



Neanderthals' hunting seasonality inferred from combined cementochronology, mesowear, and microwear analysis: case studies from the Alpine foreland in Italy

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Received: 28 October 2021 / Accepted: 19 January 2022 / Published online: 28 February 2022
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Abstract

Herbivore teeth are a valuable source of information for inferring the hunting season of past hunter-gatherers, the spatial-temporal organization of their activities, their socio-economic organization, and their adaptation to the seasonal fluctuation of the resources. Numberless of studies have been conducted on Neanderthals across Eurasia, but only few of them rely on the application of cementochronology and tooth wear analyses combined to obtain information about the ungulate paleodiet, paleoenvironments, and the time range of the mortality events. In this study, we present the results achieved through the combination of these two high-resolution techniques applied to large and medium-sized herbivore teeth yielded by two Middle Paleolithic sites in the north-east of Italy. We combined the two methodologies with the aim to overcome any possible lack of information, due to the use of a single method. This study addressed to analyze the material coming from two caves in the Venetian region, De Nadale and San Bernardino, and to produce data supporting the interpretation of the origin of the two archaeofaunal assemblages as a result of seasonal hunting events that took place mainly in winter. In this specific geographic and environmental context, our data gain a better understanding of Neanderthal subsistence strategies and occupational patterns.

Keywords Herbivore teeth analysis · Hunting season · Settlement dynamics · Middle Paleolithic · Northern Italy

Introduction

The spatial-temporal organization of the activities within the territory of Neanderthals is a key proxy to discuss their socio-economic organization and the responses they developed to cope with the seasonal fluctuation of the resources (Conard and Prindiville 2000; Rendu 2010; Delagnes and Rendu 2011; Rosell et al. 2012; Chacón et al. 2015, among others). Depending on the region and the time considered, different mobility patterns were developed by these past human populations for the exploitation of its biotope. In this context, the Mousterian record in the Italian Alpine range and foreland could disclose insights into the adaptation of Neanderthals, their scheduling capacity, and the flexibility of their economy: by exploiting at the same time mountainous, low altitude and plain environments, these natives were induced to adapt their ecological relations through designing their seasonal mobility patterns. In this scenario, zooarchaeological data play a fundamental role in inferring the seasonality of prey procurement by hominids.

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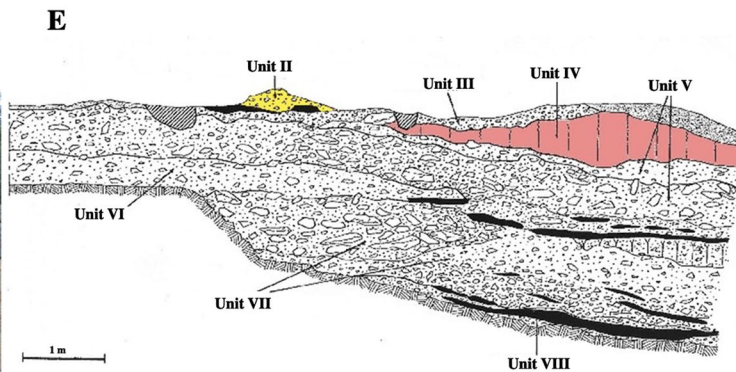
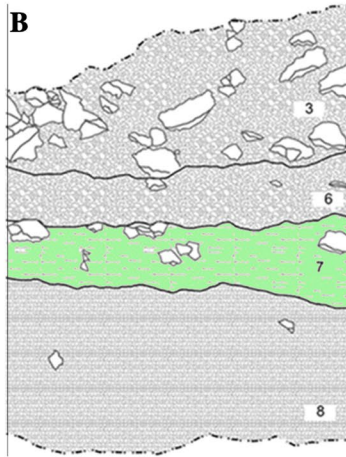
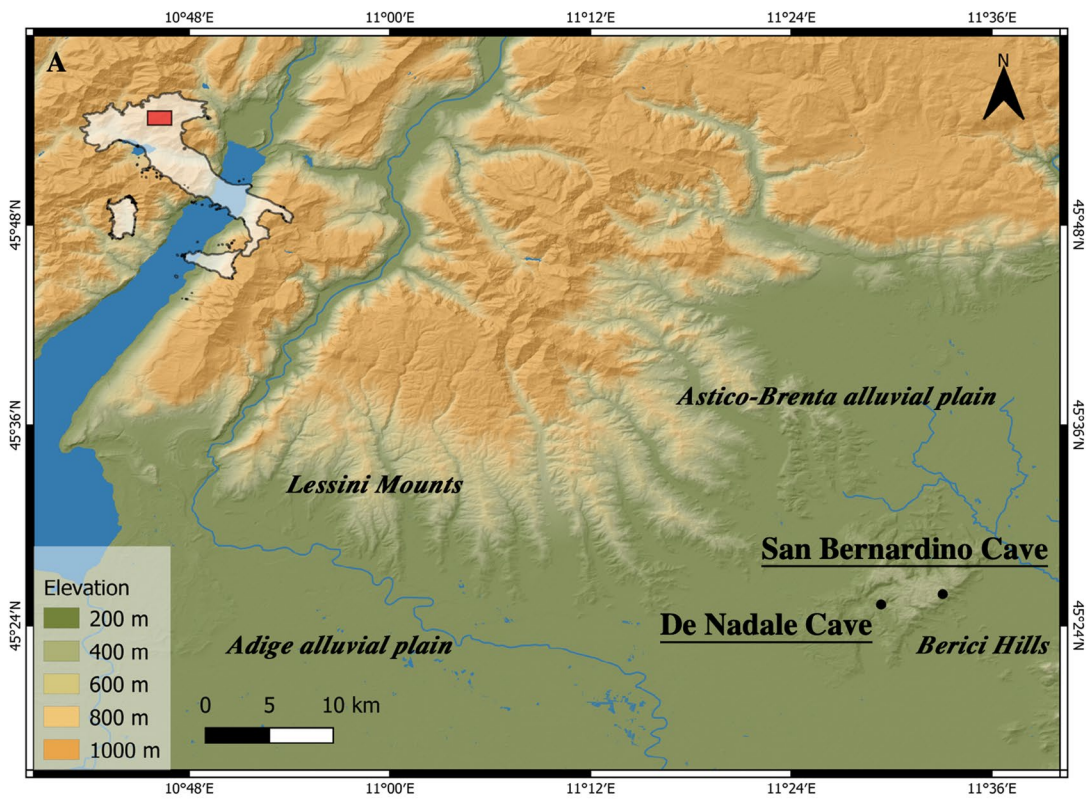


Fig. 1 **A** The geographical location of De Nadale and San Bernardino Caves in the north-east of Italy; **B** the stratigraphic sequence of De Nadale Cave (dotted lines show the roof and the bedrock of the cave; Unit 7 is colored in green); **C** the entrance of De Nadale Cave; **D** the entrance of San Bernardino Cave; **E** the stratigraphic sequence of San Bernardino Cave (Unit II is colored in yellow and Unit IV in pink)

Nowadays both seasonality and duration of occupation can be estimated through some valuable analytical methods applied to teeth, such as the analysis of carbon and oxygen stable isotopes (e.g., Feranec et al. 2009; Balasse et al. 2012; Julien et al. 2012; Blumenthal et al. 2014), the study of tooth eruption and replacement patterns (e.g. Wilson et al. 1982; Mariezkurrena 1983; Carter 1998; Bunn and Pickering 2010), the dental micro- and mesowear analyses (e.g., Rivals and Deniaux 2005; Rivals et al. 2009a, b; Rivals and Semprebon 2012; Rivals and Semprebon 2012; Sánchez-Hernández et al. 2016; Uzunidis 2020), and the cementochronology technique (e.g., Klevezal 1988; Pike-Tay 1991a,b; Lieberman 1994; Burke and Castanet 1995; Rendu 2007, 2010; Naji et al. 2015). Nevertheless, using one of these methods alone may not be always reliable, since when used independently, a certain technique may provide too low-resolution data.

