, 1991; Nowak, 1999; Rivals et al., 2009, 2015). *Equus*  
81 *hydruntinus* seems restricted to open areas and the resources available therein (Orlando et al.,  
82 2006; van Asperen et al., 2012; Crees and Turvey, 2014; Boulbes and van Asperen, 2019).  
83 Otherwise, some morphological and size aspects (a longer protocone and increased  
84 hypsodony) of their teeth suggest wider dietary plasticity (Eisenmann, 1991; Boulbes, 2009).

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

93         The study of ungulates' dental wear gives information about diet because both meso-  
94 and microwear are sensitive to dietary changes on different temporal scales (Grine, 1986;  
95 Fortelius and Solounias, 2000). Mesowear reveals the average annual diet of the last  
96 months/year (> 6 months) before death correlated with the general surrounding  
97 environmental features (Fortelius and Solounias, 2000; Ackermans et al., 2018). On the other  
98 hand, microwear reflects a very precise moment in an individual diet as it is generated by the

99 diet of the last days/weeks before death (Grine, 1986), thereby highlighting specific  
100 environmental conditions at that point and seasonal climatic changes (Merceron et al., 2004;  
101 Semprebon et al., 2004; Rivals and Semprebon, 2012). Furthermore, dental cementum  
102 analysis—also called cementochronology—provides accurate estimates of the season of death of  
103 the animals (Scheffer, 1950; Laws, 1952; Lieberman, 1991; Pike-Tay, 1991a; Gourichon, 2004;  
104 Rendu, 2007; Naji et al., 2015), allowing us to correlate the seasonal feeding patterns with a  
105 specific period of the annual cycle (Sánchez-Hernández et al., 2019). In addition, even if the  
106 taxa show homogenous feeding traits through the stratigraphic sequences or the  
107 archaeological sites, cementum analysis enables assessing whether these patterns are due to  
108 seasonal mortality (same season) or stable environmental features allowing them to feed on  
109 the same resources. In this study, dental cementum analysis was only applied to red deer  
110 because the properties of equid cementum make it difficult to interpret the observations.

111

## 112 **2. European and Iberian environmental contexts**

113 The MIS 3 is marked by extreme oscillations characterised by the predominance of  
114 notably cold and dry periods (Heinrich events (HE)) interspersed by temperature and humidity  
115 recovery events with less extreme environmental conditions (Dansgaard-Oeschger events  
116 (DO)) (Dansgaard et al., 1982; Heinrich, 1988; Johnsen et al., 1992; Rasmussen et al., 2014).  
117 These cyclical HE and DO alternations affected the European continent in different ways  
118 depending on the region because other factors such as latitude and altitude are also deeply  
119 involved (Álvarez-Lao and Méndez, 2016; Rivals and Semprebon, 2016). During the HE (also  
120 stadial periods), most of the European territory was dominated by tundra and steppe as well  
121 as ‘mammoth fauna’ in areas without ice sheets (Guthrie, 1982; Vereshchagin and  
122 Baryshnikov, 1982; Kahlke, 2014). On the other hand, mid-climate-adapted vegetation and  
123 animals were pushed toward southern areas, considered as climate refugia, such as the

124 Mediterranean peninsulas and the Balkans (Hewitt, 2000; Sommer and Nadachowski, 2006;  
125 Álvarez-Lao and Méndez, 2016). These ecologic refugees allowed a rapid recovery of forested  
126 areas and animals adapted to temperate conditions in the rest of the continent during DO.

127         The Iberian Peninsula would not have been strongly affected by the climatic changes  
128 occurring during the MIS 3 despite the marginal presence of some cold-adapted taxa like the  
129 woolly mammoth (Sánchez-Goñi et al., 2010; Álvarez-Lao and García, 2011; Álvarez-Lao and  
130 Méndez, 2016; Rivals and Álvarez-Lao, 2018). The Pyrenees Mountains act as a natural barrier  
131 in the north which isolates the Peninsula from the rest of the continent, leaving only two  
132 narrow natural paths in the occidental and oriental slopes of these mountains. The Iberian  
133 Peninsula is characterised by relatively mild environmental conditions even during the coldest  
134 phases (HE) of MIS 3 (Hewitt, 2000; Sommer and Nadachowski, 2006; Álvarez-Lao and Méndez,  
135 2016). The relative stability of the environmental features and the vegetal coverture's  
136 resilience to global climatic changes are some of the main particularities of this region. These  
137 conditions could have guaranteed the constancy of the available resources and the absence of  
138 drastic adaptive behaviours resulting in stable faunal ecological niches, especially for  
139 ungulates. Nevertheless, the orography and the several oceanic influences observed (i.e.  
140 Atlantic and Mediterranean) reflect a wide range of climatic parameters that allow us to  
141 consider the Peninsula as a mini-continent in itself. With an average altitude of 600 m a.s.l. and  
142 various mountain ranges and river valleys, this territory can be divided into three main areas  
143 characterised by distinct ecological features (i.e. latitude, orography, and altitude): the central  
144 Iberian area, and the Cantabrian and the Mediterranean basins.

145         The latitudinal and altitudinal gradients related with climate and vegetation as well as  
146 climate instability usually affect ungulate populations (Rivals et al., 2007b, 2010; Rivals and  
147 Semprebon, 2016). Along the Iberian Mediterranean basin, several studies indicate a northeast  
148 area as cold and dry as the southern area but relatively more humid (Uzquiano-Ollero, 2008;

149 Badal-García et al., 2012; Allué et al., 2017, 2018; Vidal-Matutano, 2018). The north-eastern  
150 region was dominated by vegetal coverture typical of open forested areas dominated by  
151 conifers like *Pinus sylvestris* associated with deciduous and mesophilous taxa (e.g. *Quercus*,  
152 *Betula*, and *Corylus*) that suggest warm and humid episodes (Ros-Mora, 1987; Burjachs and  
153 Julià, 1994; Rivals et al., 2017; Allué et al., 2017, 2018). Otherwise, open landscapes and dryer  
154 conditions dominated in the southern regions with the occurrence of pine forests (*Pinus nigra*-  
155 *sylvestris* and *Pinus pinea*) along with *Quercus*, *Juniperus*, and *Ephedra* taxa (Ros-Mora, 1987;  
156 Uzquiano-Ollero et al., 2008; Badal et al., 2012; Allué et al., 2017, 2018; Vidal-Matutano, 2017,  
157 2018).