In this paper, we present a twofold high-resolution approach, combining cementum increment and dental wear analyses on ungulate teeth (*Cervus elaphus*, *Megaloceros giganteus*, *Bos/Bison*, and *Capreolus capreolus*) from two Middle Paleolithic multi-layered sites, San Bernardino Cave (Grotta Maggiore di San Bernardino) and De Nadale Cave, located in the Berici Hills in north-eastern part of Italy. Our objectives are to provide a better understanding of the seasonality and the length of occupations of these sites in order to contribute to the reconstruction of mobility patterns and exploitation of the territory by Neanderthals during the late Middle Paleolithic between the Alpine fringe and foreland.

Dental wear analysis, both meso- and microwear, is easily affected by dietary changes, ruled in nature by the annual changing of seasons, but on different time scales (Grine 1986; Fortelius and Solounias 2000). Mesowear analysis records a macroscopic wear, such as the shape and the highness of the cusps of the molars, revealing the average annual diet of the last months or a whole year (Fortelius and Solounias 2000; Ackermans et al. 2018). By contrast, microwear analysis investigates microscopic features which are the recording of the diet of the last days or weeks before the death of the animal (Merceron et al. 2004; Semprebon et al. 2004; Rivals and Semprebon 2012). So, the combination of these two dental wear techniques gives access not only to the degree of attrition and abrasiveness of food in an annual cycle (mesowear), but also to any possible variations due to seasonal environmental influences (microwear) (Sánchez-Hernández et al. 2019). Moreover, microwear analysis is

also useful to assess the duration of accumulation events and, consequently, the extent of the human occupation. This approach helps to differentiate assemblages which were accumulated in a seasonal or shorter event, events longer than a season, and separated events occurring in different seasons (Rivals et al. 2015a, b, 2018).

In addition to that, the cementochronology technique, which is based on the observation of the microscopic incremental tissue of the teeth (see “Materials and methods”) enables us to estimate the age at death of each individual and the season when the animal was killed (Lieberman 1991; Pike-Tay 1991a; Gourichon 2004; Rendu 2007; Naji et al. 2015, among the others). This allows us to correlate the seasonal feeding pattern with a specific period of the annual cycle (Sánchez-Hernández et al. 2019, 2020).

The sites

The region where De Nadale and San Bernardino caves are located is dominated by three geomorphological units: the Po and the Adige alluvial plains in the south, the pre-Alps in the north, and two small sub-alpine massifs (the Berici and the Euganean Hills) in the south-east (Fig. 1). The present-day physical landscape of the Berici Hills is an ensemble of markedly different morphological zones. Above both De Nadale and San Bernardino caves, at an average elevation of 250 m, the karst plateau forms a gentle honeycomb with sinkholes and various depressions (including ponors and limestone pavements) succeeding one another, delineating an extremely uneven topography with peaks and block karst affected by surface dissolution. In De Nadale surroundings, the plateau is dissected by the Calto valley bottom, a depressed system with pocket-valleys, a swampy environment, and steep slopes all around. To the east, the Pozzolo ancient karst surface is a wide trench cutting through the plateau in a NW–SE direction at an elevation of 150 m, ending at both the SE and NW (Sauro 2002). The San Bernardino Cave opens on the Eastern slope of the Berici Hills at dominant position onto the Bacchiglione river alluvial plain, facing the southern side of the Euganean Mounts. The Berici Hills area produced an important amount of paleolithic evidence, both as open-air sites and as caves and shelters (Leonardi and Broglio 1962; Bertola and Peresani 2000; Peresani 2001a, 2015) used by Neanderthal foragers as part of a settlement system extended to the Euganean Hills, the Alpine foreland, and the southern slope of the Alps (e.g., Peresani et al. 2011, Peresani 2013).

De Nadale Cave

De Nadale cave is a small cavity at 80 m a.s.l. above the narrow Calto valley. It was first reported in 2006 and extensively

excavated since 2014. The field campaigns carried out from 2014 to 2017 and still ongoing exposed a short stratigraphic sequence composed of eight different stratigraphic units (SU), including one single anthropic layer (SU 7) embedded between Pleistocene sterile sediments (SU 6 and SU 8) (Jéquier et al. 2015). SU 7 extends on almost entirely the cavity. It yielded a cultural assemblage attributed to the Quina Mousterian (Jéquier et al. 2015; Livraghi et al. 2021) dated to $70.2 \pm 1/-0.9$ ka BP by U/Th (Jéquier et al. 2015). The anthropic layer yielded thousands of fragmented bones, charcoals, and a Neanderthal deciduous tooth (Arnaud et al. 2016). The anthracological assemblage from Unit 7 of De Nadale cave is characterized by the strong presence of spruce—larch woodland and cryophilous pine forests—and indicates the important role that montane and alpine flora played in this region during MIS 4 (Vidal-Matutano et al. 2022). The frequentation at De Nadale is framed in a landscape dominated by open woodland formations and dry meadows at the very beginning of MIS 4 (López-García et al. 2018), a period still quite unknown in the north of Italy.

Large and medium-sized ungulates—red deer (*Cervus elaphus*), giant deer (*Megaloceros giganteus*), and large bovines (*Bison priscus* and *Bos primigenius*)—dominate the faunal spectrum, both according to NISP and MNI. Smaller ungulates, such as roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), wild boar (*Sus scrofa*), and ibex (*Capra ibex*), have also been recovered although in lower quantity. Carnivore remains yielded by Unit 7 are scarce, and they have been identified mainly as belonging to cave bear (*Ursus spelaeus*) and other non-identifiable bear species, with lower percentages of wolf (*Canis lupus*), fox (*Vulpes vulpes*), and badger (*Meles meles*) (Livraghi et al. 2021).

San Bernardino Cave

The San Bernardino Cave opens at 135 m a.s.l. Several systematic archaeological excavations were carried out in the second half of the last century and focused on the atrial area: the first began in 1959, while the second stage went on from 1986 to 1994. The excavations unearthed a 4.5-m-thick stratigraphic sequence composed by eight layers spanning from the Late Middle Pleistocene to the Late Pleistocene and containing Mousterian lithic assemblages (Leonardi and Broglio 1961; Peresani 1995; Fiore et al. 2004).

Sediment composition and stratigraphy of units from VIII to I identify three main cycles (Cassoli and Tagliacozzo 1994; Peresani 2001a, b; López-García et al. 2017), dated on the basis of U/Th and electron spin resonance (ESR) and radiocarbon from MIS 7 to MIS 3 (Gruppioni 2004; Picin et al. 2014; Terlato et al. 2021): the 1st cycle is referable to the Late Middle Pleistocene and characterized by a phase of wet and temperate climatic conditions (unit VIII) with broadleaf, wooded landscapes, followed by

a phase of slightly colder oscillations (unit VII). The 2nd cycle is referable to the Late Pleistocene and characterized by temperate climatic conditions, generally forested environment with some open spaces and wetlands (unit VI). This period was followed by a colder climatic phase (units V–IV) which resulted in the formation of a steppe environment. The 3rd cycle is referable to the Late Pleistocene and characterized by a humid phase (unit III) correlated to a more wooded landscape. In particular, unit II shows an increasing in anthropogenic remains.

So far, zooarchaeological studies have been carried out in detail only on unit II. The faunal record is dominated by ungulates, among which the roe deer (*Capreolus capreolus*) is the most common species, followed by the red deer (*Cervus elaphus*) in a lower quantity. The wild boar (*Sus scrofa*), the elk (*Alces alces*), the chamois (*Rupicapra rupicapra*), and large bovines are present but scarce. The evidence of giant deer (*Megaloceros giganteus*), ibex (*Capra ibex*), and rhinoceros (*Stephanorhinus* sp.) (Romandini et al. 2018; Terlato et al. 2019; 2021) is rare. This trend seems to be common also in other units, where preliminary studies pointed out the predominance of red and roe deer over chamois and ibex, with a stable presence of few bovines, giant deer, wild boar, and elk (Cassoli and Tagliacozzo 1994; Fiore et al. 2004).

Materials and methods

The sample analyzed in this study is composed of 74 teeth, sorted among the whole faunal material yielded by the two deposits during the excavations. The material was studied at taxonomical and taphonomical levels in previous works (Cassoli and Tagliacozzo 1991; Livraghi et al. 2021; Terlato et al. 2019, 2021) and stored at the Department of Humanities of the University of Ferrara, Italy.

Among the 74 specimens, 23 out of 25 gave interpretable results when studied with the cementochronology technique and 36 out of 59 with the dental wear analyses. Despite the general good macroscopic appearance, two teeth out of the 25 specimens selected for the cementochronology were discarded. They were affected by a microbiological attack which caused extensive demineralization of the hydroxyapatite, followed by collagen lysis and, subsequently, the complete loss of the structure of the cementum itself (Geusa et al. 1999). Among the 59 teeth selected for dental wear analyses, 23 teeth were discarded since they did not present the optimal features for the study. To allow a good evaluation, we selected only the molars and the fourth premolars, and we discarded young and senile individuals—to avoid any bias due to their unworn or, on the contrary, heavily blunt surface. Moreover, some of these 23 discarded teeth had a badly preserved enamel that did not allow any observation.

Both techniques have been performed on ten specimens, but only four gave positive results with both.

The San Bernardino Cave sample is composed of 47 specimens (Table 1) coming from units II (NR: 38), IV (NR: 8), and VI (NR: 1), mostly belonging to roe deer, the most common taxon, followed by red deer, elk, giant deer, and bovids. Dental wear analysis has been carried out on 39 teeth and cementochronology on 12; among them, four remains were suitable for a directly combined study obtained applying the two techniques.

The De Nadale Cave sample is composed of 27 (Table 1) teeth coming from Unit 7 (NR: 19) and 13 (NR: 8) identified as belonging to giant deer, red deer, and roe deer. No bovid teeth were found. We carried out dental wear analysis on 20 specimens, while cementochronology was applied on 13 remains; among them, six teeth were suitable for a directly combined study obtained applying both techniques. We were not able to sample four large-sized ungulate teeth since they have been chosen for new U/Th dating, and they are currently under study.

Cementochronology

As pointed out by several biological studies, in the teeth of most temperate, sub-arctic, and arctic mammal species, the cementum surrounding the roots grows regularly, according to a predictable seasonal rhythm and starting from the complete eruption of the tooth until the death of the animal (Klevezal and Kleinenberg 1969; Gordon 1984; Klevezal 1988; Pike-Tay 1991a, b; Lieberman and Meadow 1992). This incremental tissue appears, under transmitted cross-polarized light, as a stratified deposit: somewhat regular bands are organized in pairs which correlate with a year timespan. Every couple of layers is namely the result of the annual deposition of cementum and consists of a thicker and translucent band (TB, accretion line, or growth layer), which is formed during periods of more substantial and fast tissue growth (i.e., from spring to autumn) and a thinner and opaque band (OB, the “line of arrested growth”—LAG—or *annulus*), which deposits during periods of reduced tissue growth, such as winter (Pike-Tay 1991a, b, 1995; Lieberman 1994). Therefore, the age at

death of the animal was deduced adding the number of pairs of layers to the time of tooth eruption, while the season of death was pointed out by the nature of the band observed.

This regularity in cementum growth has been observed both in cellular and acellular cementum, but only the latter seems to be reliable and suitable for this kind of approach since its deposition is more regular and rarely biased by mechanical and/or biological stress (Pike-Tay 1991a, b; Lieberman and Meadow 1992; Lieberman 1993a, 1994; Stutz 2002a; Gourichon 2004; Rendu 2007).

Among the 74 teeth we sampled, 25 (i.e., 12 specimens from San Bernardino Cave and 13 from De Nadale Cave) were analyzed with the cementochronology approach, following the well-established protocol for the archaeological application of this method (Saxon and Higham 1968; Spiess 1976; Gordon 1988; Pike-Tay 1991a, b; Lieberman and Meadow 1992; Lieberman 1993a, b, 1994; Burke and Castanet 1995; Rendu and Armand 2009; among others).

Following the literature (Lieberman and Meadow 1992; Gourichon 2004; Rendu 2007; Naji et al. 2015), we sampled as many teeth as possible, coming from different individuals, still encased in the alveolar bone or, in case of loose teeth, not showing any post-mortem damage on the roots, any presence of manganese stains, weathering cracks, or concretions. In some cases, and it will be specified, we chose more than one tooth per individual, to validate the results and to avoid any uncertainty in the observations.

We analyzed the upper half of the root, in correspondence of the cervix of the tooth, where the cementum is clearly readable. The sample was processed following the techniques for ground thin sections applied in archaeology contexts (Rendu 2007; Naji et al. 2015; Gourichon and Parmegiani 2016):

- Extraction (if necessary) of the tooth from the alveolar bone.
- Cleaning of the specimen with ethyl alcohol.
- Embedding of the roots of the tooth in translucent epoxy resin. The specimen is located vertically in a plastic mold, filled with epoxy resin, and put into a vacuum pump for 12–24 h, in order to remove bubbles and let

Table 1 Taxa and number of specimens selected for this study and their stratigraphic provenance

Taxa	De Nadale Cave (CN)			San Bernardino Cave (SB)			
	7	13	tot	II	IV	VI	tot
<i>Alces alces</i>				3			3
<i>Megaloceros giganteus</i>	6	5	11	2			2
<i>Cervus elaphus</i>	8	3	11	15	5		20
<i>Capreolus capreolus</i>	5		5	15	2	1	18
Bovinae				3	1		4
Total	19	8	27	38	8	1	47

the resin completely permeate the tooth tissue. There, the polymerization process begins.

- Cutting of the block of resin containing the tooth, using a slow-speed diamond saw. Sections are made both transversally and longitudinally, after the removal, when possible, of the tooth crown to preserve it for further analyses. To avoid optical superimposition of the cementum layers within the section, the transverse cuts are made orthogonally, and the longitudinal cuts are made as much parallel as possible to the major axis.
- Gluing the obtained slice (0.5–1 mm) on glass-slide with epoxy glue. The slice is heated and pressed for 8 h so that it can adhere perfectly to the glass.
- Abrading of the upper face of the slice until it reaches the thickness of 30–50 μm . The obtained thin section is also polished with the diamond powder to erase scratches that can hinder the observation under the microscope.

We examined the thin sections with a transmitted light polarizing microscope (Leica DM2500P) at $\times 10$, $\times 20$, $\times 40$, and $\times 50$ magnifications, in order to recognize the best regions of interest for the observation. We counted the incremental bands, and we identified the last deposits through optical images by using three distinct light filters: plane-polarized light, cross-polarized light, and full-wave retardation plate (λ plate). The use of the λ plate allowed us to identify the eventual presence of microbiological alterations (fungi or bacteria), diagenetic alterations of the cementum (recrystallization, false increments, collagen leaching), or the effect of weathering (Stutz 2002b; Rendu et al. 2009). The whole process was carried out at PACEA laboratories of the University of Bordeaux.