158

### 159 **3. Archaeological sites**

#### 160 **3.1. Arbreda Cave**

161 The Arbreda Cave is an archaeo-palaeontological site located in the Serinyà locality  
162 (42° 9' 38" N, 2° 44' 49" E) (Fig. 1A). Along with other cavities such as Reclau Viver or Mollet I, it  
163 forms part of a karstic system belonging to the Banyoles-Besalú basin (Julià, 1980; Roqué et al.,  
164 1999). The cave is located in a low area of the pre-Pyrenean region, in an elongated but  
165 narrow travertine strip of the river Serinyadell valley. In its surroundings, there is a platform of  
166 lacustrine origin called Pla d'Usall to the west and small rivers. The 10 m sedimentary sequence  
167 comprises 14 levels from the Middle Pleistocene at the bottom to the Holocene at the top (Fig.  
168 1B) (Soler et al., 1987a, 2014; Bischoff et al., 1989; Kehl et al., 2014). The Mousterian sequence  
169 shows an extensive chronological frame: the basal level (i.e. N) was dated by U-series/ESR ca.  
170 120 ka BP (Soler i Subils et al., 2012, 2014), whereas the upper Mousterian level (i.e. I) is dated  
171 to 45.840–41.410 cal BP based on AMS radiocarbon dates (Maroto et al., 1996a, 2005, 2012;  
172 Wood et al., 2014). The sequence presents alternating occupations by human groups and  
173 carnivores. The faunal assemblage documented for the Late Mousterian levels corresponds to



174 a broad spectrum of both herbivore and carnivore mammals adapted to Eurosiberian and  
175 Mediterranean environmental conditions (Soler et al., 1987b, 2014; Galobart et al., 1996;  
176 Lloveras et al., 2010, 2018; Rufí et al., 2018). These include a few species from semi-open and  
177 wooded areas, like *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, and *Capra pyrenaica*,  
178 as well as species typical of open areas, like *Equus ferus* and *Equus hydruntinus*. A calf tooth of  
179 *Mammuthus primigenius* represents cold-adapted fauna in level J, whereas a molar of *Castor*  
180 *fiber* indicates running rivers in the vicinity. Carnivores are represented by *Ursus spelaeus*,  
181 *Crocota crocuta*, *Canis lupus*, *Vulpes vulpes*, *Felis silvestris*, *Panthera pardus*, and *Lynx cf.*  
182 *spelaea*. Among lagomorphs, *Oryctolagus cuniculus* predominates versus the marginal  
183 presence of *Lepus europaeus* (Soler i Masferrer and Maroto, 1987b; Maroto et al., 1996;  
184 Lloveras et al., 2010). Level I is the unique Mousterian level where small mammal assemblage  
185 has been recovered and studied (Alcalde, 1987; Galobart et al., 1996; Alcalde and Galobart,  
186 2002; López-García et al., 2015). This assemblage, which may be used as a reference for level J  
187 on which the present research focuses, is dominated by species with Eurosiberian climatic  
188 preferences, such as *Microtus arvalis* or *Talpa europaea*, as well as by generalist taxa such as  
189 *Microtus agrestis* or *Apodemus sylvaticus*. There is also an important component of species  
190 with Mediterranean requirements, like *Eliomys quercinus*. The climatic and environmental  
191 conditions had lower annual temperatures and higher degree of humidity than those seen  
192 nowadays (Sans-Fuentes and Ventura, 2000). An alternation between two warm and humid  
193 periods and another cold and dry one was identified for level I (López-García et al., 2015).  
194 Previous palynological and anthracological studies suggest a landscape of open-wet and  
195 forested areas dominated by *Pinus sylvestris* and herbaceous vegetation around the cave (Ros-  
196 Mora, 1987; Burjachs and Renault-Miskovsky, 1992; López-García et al., 2015).

### 197 **3.2. Teixoneres Cave**

198 More than 60 km southwest of the previous site, Teixoneres Cave (41° 48' 25" N, 2° 09'  
199 02" E) (Fig. 1A) belongs to the 'Coves del Toll' karstic system (Rosell et al., 2010a, 2017). The  
200 cave is located south of the pre-Pyrenean region (Moià, Barcelona, Spain) in a zone of  
201 transition between the Mediterranean coast and the hinterland of the North-East region (Fig.  
202 1A). The surrounding landscape is characterised by highlands with the presence of small hills  
203 and rivers of little importance, except for the Llobregat River to the south and the Ter River to  
204 the north which delimit the region. The cavity presents ~8 m deep sedimentary sequence  
205 where nine stratigraphic units were identified (Fig. 1C) (Serra et al., 1957, 1973; Rosell et al.,  
206 2017). The present research focuses on unit III, divided into two sub-units (i.e. IIIa and IIIb) and  
207 ranging from >51 ka <sup>14</sup>C BP to 43.4 ka cal BP (Talamo et al., 2016). Unit III is characterised by an  
208 alternation between human occupation at the entrance of the cave and carnivore occupation  
209 in the back and darker areas (Rosell et al., 2010b).

210 In the faunal record, up to 19 different taxa were identified, including carnivores and  
211 herbivores. In the unit III, the carnivores correspond to *Ursus spelaeus*, *Crocuta crocuta*, *Canis*  
212 *lupus*, *Vulpes vulpes*, *Lynx spelaea*, and *Meles meles*. The broad spectrum of ungulates  
213 recovered in this unit indicates a complex environment formed by different habitats such as  
214 steppe-like, open forest, and mountains areas (Álvarez-Lao et al., 2017; Rosell et al., 2017). The  
215 presence of mixed wooded and semi-open areas is indicated by *Sus scrofa*, *Cervus elaphus*,  
216 *Capreolus capreolus*, and *Bos primigenius*. The open spaces around the cave are suggested by  
217 the occurrence of *Equus ferus* and *Equus hydruntinus* and by the cold-adapted taxa *Coelodonta*  
218 *antiquitatis* and *Mammuthus primigenius*. Finally, remains of *Capra pyrenaica* and *Rupicapra*  
219 *rupicapra* were found in the assemblage. The small vertebrate assemblage shows differences  
220 in composition and proportion between the sub-units IIIa and IIIb (López-García et al., 2012,  
221 2014). Generalist species like *Apodemus sylvaticus*, *Eliomys quercinus*, or *Bufo calamita*  
222 dominate the entire unit III. The Mediterranean species take a significant part, such as  
223 *Microtus (Terricola) duodecimcostatus*. The strict Eurosiberian species present in both sub-