The results of the observations and the pictures taken with a high-resolution camera connected to the microscope were digitally reworked and enhanced with the support of the software Image J, following the standard protocol (Lieberman et al. 1990). This allowed us to achieve a more accurate estimation when the last cementum accretion was a growth layer, avoiding potential subjective mistakes due to the competence and the experience of the observer (Lubinski and O'Brien 2001). By comparing the mean thickness of the proceeding and fully formed bands, the “good season” to which the growth layer corresponds can be divided into three sub-periods: the beginning (up to one-third of the mean thickness, 1–33.3%), the middle (from one- to two-thirds, 33.4–66.6%), and the end (more than two-thirds, 66.7–100%) (Gourichon 2004; Rendu 2007; Sánchez-Hernández et al. 2020).

Tooth mesowear

We carried out the mesowear technique through evaluating the relief and the degree of sharpness of the molars'

cusps, by observing the buccal side of the upper molars and lingual side of the lower molars, with the naked eye. The sharpness and the morphology of the cusps point out different degrees of attritive or abrasive dental wear, which are the result of different kinds of diets, registered within the animal's lifespan (Ackermans et al. 2020). In general, by applying this method, herbivores can be grouped in three main feeding categories:

- Browsers: feeding on leaves from shrubs and trees. The molars present high relief and sharp apices, due to the low degree of abrasion and the high degree of attrition.
- Grazers: feeding on grass. The molars present low relief and blunt apices, due to the high degree of abrasion and the low degree of attrition.
- Mixed feeders: the molars present intermediate values of abrasion and attrition, with a variable morphology of the tooth outline, according with the feeding preference of an individual.

Tooth mesowear analysis was applied to 19 specimens, 9 of which from De Nadale Cave and 10 from San Bernardino Cave.

Following Fortelius and Solounias (2000) and Mihalbachler et al. (2011), each tooth was scored with a 0 to 6 value, where stage 0 corresponds with a high and sharp cusps type and stage 6 to a completely blunt with no relief profile molar. The averaged value of the mesowear measurements taken on teeth from an assemblage corresponds to the mesowear score (MWS). To avoid biased results, this technique was applied to non-fractured teeth, in which the crown and the occlusal surface do not show any damage or taphonomical alterations (Fortelius and Solounias 2000; Kaiser and Fortelius 2003). Teeth that do not present significant wear as well as those that are heavily worn, depending on the age of the individual, were not suitable for the evaluation and were discarded (Rivals and Semprebon 2006; Rivals et al. 2007).

Tooth microwear

The microwear technique describes and analyzes a pattern of microscopic features readable on the occlusal surface enamel, which provides information about the diet of an individual at the time of its death (Grine 1986; Solounias and Semprebon 2002; Semprebon et al. 2004). These marks are indeed left by the abrasive particles present in food, which may leave scratches and pits during the masticatory process, with a rapid overprint of these marks within each food intake (Grine 1986).

We prepared and described the sample to be analyzed following the well-established protocol (Solounias and Semprebon 2002; Semprebon et al. 2004; Rivals and Semprebon

2011, 2012; Rivals et al. 2007, 2009a, b, c a, b, Rivals et al. 2015a, b, Rivals et al. 2018; Sánchez-Hernández et al. 2019, 2020, among the others). The occlusal surface of each specimen was cleaned with acetone and then 96% ethanol, and once dry, it is molded with vinylpolysiloxane, a high-resolution dental silicone. The molds obtained were filled with transparent epoxy resin, in order to create highly detailed casts. Every cast was carefully screened under the transmitted light of the stereomicroscope (a Zeiss Stemi 2000C) at $\times 35$ magnification with an ocular reticle delimitating a 0.16 mm^2 square area. The microscopic features of the enamel were easily observed and quantified, thanks to the refractive properties of the clear epoxy cast. These microfeatures were classified into three categories: pits (circular or sub-circular scars), scratches (elongated scars with a straight direction), and gouges (larger and deeper pits with irregular outline). We quantified the micro-features on the enamel of the paracone of the upper molars and the protoconid of the lower molars. We sampled two different areas on each specimen, in order to average the microwear features per tooth. The results were compared with a database containing information on extant and wild ungulate taxa (Solounias and Semprebon 2002). The number of scratches (from now on, Nscr) and the number of pits (Npit) are strongly linked to the dietary habit of the ungulates. In modern populations, browsers show a wear pattern with a low Nscr, while grazers display a high Nscr. As predictable, mixed feeders are characterized by the overlap of the two other patterns, since they switch seasonally (and/or regionally), between diets based either on browse or on grass. To better discriminate mixed feeders from browsers or grazers, we applied the well-established method developed by Semprebon and Rivals (2007) which gave significant results when applied both to extant and to fossil samples (e.g., Rivals et al. 2018; Sánchez-Hernández et al. 2019). Thus, we calculated the percentage of individuals in a population with scratch numbers that fall between 0 and 17 scratches in the 0.16 mm^2 area (i.e., the LSR, low scratch range): the browsers have LSR values that fall between 0 and 22.2%, browsers show values comprised in the range of 72.73–100%, and the mixed feeders overlap partially with the other two categories, being comprised between 20.93 and 70% (Solounias and Semprebon 2002; Semprebon and Rivals 2007; Rivals and Semprebon 2010). Qualitative features were evaluated too: the scratch width score (SWS) defines the thickness of the scratches using a scoring system from 0 to 4 (from “fine” to “mixed coarse/hyper-coarse”). This scale varies according to the abrasive properties of food consumed by the individual. Moreover, the frequency of cross scratches (%XS) refers to the presence of scratches with different directions relative to the main orientation.

Beside this, microwear analysis gives information about the relative duration of the occupation through the estimation

of the duration of the mortality event(s) of the ungulates (Rivals et al. 2009b, 2015b). Following Rivals et al. (2015b), we calculated the coefficient of variation (CV) and the standard deviation (SD) of a species' scratch variability, and we plotted the values into a heat map which was divided in three areas, corresponding to different durations of event(s): (A) a season-long (or shorter) period, (B) a timespan longer than a season; and (C) at least two separated events that occurred in different non-contiguous seasons (Rivals et al. 2015b). Taxa with a minimum of four individuals suitable for the analysis were selected to get a picture of each population's variability. As some of the samples used here are too small to detect the true CV and SD values of the larger population that they represent, we applied a joint bootstrapped function of CV and SD ($n = 500$, with replacement) using the R code by Domínguez-Rodrigo et al. (2019).

Results

Cementochronology

De Nadale Cave When analyzed with the cementochronology method, 12 (92.3%) of the 13 teeth we selected gave positive results (Table 2), presenting at least one suitable region of interest to perform the observation. Fungi or bacterial alteration and recrystallization are present, affecting especially the dentine, but they do not bias the analysis of the cementum. The sole exception consists of a giant deer's molar (CN661), which does not show any presence of cementum, probably due to the heavy microbiological alteration that affected the dentine and lead to the collapse of the structure of the layers.

The cementum bands are clearly readable and measurable, and the dental tissue is generally well preserved. This made possible the digital enhancement to be performed on each specimen, except for a red deer incisor (CN929): in this case, it was not possible to recognize the end of the last band (LCB), making the measurement not reliable.

Among the three taxa sampled, the results are homogeneous for *Cervus elaphus* and *Capreolus capreolus*, but they show a certain degree of intraspecific variability for *Megaloceros giganteus*. Namely, the only sampled tooth of roe deer presents an opaque band (OB) as LCB; the same was observed for all the specimen of red deer, except for two teeth, presenting a very thin translucent band (TB) in one case and a complete TB on the other case.