224 units include *Rana temporaria*, *Microtus arvalis*, and *Sorex coronatus*. Sub-unit IIIa is  
225 characterised by species with a preference for high altitude and rocky terrain, such as  
226 *Chionomys nivalis* and *Terricola gerbei* and Mediterranean taxa such as *Anguis fragilis*. This  
227 combination suggests a decrease in temperature but still humid conditions, as indicated by the  
228 presence of forest. Instead, sub-unit IIIb yielded species of generalist and Mediterranean  
229 requirements which are absent in IIIa: *Natrix cf. natrix*, *Coronella austriaca*, *Glis glis*, and  
230 *Rhinolophus ferrumequinum*. They show a predominance of forested areas and humid  
231 conditions. The pollen and charcoal studies indicate the prevalence of humid and temperate  
232 environments in a Mediterranean region characterised by open forest landscape mostly  
233 comprising *Pinus sylvestris* and *Quercus* sp., whereas herbaceous taxa (Poaceae,  
234 Amaranthaceae, Asteraceae) dominated in open areas (López-García et al., 2012).

235

#### 236 **4. Material and Methods**

237 The material involved in the present research was selected following specific protocols  
238 related to each technique (see below) and by taking as a basic premise a good preservation of  
239 the morphological integrity and dental tissues. Ideally, it is preferable to perform the whole  
240 study on a single type of molar (e.g. the second upper molar). Nevertheless, owing to the  
241 relatively high degree of fragmentation in the assemblages (especially those from Arbreda  
242 Cave) and to the low amount of cheek teeth, the upper and lower molars as well as the forth  
243 premolar were chosen for all the analyses, in particular for microwear. Xafis et al. (2017)  
244 suggested that differences between the microscopic patterns of premolars and molars are not  
245 significant, which was also observed for the Schöningen equids by Rivals et al. (2015). We also  
246 tested for differences between tooth positions in our material (see section 5.2). The teeth  
247 sampled for dental wear belong to *Cervus elaphus* (n = 132) *Equus ferus* (n = 120) from Arbreda  
248 and Teixoneres caves and *Equus hydruntinus* (n = 43) which was only present at Teixoneres

249 Cave (Table 1; see Table S1 and S2 from supplementary data). The teeth sampled for  
250 cementum analysis belong exclusively to *Cervus elaphus*: seven teeth from sub-unit IIIb of  
251 Teixoneres Cave (n = 7) as well as three from Arbreda Cave (n = 3) (Table 3; see Table S3 from  
252 supplementary data). It should be noted that one tooth from sub-unit IIIa was sampled but  
253 excluded as it presented taphonomic alterations hiding/obliterating cementum increments. All  
254 the mesowear and microwear analyses performed were ran by a single observer (CSH) to avoid  
255 possible inter-observer errors. The complexity of cementum analysis required a combined  
256 observation between two observers (i.e. CSH and LG).

257         The success rate of the analysis varies between techniques and the general state of  
258 conservation of the different type of teeth (position and laterality) (Table 1; see Table S4 from  
259 supplementary data). We developed an ANOVA (Kruskal-Wallis) and Tukey's test to check  
260 whether there are or not statistical differences between the dietary traits of the studied teeth  
261 (premolars and molars) (see Table S5 from supplementary data). All the samples studied were  
262 recovered at levels with a clear anthropic context, associated with invariable evidences of  
263 faunal processing, lithic industry, and hearths (Rosell et al., 2010b, 2017; Soler i Subils et al.,  
264 2014). The material from Arbreda Cave is curated at the local museum of Banyoles (Girona,  
265 Spain) and at the Universitat de Girona (Girona, Spain). The material belonging to Teixoneres  
266 Cave is curated at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES)  
267 (Tarragona, Spain).

268 *Tooth mesowear*. The technique developed by Fortelius and Solounias (2000) macroscopically  
269 describes the physical modifications over individual dentition owing to the relative amount of  
270 attritive-abrasive dental wear caused by the diet. There are two variables to consider, namely,  
271 sharpness (sharp, rounded, or blunt) and relief (high or low) of tooth cuspids, which are  
272 directly affected by the intrinsic (plant phytoliths) and extrinsic (dust, sand, and grit) abrasive  
273 items present in the resources consumed. Precisely, browsers (i.e. feeding on concentrate  
274 resources: leaves, shrubs, forbs, and woody plants) are characterised by diets with relatively

275 low levels of abrasion and high attrition producing sharp apices and high relief, whereas  
276 grazers (i.e. eating grass and pasture) feed on items of high abrasion and low attrition  
277 producing blunt apices and lower relief than browsers. The mixed feeders occupy the gap  
278 between the last two dietary groups and are characterised by rounded cusp sharpness and  
279 intermediate relief. We follow the Mesowear Score (MWS) developed by Muhlbachler et al.  
280 (2011) on equids, which improve the previous scoring method applied for several taxa and  
281 based on a four points scale (i.e. from 0 to 3). It was tested on cervids by Rivals and Takatsuki  
282 (2015). The new score consists on seven points referring to different cusps shape and relief,  
283 where the highest attrition value is represented by stage 0 and the highest abrasion value by  
284 stage 6. The selection protocol for the mesowear study includes adult teeth presenting good  
285 integrity of both the crown and the cusps (especially in the buccal facet), and teeth with low or  
286 high wear rates from young and senile individuals were discarded (Fortelius and Solounias,  
287 2000; Rivals et al., 2007a).

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

301 preferences/tendencies for one type of resource (i.e. attritive or abrasive) on a daily or  
302 seasonally based pattern, including a slightly higher proportion of attritive or abrasive items.  
303 They are referred to as browse- or grass-dominated mixed-feeders, respectively (Solounias and  
304 Semprebon, 2002). The average NS and NP obtained from the archaeological record are  
305 represented in a bivariate plot. Similarly, calculating the low range of scratches (LSR) of  
306 individuals per taxon (i.e. individuals with NS between 0 and 17) allows recognising the dietary  
307 particularities of a given population (Solounias and Semprebon, 2002; Semprebon and Rivals,  
308 2007). Browsers show an LSR between 72.73% and 100%, whereas grazers show an LSR  
309 between 22.2% and 0%. Mixed-feeders show an intermediate LSR between 20.93% and 70%.  
310 Other qualitative variables are recorded, such as the scratch width score (SWS) (0 = fine; 1 =  
311 mixture of fine and coarse; 2 = coarse; 3 = hyper-coarse, 4 = mixture of coarse and hyper-  
312 coarse), the presence of large pits (LP), and gouges (G) (Solounias and Semprebon, 2002;  
313 Semprebon et al., 2011). The sampling protocol includes adult teeth presenting occlusal wear  
314 facets without strong damage (Solounias and Semprebon, 2002). Initially, the occlusal surfaces  
315 are washed using acetone and 96% ethanol. Then, for each tooth, a mould of the occlusal  
316 surface is created using a high-resolution silicone (vinylpolysiloxane HeraeusProvil Novo Light  
317 Regular Set). Finally, positive casts are made with a transparent and high-resolution epoxy  
318 resin (C.T.S.® EPO 150) and catalyst (K 151). Teeth presenting post-depositional damages are  
319 excluded (King et al., 1999; Martínez and Pérez-Pérez, 2004). For quantifying the microscopic  
320 features, we use a Zeiss-Stemi 2000C stereomicroscope of transmitted light at x35  
321 magnification with an ocular reticule delimiting a 0.16 mm<sup>2</sup> square area. The counting process  
322 took place in two independent enamel areas, which were also separately analysed in duplicate  
323 to obtain the average of microwear features per tooth (Semprebon et al., 2004; Solounias and  
324 Semprebon, 2002). This system allows minimizing intra-observer errors (Semprebon et al.,  
325 2004). The analysis in those teeth with an integral structure conservation were focused on the  
326 protocone (upper molars) and the protoconid (lower molars) (Semprebon et al., 2004;

327 Solounias and Semprebon, 2002). Otherwise, we also analysed small good preserved enamel  
328 zones in tooth partially broken or taphonomically affected to increase the sample size.

329 *Dental cementum*. The technique is based on the study of the growth marks registered  
330 seasonally within the dental cementum which covers the root surface (Scheffer, 1950; Laws,  
331 1952; Sergeant and Pimlott, 1959; Klevezal and Kleinenberg, 1969; Grue and Jensen, 1979;  
332 Stott et al., 1982). The analysis is primarily focused on the acellular cementum (specifically, the  
333 Acellular Extrinsic Fibre Cementum (AEFC)) owing to its regular and predictable growing  
334 pattern throughout the annual cycle (Schroeder, 1986; Sequeira et al., 1992; Naji et al., 2015).  
335 The acellular cementum growth is characterised by two types of increment layers which differ  
336 by the collagen deposition rate and the mineralisation degree (Klevezal and Kleinenberg, 1969;  
337 Jones, 1987; Burke, 1993; Gordon, 1993; Gourichon, 2004). Viewed in transmitted light, these  
338 increments appear respectively as translucent (TB) and opaque bands (OB) (Fig. 3) (Scheffer,  
339 1950; Lieberman, 1991, 1993, 1994; Lieberman and Meadow, 1992; Burke and Castanet, 1995;  
340 Pike-Tay, 1995; Gourichon, 2004). The hypo-mineralised TB, also called 'growth zones', result  
341 from a fast growth pattern and are generally thicker than the OB. The hyper-mineralised OB,  
342 also called '*annuli*' or 'rest line', result from a slow growth pattern and may sometimes appear  
343 as thin lines of arrested growth (Fig. 3) (LAG; e.g. Burke and Castanet, 1995). A wide range of  
344 mammals from temperate regions is characterised by presenting seasonality within the  
345 increment growing patterns (e.g. cervidae, bovidae, caprinae). The causes of seasonal  
346 increment depositions cannot be strictly defined although multiple factors (exogenous and  
347 endogenous) could be involved in the process; however, latitude seems to play an important  
348 role (i.e. arctic, temperate, or tropical regions). It is also suggested that not all mammals  
349 cohabiting the same region (e.g. some carnivores from Denmark) necessarily follow the same  
350 increment deposition schedule (Grue and Jensen, 1979). In other words, for the ungulates  
351 studied here, the TB are generally deposited during seasons of greater amount of daily light,  
352 also called 'good seasons' (i.e. spring to fall) (Pike-Tay, 1991a, 1991b, 1995), whereas the OB

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

372 The tooth samples were prepared following the standard techniques used for ground thin-  
373 sections (Lieberman et al., 1990; Pike-Tay, 1991a; Stutz, 2002; Gourichon, 2004; Rendu, 2007;  
374 Naji et al., 2015). As recommended by one of us (LG), only one root was extracted to keep the  
375 maximum tooth integrity. Upper and lower molar with apparent good preservation state (no  
376 or only few fractures on the cementum surfaces) were chosen for the analysis. Primarily, the  
377 root was embedded within a transparent epoxy resin and, after drying, was separated from  
378 the crown. Next, 2–4 sections with thickness of 0.5–1 mm were cut from the root using a slow-



379 speed rotating saw (Buehler Isomet 1000 or 5000), glued separately on a glass support, and  
380 then abraded to the required thickness using a semi-automatic grinding device (Buehler  
381 PetroThin) (Gourichon, 2004; Rendu, 2007; Naji et al., 2015). The analysis was performed using  
382 a polarising light microscope Leica 2500P with x100, x200, x400, and x500 magnifications and  
383 connected to a computer via a high-resolution digital camera (full-screen video) using three  
384 distinct light filters: plane-polarised light, cross-polarised light, and full-wave retardation plate  
385 ( $\lambda$  plate) (Stutz, 2002).