Giant deer shows some significant discrepancies from the pattern of the two taxa mentioned: in two cases, the LCB is an opaque band (bad season), two other cases are halfway through the translucent band development, and one

Table 2 Summary of cementum data obtained at the De Nadale Cave. Abbreviations: *Ref.* reference number assigned by the authors, *N° CB* number of pairs of bands observed in the acellular cementum, *LCB* last cementum band observed, *%* % growth ratio of the last cementum increment, *Season of death* season of the individual death, *OB* dark and high mineralized (opaque) cementum band, *TB* clear and low mineralized (translucid) cementum band, *UM* non-identified upper molar, *L/R* left or right

Taxa	Level	Ref	Tooth	N° CB	LCB	%	Season of death	
<i>Megaloceros giganteus</i>	7	CN181	I ₂ R	3 (+TB)	TB	71.98	End of good season	
		CN2146	P ⁴ L	4 (+TB)	TB	51.68	Middle good season	
		CN41	UM	4	OB	OB		Bad season
		CN661	M ₃ R	–	–	–		No data
		CN3198	M ₃ L	5	OB	OB		Bad season
		CN3138	M ₃ L	2 (+TB)	TB	47.38		Middle good season
<i>Cervus elaphus</i>	7	CN1446	UM	4	OB	OB	Bad season	
		CN321	M ¹ R	3	OB	OB	Bad season	
		CN929	I ₂ L	3 (+TB)	TB	– *		End of the good season
		CN1027	I ₄ R	2	OB	OB		Bad season
		CN2400	I ₂ L	3 (+TB)	TB	32.91		Early good season
		CN2401	I ₂ L	5	OB	OB		Bad season
<i>Capreolus capreolus</i>	7	CN2145	M ₁ R	3	OB	OB	Bad season	

*Digital enhancement was not possible due to bad preservation of the cementum

tooth shows a nearly complete translucid band, which corresponds to the end of the good season.

San Bernardino Cave Cementochronology gave positive results from 11 (91.6%) out of 12 teeth (Table 3). The structure of the cementum is visible and reliable in most of the sample, even though the dentine often presents microbiological and diagenetic alterations. Only one specimen, a roe deer lower third molar, gave no readable data, due to the recrystallization of the cementum itself.

For unit VI, only one tooth was suitable for the analysis, a *C. capreolus* lower third molar, which clearly shows an opaque band as LCB.

For unit IV, the sample consist of only one *C. elaphus* tooth, with clear cementum stratification, including the LCB which was recognized as a very thin opaque band, corresponding to the beginning of the bad season.

The largest sample came from unit II, and it is composed of one lower molar of *M. giganteus*, one premolar from a Bovidae, four teeth from *C. capreolus*, and four from *C. elaphus*. Both the giant deer’s and the bovine’s specimens show a very thin opaque band as LCB, which points out a bad season mortality. The data for *C. capreolus* are quite homogeneous, too: three teeth show a last opaque band (bad season), while one specimen ends with a halfway grown translucid band (middle of the good season).

The red deer, instead, shows a slightly higher intraspecific variability: two teeth show a very thin translucid band

Table 3 Summary of cementum data obtained at the San Bernardino Cave. Abbreviations: *Ref.* reference number assigned by the authors, *N° CB* number of pairs of bands observed in the acellular cementum, *LCB* last cementum band observed, *%* percentage of growth ratio of

the last cementum increment, *Season of death* season of the individual death, *OB* dark and high mineralized (opaque) cementum band, *TB* clear and low mineralized (translucid) cementum band, *LM* non-identified lower molar, *L/R* left or right

Taxa	Level	Ref	Tooth	N° CB	LCB	%	Season of death	
<i>Megaloceros giganteus</i>	II	SB914	LM	5	Thin OB/complete TB	OB	End of good season/beginning of bad season	
<i>Cervus elaphus</i>	IV (6d)	SB1055	I ₄ L	4	Thin OB	OB	Beginning of bad season	
		II	SB1	M ² L	2 (+TB)	TB	– *	Beginning of good season
	VI (24a)	SB3	LM	2 (+TB)	TB	– *	End of good season	
		SB991	I ₂ R	1 (+TB)	TB	55.50	Middle of the good season	
		SB1011	P ₄ L	4 (+TB)	TB	9.35	Beginning of good season	
<i>Capreolus capreolus</i>	VI (24a)	SB121	M ₃ R	5	OB	OB	Bad season	
		II	SB117	M ₁ , M ₂ R	4 (+TB)	TB	59.75	Middle of good season
		SB640	M ₃ L	–	–	–		No data
		SB1182	P ² L	4	OB	OB		Bad season
		SB1186	P ₂ L	4	OB	OB		Bad season
Bovinae	II	SB911	P ² R	7	Thin OB/complete TB	OB	End of good season/beginning of bad season	

*Digital enhancement was not possible due to bad preservation of the cementum

(very beginning of the good season), one ends with an almost fully grown TB, and one ends with half of a full TB (Fig. 2).

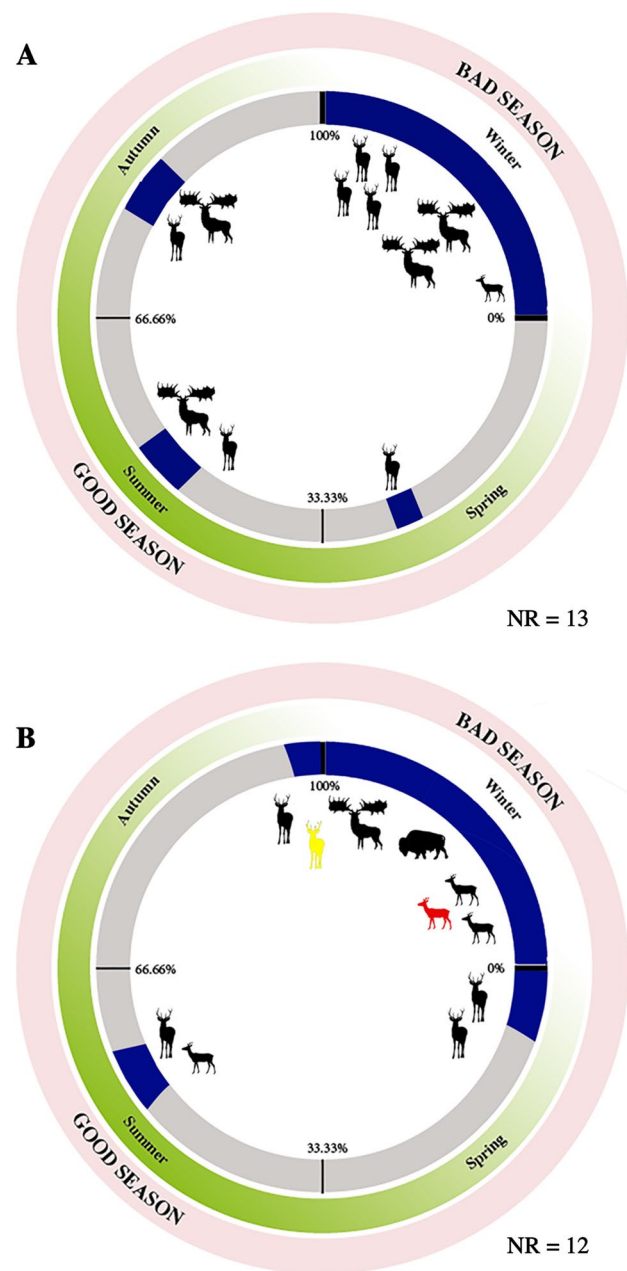


Fig. 2 **A** Schematic representation of hunting events for *Megaloceros giganteus*, *Cervus elaphus*, and *Capreolus capreolus* at De Nadale Cave. **B** Schematic representation of hunting events for *Megaloceros giganteus*, *Cervus elaphus*, *Capreolus capreolus*, and bovids at San Bernardino Cave. (black, sample from Unit II; yellow, sample from Unit IV; red, sample from Unit VI). Percentages correspond to the degree of development of the last translucent cementum band (TB)

Meso- and microwear analyses

De Nadale Cave Unit 7 yielded very few specimens suitable for the mesowear analysis: among the totality of the teeth sampled from the site, only 9 of them (Table 4) gave positive results, since the cusps were not always well preserved, fractured, or biased by post-depositional events.