386

## 387 **5. Results**

### 388 **5.1. Mesowear analysis**

389 The tooth mesowear values (MWS) observed for *Cervus elaphus* from both sites  
390 present a remarkable heterogeneity ranging from 1 to 4.5 (Table 2), that is, from browsers  
391 (concentrated resource feeders) to grazers (grass and other herbaceous plant feeders). Red  
392 deer from sub-units IIIa (n = 14) and IIIb (n = 34) of Teixoneres Cave have values corresponding  
393 to animals with a typical annual diet pattern of mixed feeders (Table 2, Fig. 4A). Although the  
394 *Cervus elaphus* sample from Arbreda Cave is too small to obtain reliable results (Table 2), we  
395 obtained approximate information from all levels where the red deer is present except for  
396 levels J and N. Data from level I (n = 3) suggest mixed feeders, whereas that from level K (n = 1)  
397 suggested a browser diet. Levels L (n = 1) and M (n = 2) show the highest values (MWS = 3 and  
398 4.5, respectively) (Table 2, Fig. 4A). These results suggest grass-dominated mixed-feeding for  
399 level L, whereas higher levels of abrasion characterised the pure grazer, namely, red deer, for  
400 level M (Fig. 4A).

401 *Equus ferus* teeth display similar MWS values ranging from 4 to 6 from an intra- and  
402 inter-site perspective at both Mediterranean sites (Table 2). Horse are well-represented at  
403 Teixoneres Cave, where sub-units IIIa (n = 17) and IIIb (n = 10) are representative of annual

404 dietary traits typical of pure grazers (Table 2, Fig. 4A). Regarding the horse from Arbreda Cave,  
405 the small sample size limits the interpretation of the results (Table 2). However, the MWS  
406 values from all levels suggest dietary patterns based on very abrasive items such as grass  
407 (Table 2, Fig. 4A). It is therefore possible to observe small intra- and inter-site variations but  
408 always within the same dietary group, namely, the grazers.

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

## 412 **5.2. Microwear analysis**

413 The ANOVA (Kruskal-Wallis) and Tukey's test indicate non-significant differences  
414 between the six molar positions (upper and lower M1 to M3) both in *Cervus elaphus* (F =  
415 0.782; p= 0.568) and *Equus ferus* (F = 2.631; p= 0.083). The comparison of the different dental  
416 position in the red deer from Teixoneres sub-units IIIa and IIIb did not show any significant  
417 difference (F = 1.189; p= 0.334). Similarly, the statistical analysis between the samples from  
418 sites do not show significant differences: *Cervus elaphus* (F= 0.104; p= 0.748) and *Equus ferus*  
419 (F= 0.191; p= 0.670) (see Table S5 from supplementary dataset). Premolars were excluded  
420 from the analysis due to the extremely low sample size. We can conclude that there are no  
421 significant differences in microwear patterns among the different dental positions in red deer  
422 and horse, and that all molars can be lumped together to increase sample size.

423 *Cervus elaphus* do not show strong variations in dental microwear at the two sites, as  
424 evidenced by the average NS and NP (Fig. 5A) as well as by LSR (Fig. 4B) (Table 2). Red deer  
425 from sub-units IIIa (n = 15) and IIIb (n = 42) of Teixoneres Cave and level J (n = 14) of Arbreda  
426 Cave were mixed-feeders (Table 2, Fig. 4B and 3A). Nevertheless, the sample from level I of  
427 Arbreda Cave (n = 3) suggests grass-dominated mixed-feeders and that from level L (n = 2)  
428 suggests a mixed-feeder diet (Table 2, Fig. 4B and 3A); however, they do not allow obtaining

429 statistically reliable results because the number of teeth is very low. Instead, the approximate  
430 results from level K (n = 1) appear to be shifted toward the browser zone of the confidence  
431 ellipse and differ from the general dietary features evidenced for the other levels (Fig. 5A).  
432 Level M (n = 2) show NS and NP values that suggest mixed-feeder traits (Fig. 5A).

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

443 *Equus ferus* shows similar grazer dietary traits at an intra- and inter-site level (Table 2).  
444 The horse tooth samples from sub-units IIIa (n = 29) and IIIb (n = 12) of Teixoneres Cave and  
445 from level J (n = 10) of Arbreda Cave (with slightly higher NP) lie outside the grazer confidence  
446 ellipse despite their NS values being representative of grazers (Fig. 5B). Otherwise, the LSR  
447 values indicate grazer dietary patterns (Table 2, Fig. 4B) and agree with the NS values (Fig. 5B).  
448 Therefore, although the high NP values are placed three levels above the grazer confidence  
449 ellipse, the NS range still corresponds to typical grazers, highlighting a very abrasive diet for  
450 horse (Table 2, Fig. 5B). Regarding the levels of Arbreda Cave with small sample size (i.e. I, K, L,  
451 M, and N) (Table 2), all showed NS and NP values as well as LSR values close to the three levels  
452 described previously, which are typical of a grazer dietary pattern (Table 2, and Figs. 2B and  
453 3B).

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

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

### 469   **5.3. Cementum analysis**

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

477           Concerning Arbreda Cave, data from only three *Cervus elaphus* teeth are available  
478 owing to the extreme fragmentation and bad preservation of the dental assemblage. In the

479 two samples from level L, the cementum sequence ends with a TB in its intermediate growth  
480 stage, whereas the single tooth from level M shows a final OB (Table 3 and Table S3 from  
481 supplementary data). However, the samples from these levels (i.e. L and M) is not large  
482 enough to provide interpretable data, neither to be integrated into the discussion.

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

493

## 494 **6. Discussion**

### 495 **6.1. Ungulates' dietary traits**

496 The vegetation composition and distribution in the Iberian Peninsula have been  
497 affected by the climatic fluctuations of the MIS 3 (Roucoux et al., 2005; Sánchez-Goñi and  
498 D'Errico, 2005; Uzquiano-Ollero, 2008; Sánchez-Goñi et al., 2010; Uzquiano-Ollero et al., 2016;  
499 Allué et al., 2017). In addition, the latitudinal location of the Peninsula along with the complex  
500 orography favours a broad diversity of faunal and vegetal resources. Consequently, substantial  
501 changes can be expected in the quality and type of vegetal cover along with the environmental  
502 conditions within a small area and over short distances. While located in a relatively stable

503 climatic Mediterranean zone characterized by patchy landscapes as attested in several  
504 stratigraphic sequences of the MIS 5 to 3, e.g. Abric Romaní, Cova Gran, Coll Verdaguer, Riera  
505 de les Terrasses dels Canyars, or Cova del Rinoceront (Allué et al., 2018, 2017; Daura et al.,  
506 2017, 2015; Fernández-García, 2019; Fernández-García et al., 2016; López-García et al., 2015),  
507 the latitude and altitude characteristics of Arbreda and Teixoneres Caves could have  
508 influenced the feeding strategies of the fauna living around. However, the dietary behaviour  
509 observed for the two most common ungulates, *Cervus elaphus* and *Equus ferus*, do not show  
510 adaptive changes irrespective of the site and stratigraphic level (Ramírez-Pedraza et al., 2019).  
511 The same was not true of *Equus hydruntinus*, which showed seasonal variations in its dietary  
512 behaviour.

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

529 scratches type and gouges suggest that the high percentage of large pits could not be  
530 exclusively attributed to browsing episodes during the mixed diet. Indeed, in mixed-feeders,  
531 grass consumption close to the ground may also increase the number of large pits owing to the  
532 abundance of extrinsic particles in the bolus (i.e. dust, grit) (Solounias and Semprebon, 2002;  
533 Semprebon and Rivals, 2007).

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

540           *Cervus elaphus* seems to alternate between concentrate resources and grasses (i.e.  
541 attritive and abrasive) as long as they are available in the surroundings of both sites and their  
542 quality is enough to cover their nutritional demands for survival. This perspective could be  
543 reinforced by the combined results of Arbreda Cave levels M and L, where annual and  
544 daily/weekly diets show different results (i.e. grazer and mixed-feeder, respectively). It seems  
545 to be a common feeding behaviour within the region because red deer from the Abric Romaní  
546 (Capellades, Barcelona, Spain) shelter also show a wide dietary pattern (i.e. from browser to  
547 grass-dominated mixed-feeders) (Fernández-Laso et al., 2011; Allué et al., 2012; Burjachs et al.,  
548 2012).

549           Similarly, *Equus ferus* shows a stable average annual and daily/weekly dietary pattern  
550 at both sites that is focused exclusively on grass consumption (abrasive items). These dietary  
551 traits are indicative of strict grazer behaviour and are supported by the high proportion of  
552 coarse scratches on the enamel surface. Nevertheless, an unexpectedly high number of pits is  
553 seen for typical grazers, which could initially suggest concentrate resource ingestion (attritive

554 wear). This may be conceivable because it has been suggested that modern (Duncan, 1991;  
555 Nowak, 1999; Baskin and Banell, 2003; Ungar, 2010) and ancient horse populations (Rivals et  
556 al., 2009, 2015; Ecker et al., 2013) occasionally browsed. However, MWS and LSR values  
557 unequivocally indicate a grazing diet at both sites, with no suggestion of concentrate item  
558 consumption and opening new alternatives to explain the high number of pits. The grazing  
559 behaviour combined with the high number of pits have already been seen in the  
560 archaeological record of Payre level D (Rhône Valley, France), Wallertheim level F (Mainz,  
561 Germany), and Covalejos levels 8 and 7 (Cantabria, Spain) (Rivals et al., 2009; Sánchez-  
562 Hernández et al., 2019). Specifically, Wallertheim (level F) and Covalejos (levels 8 and 7) caves  
563 are related to the appearance of colder and dryer pulsations that increase dust particles in the  
564 ingested resources. We suggest that this explanation is also relevant for Arbreda and  
565 Teixoneres caves, where both concentrate resources and grasses would contain elevated  
566 amounts of extrinsic particles.

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



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

601           Indeed, neither the latitude nor the almost 600 m difference in altitude between the  
602 two sites seem to have strongly modified the surrounding resources because the red deer and  
603 horse were not forced to adapt their annual feeding strategies. The natural course of the  
604 annual cycle seems to have a low impact on available resources except for sub-unit IIIb, where

605 grasses are temporarily reduced, thus modifying the diet of the wild ass. Therefore, although  
606 we could consider that the annual dietary homogeneity of these taxa was due to the low  
607 mesowear sensitivity in detecting seasonal variations (i.e. suitable for long-term  
608 measurements), the microwear results are conclusive with the annual dietary pattern.  
609 Thereby, no long-term shifts and interspecific competition between cervids and equids related  
610 to latitude or altitude can be detected for these contexts; they are seen only at the  
611 intraspecific level for equids.

## 612 **6.2. Seasonality of diet**

613 The feeding behaviour of red deer at sub-unit IIIb shows a slight seasonal pattern with  
614 increased consumption of grasses and other herbaceous plants during winter, as evidenced by  
615 the correlation of daily/weekly feeding traits and the season of death. This trend contradicts  
616 the expected seasonal variation observed for the extant European red deer, which usually tend  
617 to increase browsing during winter as a result of nutritional constraints (Staines and Crisp,  
618 1978; Gebert and Verheyden-Tixier, 2001). However, Mediterranean environments reach the  
619 richest nutritional period at the end of autumn and during winter. During this period, the  
620 extant red deer prioritises grasses and other herbaceous items because the tissue of  
621 concentrate resources would lignify, thus hindering the digestive process (Gutman and  
622 Seligman, 1979; Seligman, 1996; Bugalho et al., 2001; Bugalho and Milne, 2003; Weladji et al.,  
623 2002; Azorit et al., 2012). This could explain the increased NP and NS. In addition, this case is  
624 not isolated; the same trend has also been observed in the M level of Abric Romaní, whose  
625 individuals were hunted from October to December and showed a predominance of grass  
626 consumption within the mixed diet (Fernández-Laso et al., 2011a).