The three taxa analyzed show a quite homogeneous trend, with mesowear scores (MWS) ranging from 0.75 for *C. capreolus* ($N=4$) to 2 for *M. giganteus* ($N=2$). *C. elaphus* ($N=3$) has a MWS of 1, falling between the two above-mentioned species. Accordingly, data suggest that the roe deer and the red deer have a browser diet, while giant deer tends toward a browse-dominated mixed feeder diet. Nevertheless, the number of specimens that allowed us to apply the methodology is too modest to give a meaningful interpretation of the data.

Microwear analysis was applied to a broader sample: 16 teeth, out of the 20 specimens sampled from De Nadale Cave, gave positive results when observed under the microscope.

The average numbers of pits (Npit) and scratches (Nscr) are very close for all the three species considered, and, when plotted, they fall within the limits of the confidence ellipse for modern browsers (Fig. 3A). This result is consistent with the microwear score (LSR) that indicates pure browser values since no individual presents a Nscr higher than 17. From a qualitative point of view, the three taxa have high rates of individuals showing large pits (LP) and significant percentages of gouges, which are features of a browse dietary preference with the possibility of fruit and seed consumption. No giant deer or roe deer individuals show cross scratches (XS), which are present only on a low percentage of red deer specimens. The scratch width score (SWS) observed shows a predominance of fine and mixed fine-coarse scratches, related to the high level of attrition typical of the browse diet and consistent with all the above-mentioned data.

When plotted into the heat map (Fig. 3B), data available give significant results for all the taxa sampled: all the three populations have low standard deviations (SD) and low coefficient of variation (CV) of the numbers of scratches (Table 4). They plot in area [A] of the heatmap, indicating a short duration of the accumulation event(s).

San Bernardino Cave Only a few specimens (Table 4) from Unit II of San Bernardino Cave were suitable for the mesowear analyses, mainly because of the not optimal state of preservation that characterizes the archaeological material. The most common damage that affected the sample was the presence of several broken tips that could bias the evaluation of the MWS and that were discarded. Nevertheless, the trend is homogeneous for the three species taken into account, with a MWS ranging from 0.40 of *C. capreolus* ($N=5$), to

Table 4 Summary of meso- and microwear data for the De Nadale Cave and from San Bernardino Cave. Abbreviations: *N* number of specimens, *MWS* mesowear score, *LSR* microwear score, *Nscr* average number of scratches, *CV* corrected coefficient of variation, *SD* standard deviation, *Np* average number of pits, *%LP* percentage of individuals with large pits, *%G* percentage with gouges, *%XS* percentage with cross scratches, *SWS* scratch width score

Site	Taxa	Labels	Level	Mesowear		Microwear										
				N	MWS	N	Np	SD	CV	Nscr	SD	CV	%LP	%G	%XS	SWS
De Nadale Cave	<i>Megaloceros giganteus</i>	Mg	7	2	2.0	6	6.75	2.16	0.31	10.25	0.36	0.13	66.67	50	0	1.5
	<i>Cervus elaphus</i>	Ce	7	3	1.0	5	4.9	1.60	0.33	10.4	2.01	0.20	100	60	40	1.2
	<i>Capreolus capreolus</i>	Cc	7	4	0.75	5	4.5	1.41	0.31	7.0	2.09	0.20	80	100	0	1.2
S. Bernardino Cave	Bovinae	BB_IV	IV			1	4.5			9.5			100	0	0	0
	<i>Cervus elaphus</i>	Ce_IV	IV			2	9.75	3.18	0.33	6.5	0.71	0.11	50	50	0	0.5
	<i>Capreolus capreolus</i>	Cc_IV	IV			1	5.0			9.0			0	0	0	2
	<i>Alces alces</i>	Aa_II	II	1	2.0	3	4.5	0.50	0.11	8.0	0.87	0.11	66.67	33.33	0	1
	<i>Cervus elaphus</i>	Ce_II	II	4	1.25	7	5.86	1.41	0.24	8.86	1.49	0.17	71.42	42.85	14.28	1.34
	<i>Capreolus capreolus</i>	Cc_II	II	5	0.4	6	6.5	2.37	0.36	8.5	1.79	0.21	16.67	16.67	0	1.17

1.25 of *C. elaphus* (*N*=4), to 2 of *A. alces* (*N*=1). Once again, data show that the roe deer and the red deer have a pure browser diet, while elk tends toward a browse-dominated mixed feeder diet; however, for the latter, the sample size is too small to get a definite interpretation.

The number of specimens sampled for microwear analysis, however, is more consistent, with a total of 20 teeth out of 39 that gave positive results. Most of them were yielded by Unit II (*N*=16), while only 4 teeth came from Unit IV, which was less rich in archaeological evidence than Unit II.

The material sampled from Unit IV, which belongs to red deer (*N*=2), roe deer (*N*=1), and bovids (*N*=1), is characterized by a low number of scratches (*Nscr* from 6.5 to 9.5 per counting unit) and a low number of pits (*Npit* from 4.5 to 9.75 per counting unit). Large pits are present on the bovid and on the *C. elaphus* specimens but completely absent on the *C. capreolus* molar. In the three taxa, gouges and cross scratches are absent, except for one of the red deer's molars examined which presents some gouges. The SWS indicates a mix of fine and coarse scratches in the sample. The bivariate distribution of the numbers of scratches and pits, as well as the LSR, classifies the three taxa among the pure browsers (Fig. 4A).