627 However, this dietary particularity in sub-unit IIIb cannot be considered a drastic  
628 adaptive response to seasonal environmental oscillations because it occurs within the same  
629 dietary group: mixed-feeder. Instead, it could suggest that the dietary behaviour of Palaeolithic

630 red deer at these sites was closer to that of current Iberian cervids than in the rest of the  
631 European continent. This implies that their current dietary behaviour in this area could have  
632 begun to generalise during the Middle Palaeolithic. The previous interpretation also reinforces  
633 the idea of the Iberian Peninsula as a climatic refuge during the Palaeolithic climatic  
634 oscillations and supports the important role of the Mediterranean as a determining factor for  
635 the environmental, vegetal, and faunal development of this area in this period. With regard to  
636 vegetal issues, the Mediterranean winter would favour an increase in grass quality and a  
637 decrease in concentrate resources and their availability. Therefore, the seasonal increase in  
638 the consumption of concentrate resources by the wild ass could be indirectly placed during the  
639 summer because the expected lower quality or availability of grasses in this season could push  
640 them to complement their diet with leaves or shrubs (Rodríguez-Berrocal, 1978; Gutman and  
641 Seligman, 1979; Bugalho et al., 1998; Seligman, 1996).

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

### 648         **6.3. Palaeoenvironmental conditions**

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

655 of both sites, whereas that of *Equus hydruntinus* indicates some seasonal fluctuations within a  
656 relatively stable environment for Teixoneres Cave during the year. Therefore, ungulates'  
657 dietary patterns as observed at Arbreda and Teixoneres caves suggest similar landscapes  
658 mainly comprising patched areas with comparable proportions of open and wooded areas.  
659 This landscape reconstruction is in accordance with the temperate environmental  
660 requirements of large and small vertebrates and the vegetal assemblages identified at these  
661 sites (López-García et al., 2012, 2015; Álvarez-Lao et al., 2017; Luzi et al., 2017; Rosell et al.,  
662 2017; Rufí et al., 2018). The dietary features observed for ungulates correlate well with the  
663 relative temperate and humid conditions for the three studied assemblages.

664         Regarding Arbreda Cave, such conditions as described above for level J could have  
665 been similar to those proposed for level I through the study of micro-vertebrates (as data are  
666 not available yet for level J), where the relative degree of humidity could occasionally decrease  
667 (López-García et al., 2015). For Teixoneres Cave, temperate and humid conditions were also  
668 recognised for the whole unit III by other micro-vertebrate studies (López-García et al., 2012;  
669 Luzi et al., 2017). However, our data allow identifying small variations for sub-units IIIa and IIIb.  
670 Specifically, the seasonal increase in the consumption of concentrate items by the wild ass  
671 indicates a major pressure over grasses, probably because of the seasonal intensification of  
672 humidity around the cave. On the contrary, sub-unit IIIa is characterised by an increase in grass  
673 consumption by both the red deer and the wild ass along with the strict grazer diet of the  
674 horse, suggesting the presence of open areas around the cave. It could also evidence the  
675 worsening of environmental features toward colder and dryer conditions with respect to sub-  
676 unit IIIb, as identified previously, which eventually culminate in unit II (López-García et al.,  
677 2015; Fernández-García, 2019).

678         Deriving out from a regional perspective, the unexpectedly high number of pits for  
679 horse at both sites could be a consequence of the occurrence of dry pulsations, especially for

680 level J and sub-unit IIIa. This was previously observed at Covalejos Cave (Cantabria, Spain) and  
681 was attributed to an aridity increase (Sánchez-Hernández et al., *in press*). At the two caves, the  
682 marginal and occasional presence of cold-adapted taxa such as *Mammuthus primigenius* (level  
683 J and sub-unit IIIa) and *Coelodonta antiquitatis* (sub-unit IIIb) support the hypothesis about the  
684 persistence of open areas (i.e. steppes) and the effects of cold and dry pulsations (Álvarez-Lao  
685 et al., 2017; Rufí et al., 2018).

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

706 colder-dryer environmental pulsations. This trend will culminate in the worsened  
707 environmental features identified at unit II of Teixoneres Cave and Terrasses de la Riera dels  
708 Canyars (López-García et al., 2012; Daura et al., 2013; Allué et al., 2017; Fernández-García,  
709 2019). The contextualisation of our results highlighted that even during pulsations of severe  
710 climate deterioration, the region remained an environmental refuge with relatively temperate  
711 and humid conditions and without complete disappearance of woodland areas. The features of  
712 these landscapes could generate an environmental context conducive to the survival of  
713 Neanderthal groups, where the availability of different preys would guarantee their acquisition  
714 at any time of the year (Sánchez-Hernández et al., 2019). The new perspective could suggest as  
715 hypothesis that the short but repetitive occupations observed for Teixoneres Cave (Sánchez-  
716 Hernández et al., 2016, 2014) would not be determined by factors such hominin ecological  
717 pressure over the resources, but that other factors would be involved in decision-making  
718 within the dynamics of settlement and movement of these populations.

719

## 720 **7. Conclusion**

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

728 This combination also proved itself useful in identifying and placing the dietary trends  
729 of red deer within the annual cycle and in linking them to possible seasonal environmental

730 factors. Nevertheless, a larger sample size for cementum analysis is required to assess whether  
731 the dietary trend of the red deer in sub-unit IIIb is due to seasonal influences or the  
732 circumstantial behaviour of these seven individuals with a meal-by-meal mixed-feeder diet.  
733 The more accurate knowledge of ungulate palaeodiets would help in further research with  
734 archaeological perspectives to precise the relevance of the ungulates preys and environmental  
735 features within the decision taken by Neanderthal groups for survival within the  
736 Mediterranean region of the Iberian Peninsula.

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

743

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

755

756 **Author contributions.** CSH conceived/designed the study in collaboration with FR and LG. JR,  
757 RB, FR, JS, and NS provided materials for the research. CSH performed the dental wear and  
758 cementum sampling processes. CSH analysed the materials and the results with contributions  
759 from LG and FR. CSH wrote the original draft with inputs from FR and LG. All authors have read  
760 and approved the manuscript.

761 **Data Availability.** All data generated during this study are included here and in the  
762 Supplementary Information file.

763 **Competing Interests.** The authors declare no competing interests.

#### 764 **Figure captions**

765 **Figure 1.** Location (A) and stratigraphy of Arbreda Cave (B) and Teixoneres Cave (C).