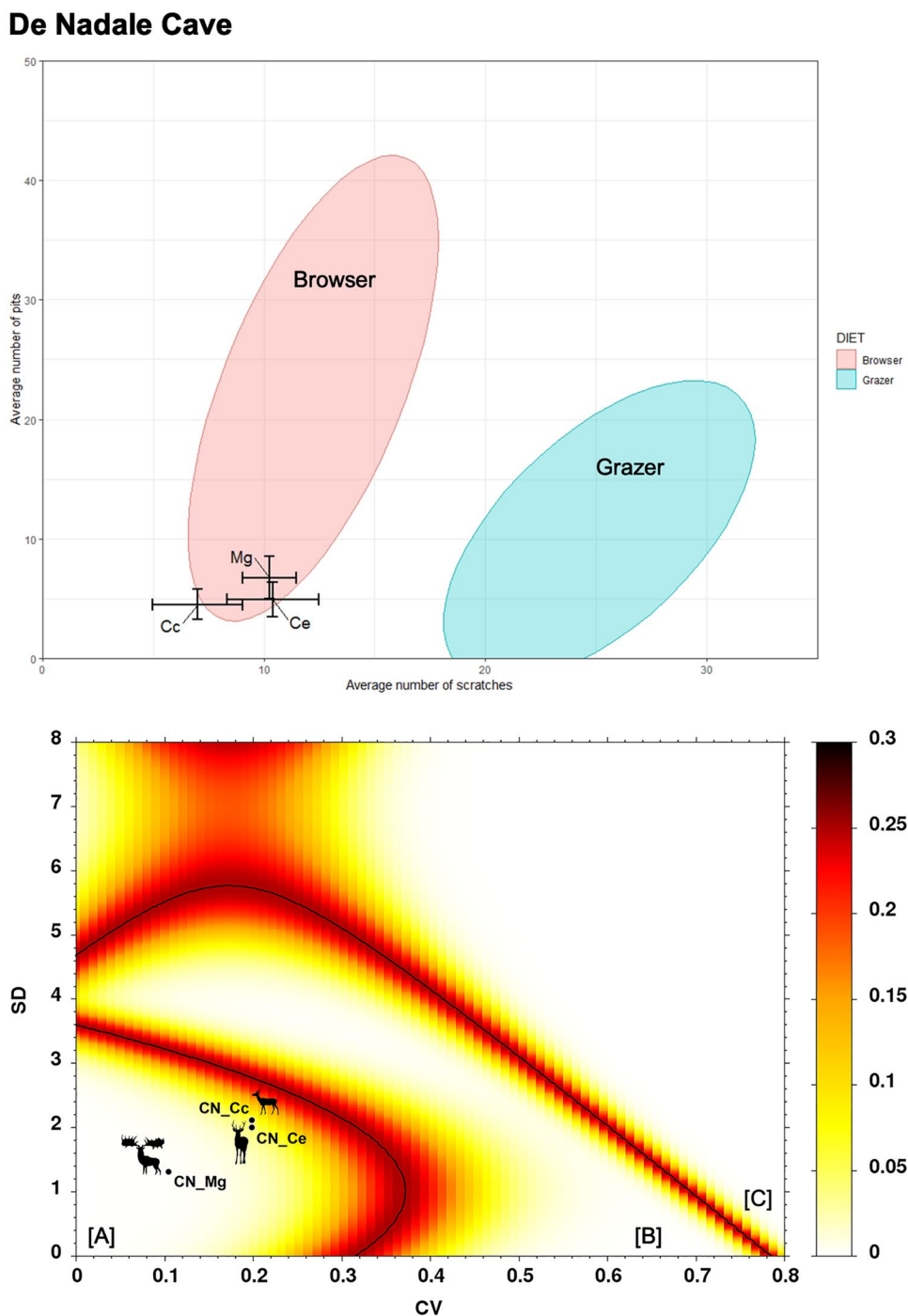
The evidence yielded by Unit II is more robust: 5 teeth from *C. capreolus*, 4 from *C. elaphus*, and one from *A. alces* show a *Nscr* ranging from 8 to 8.86 and a *Npit* from 4.5 to 6.5. Large pits are frequent on elk and red deer teeth. The range of specimens showing gouges is significant for, again, elk and red deer. Large pits and gouges are present on roe deer molars as well, but the values are significantly lower. Cross scratches were observed only on few red deer's specimens. The SWS points out the presence of a mixture of fine and coarse scratches on the surface of the teeth, related to the high level of attrition of the browse diet. The bivariate plot shows that the three species fall within the limits of the confidence ellipse for modern browsers (Fig. 4A).

When plotted into the heat map (Fig. 4B), data available for Unit IV gave positive results only for *Cervus elaphus*, despite the smallness of the sample. The microwear values (Table 4) show a low intraspecific variability and lie within zone [A]. The same scenario emerged for Unit II: all the three species taken into account—*Alces alces*, *Cervus elaphus*, and *Capreolus capreolus*—fall within the boundary of zone [A], attesting a low intraspecific variability.

Discussion

According to cementochronology and meso- and microwear analyses on the teeth of the most abundant taxa at De Nadale and San Bernardino Caves, we estimated the extent and the seasonality of mortality event(s) for each population.

Fig. 3 Above: bivariate plot of the average number of pits and scratches in the selected taxa from De Nadale Cave: *Megaloceros giganteus* (Mg); *Cervus elaphus* (Ce), *Capreolus capreolus* (Cc). Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ($p=0.95$) on the centroid for the extant leaf browsers and grazers from Solounias and Semprebon (2002). Below: boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C)



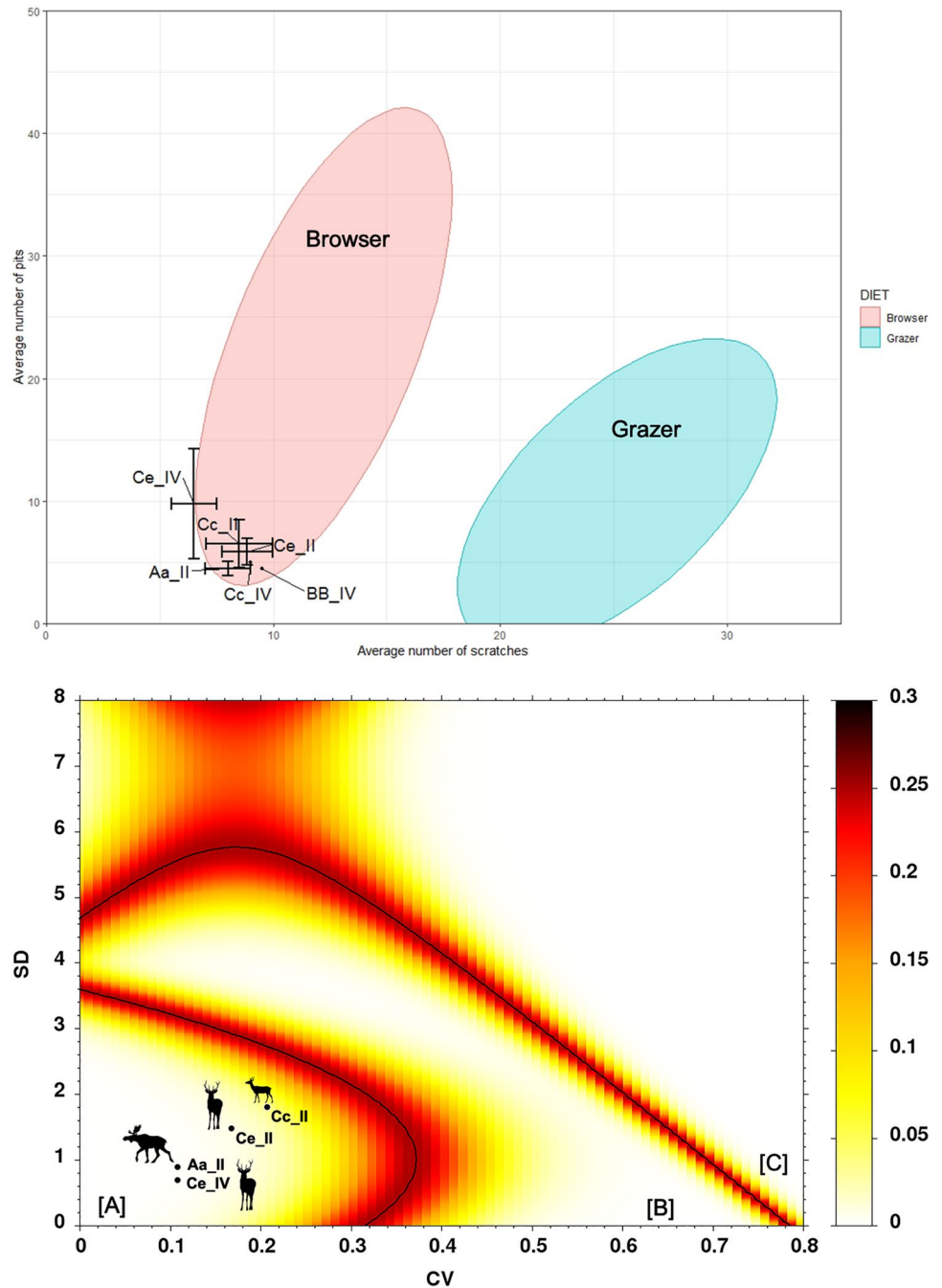
Consequently, knowing that the two deposits have an anthropogenic origin (Cassoli and Tagliacozzo 1994; Peresani 2001a, b; Jéquier et al. 2015; Livraghi et al. 2021; Terlato et al. 2021), we inferred the duration and the seasonality of the occupation of the Neanderthal groups that exploited them.