766 **Figure 2.** Microscopic images (x35) of molar enamel surfaces with observable microwear  
767 features (i.e. scratches and pits). From left to right: (A) *Cervus elaphus* from Arbreda Cave; (B)  
768 *Equus ferus* and (C) *Equus hydruntinus* from Teixoneres Cave.

769 **Figure 3.** Microscopic view with natural (A) and polarized light plus  $\lambda$  lame (B) of translucent and  
770 opaque cementum bands (TB & OB). Crosses point out the observed translucent bands (TB); Red  
771 square represents a small zone of cementum, which extends on a northeast / southwest axis.

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

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

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

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

791

#### 792 **Table captions**

793 **Table 1.** Summary of Sample Size by Taxa Site and Techniques. Abbreviations: TX = Teixoneres  
794 Cave; ARB = Arbreda Cave; N = number of specimens with interpretable data per technique.

795 **Table 2.** Summary of meso- and microwear data of Arbreda and Teixoneres caves.  
796 Abbreviations: N = number of specimens; MWS = mesowear score; LSR = microwear score; NS  
797 = average number of scratches; NP = average number of pits; %LP = percentage of individuals



798 with large pits; %G = percentage of individuals with gouges; and SWS = scratch texture  
799 analysis.

800 **Table 3.** Summary of cementum data from levels L and M of Arbreda Cave and sub-unit IIIb of  
801 Teixoneres Cave. Abbreviations: Ref = reference number attributed by the authors; N° CB=  
802 number of pairs of bands observed in the acellular cementum; LCB = last cementum band  
803 observed; % Dev = % growth ratio of the last cementum increment; Seasonality = season at the  
804 individual's death; OP = dark and hyper-mineralised cementum band; TB = clear and hypo-  
805 mineralised cementum band; M = upper molar; and m = lower molar.

806 **Table 4.** Summary of cementum and NS/NP data from sub-unit IIIb of Teixoneres Cave.  
807 Abbreviations: Ref = reference number attributed by the authors; N° CB= number of pairs of  
808 bands observed in the acellular cementum; LCB = last cementum band observed; % Dev = %  
809 growth ratio of the last cementum increment; OB = dark and high mineralized (opaque)  
810 cementum band; TB = clear and low mineralized (translucid) cementum band; NS = number of  
811 scratches; NP= number of pits; NS/NP= ratio of number of scratches and pits; NP/NS= ratio of  
812 number of pits and scratches; M = upper molar; and m = lower molar.

813

814

815

816

817

818

819

820

821

822

823

824

825

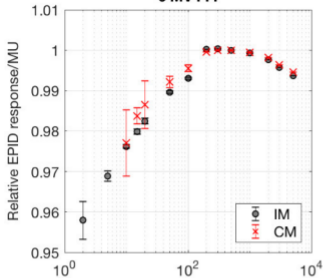
826

827

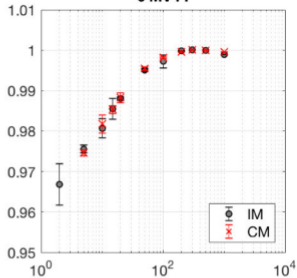
828

829

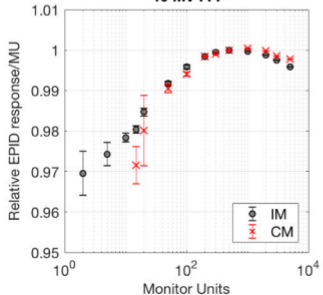
6 MV FFF



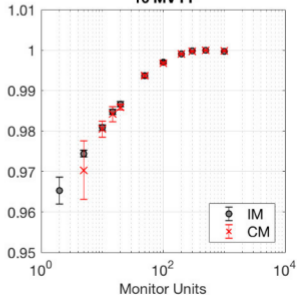
6 MV FF

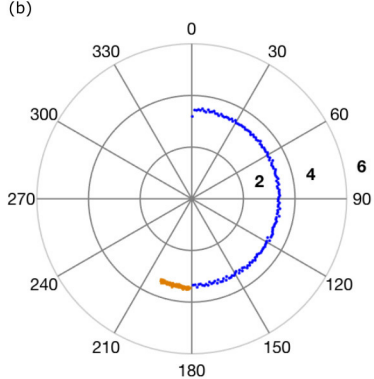
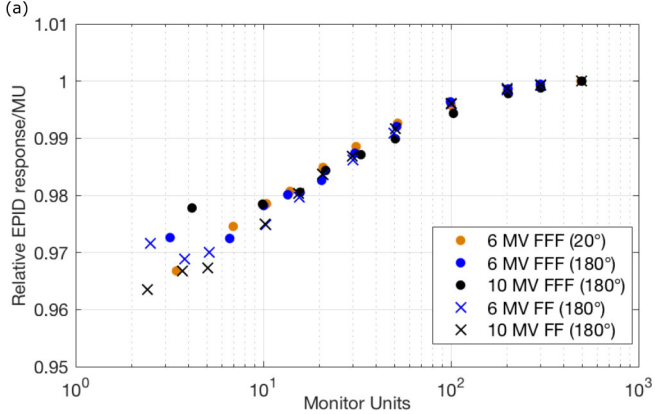


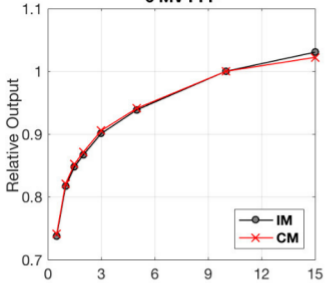
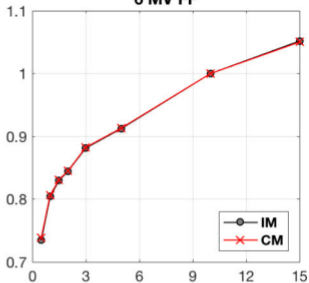
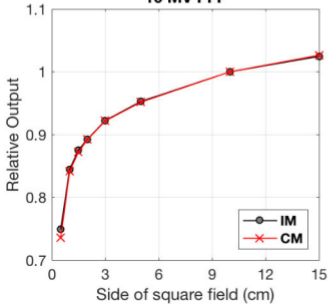
10 MV FFF



10 MV FF





**6 MV FFF****6 MV FF****10 MV FFF****10 MV FF**