The three taxa dominating Unit 7 of De Nadale Cave—*C. elaphus*, *M. giganteus*, and *C. capreolus*—show a homogeneous dietary pattern characterized by the high

consumption of attritive resources (mainly leaves and shrubs). This low variability, which is highlighted both by the MWS and by the LRS, places them within the limits of the confidence ellipse of the extant browsers (Fig. 3A) and seems to indicate that the three cervid species fed on similar vegetation. Due to competition for the same ecological niche, they probably partitioned the resources occupying different habitats with similar vegetation.

Fig. 4 Above: bivariate plot of the average number of pits and scratches in the selected taxa from San Bernardino Cave: *Alces alces* (Aa); *Cervus elaphus* (Ce), *Capreolus capreolus* (Cc), and bovids (BB). Roman numbers next to the abbreviations of the taxa indicate the unit of provenance (II, Unit II; IV, Unit IV). Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ($p=0.95$) on the centroid for the extant leaf browsers and grazers from Solounias and Sempredon (2002). Below: boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C)

San Bernardino Cave



The presence of red deer and roe deer relates to a landscape with a predominance of woodlands over open spaces under relatively cold-temperate climatic conditions and in proximity of a humid area. This view is not in conflict with the massive presence of giant deer (Chritz et al. 2009), and it is consistent with data inferred from the study on micromammals (López-García et al. 2018).

The low standard deviation and coefficient of variation, falling into zone [A] of the heatmap, indicate that the

accumulation event(s) lasted for a limited period in a timespan of a year, less than or equal to a season (Fig. 3B).

Moreover, the cementochronology data confirm the presence of more than a single occupation: thin sections indicate that most of the game animals were killed during the bad season, namely winter (at least four red deer, two giant deer, and one roe deer), but other minor hunting events occurred in the middle and at the end of the good season (Fig. 2A). No pattern of seasonal prey selection can be recognized,

since the three taxa were exploited homogeneously during each short occupational event (i.e., red deer, giant deer, and roe deer were hunted during winter and the good season as well).

Combining the results coming from the two methodologies, thus, De Nadale Cave takes the form of a short-term occupational site, with multiple accumulation events that took place mostly during winter and some minor events during the good season. Results are consistent with the presence of 38 bone fragments of large-sized ungulates which were recognized as infants (0–5 months) or early juvenile, not older than 1 year, that were probably part of the herds exploited by the human groups (Livraghi et al. 2021).

A similar situation can be depicted for the teeth sampled from Unit II at San Bernardino Cave: the three cervid taxa—*A. alces*, *C. elaphus*, and *C. capreolus*—have the same patterns of dietary traits, specific of the pure browsers (Table 4, Fig. 4A). This result fits well with the palaeoecological reconstruction that underlines the presence of generally temperate conditions in a forested landscape, interspersed by wetlands and humid areas (Cassoli and Tagliacozzo 1994; Peresani 2001a, b; López-García et al. 2017; Terlato et al. 2021). Also in this case, the low SD and CV point out one or more short mortality events, plotting in zone [A] of the heatmap (Fig. 4B).

Cementochronology results indicate the presence of a major mortality event during the bad season and a very small one, represented by an individual of red deer and an individual of roe deer, in the middle of the good season. Two other teeth slightly deviate from the standard results, but they can be placed at the very end of the bad season (Fig. 2B). There is no evidence of a preferential or seasonal exploitation of a single species rather than the others.

For Unit IV, data are too exiguous to be reliable: only one incisor of a red deer was suitable to be cut for the cementochronology, while tooth wear analyses were applied to four teeth, one recognized as Bovidae, one as roe deer, and two as red deer. The small sample is aligned with the results from Unit II, plotting into the limits of the extant browsers, but only the two molars from red deer were suitable for the evaluation of the extent of the occupation, falling into zone [A].

Interpreted as a whole, all the data point out a high mobility pattern of the human groups that inhabited the region. This scenario fits well with other studies based on dental wear analyses on Middle Paleolithic materials from Western European sites. They suggest similar conclusions related to high and diversified mobility of the human groups in relation to seasons and environmental context. For example, similar evidence is reported in France at Payre, level F (MIS 8–7) interpreted as a short-term occupation associated with other activities (Rivals et al. 2009c; Moncel and Rivals 2011), and at the specialized reindeer hunting camp of Les Pradelles (MIS 4–3) (Costamagno et al. 2006), in Belgium at Scladina

Cave (Moncel et al. 1998; Patou-Mathis and Bocherens 1998), and in Germany at Salzgitter Lebenstedt (MIS 5–3), where the accumulation of reindeer remains corresponds to seasonal (or shorter) events (Gaudzinski and Roebroeks 2000).

Unlike the data given by De Nadale and San Bernardino Caves, some studies underline a different scenario: at Portel-Ouest (France), the samples, corresponding to four taxa from the same level, fall in two distinct areas of the heatmap. The accumulation of reindeer, red deer, and large bovids is linked to seasonal or shorter events, while the horse corresponds to a longer event. This prey procurement pattern can be easily related to known human hunting strategies for different prey at different moments of the year (Rivals et al. 2015b).

Moreover, another different occupational pattern for Neanderthal groups was recognized at Taubach (Germany), where the remains of bison show a long-term event of accumulation (Rivals et al. 2015b), and at Covalejos Cave (Spain), which is therefore characterized as either long-term occupations or as a succession of short-term occupations throughout the year (Sánchez-Hernández et al. 2019).

Conclusion

Despite the difficulty to assess the nature of Neanderthal occupations and to identify the type of settlement (i.e., butchery halt, unspecialized short or long occupation camp, etc.), both De Nadale Cave and San Bernardino Cave shed new light on the organization of the territory.

Both sites attest to a high mobility pattern of the human groups that occupied the caves for short periods of time, during a timespan shorter or equal to a season. From the study, the tendency to settle in the two sites during winter emerged, with some brief occupations during the good season.

From the methodological point of view, the integrated application of cementochronology and tooth wear analyses allowed us to confirm the significance of combining these two high-resolution methods. The usefulness of this combination is in the possibility to obtain more detailed data and to avoid any lack of information due to the application of a single methodology. Specifically, the combination of both approaches suggests that the lack of variability in the microwear signal does not necessarily indicate a long-term or a succession of short-term prey procurement events.

Acknowledgements Research at the De Nadale and at San Bernardino Caves is coordinated by the University of Ferrara (M.P.) in the framework of a project supported by the Ministry of Culture-Veneto Archaeological Superintendence (SABAP – Verona, Vicenza e Rovigo) and the municipalities of Zovencedo and Mossano. The project has been financed by the Hugo Obermaier Society, local private companies (R.A.A.S.M. and Saf), and local promoters. The authors thank all the students and anyone who took part in the excavation,

Carlos Sánchez-Hernández for helping with the digital enhancement of cementum images, Davide Delpiano for providing inputs to the paper, Diana Marcazzan and Mirka Govoni for the digital elaboration and map creation, and anonymous reviewers for contributing to ameliorate the manuscript. Special thanks go to Eric Pubert and the PACEA laboratory and the cementochronology department at the University of Bordeaux for helping during the cementum analysis.

Author contribution All authors have contributed to this manuscript and have approved the final version.

Alessandra Livraghi: Conceptualization, investigation, formal analysis, validation, writing (original draft), and writing (review and editing). Florent Rivals: Conceptualization, investigation, methodology, validation, formal analysis, writing (review and editing), and supervision. William Rendu: Investigation, validation, and writing (review and editing). Marco Peresani: Supervision, conceptualization, funding acquisition, resources, project administration, and writing (review and editing).

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Declarations

Conflict of interest The authors declare no competing interests.

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