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NEANDERTHAL SUBSISTENCE STRATEGIES IN THE NORTH-EAST OF ITALY: INFERRING SEASONALITY OF OCCUPATIONS AT DE NADALE, SAN BERNARDINO AND FUMANE CAVES, COMBINING DENTAL WEAR ANALYSES AND CEMENTOCHRONOLOGY

Alessandra Livraghi

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Alessandra Livraghi - Neanderthal subsistence strategies in the North-east of Italy - Doctoral Thesis

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Doctoral Thesis

Department d'Història I Història de l'Art, Universitat Rovira I Virgili
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Tarragona
2017-2022

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FAIG CONSTAR que aquest treball, titulat “Neanderthal subsistence strategies in the Northeast of Italy: Inferring seasonality of occupations at De Nadale, San Bernardino and Fumane caves combining dental wear analyses and cementochronology”, que presenta Alessandra Livraghi per a l’obtenció del títol de Doctor, ha estat realitzat sota la meva direcció al Departament d'Història i Història de l'Art d’aquesta universitat.

HAGO CONSTAR que el presente trabajo, titulado “Neanderthal subsistence strategies in the Northeast of Italy: Inferring seasonality of occupations at De Nadale, San Bernardino and Fumane caves combining dental wear analyses and cementochronology”, que presenta Alessandra Livraghi para la obtención del título de Doctor, ha sido realizado bajo mi dirección en el Departamento de Historia e Historia del Arte de esta universidad.

I STATE that the present study, entitled “Neanderthal subsistence strategies in the Northeast of Italy: Inferring seasonality of occupations at De Nadale, San Bernardino and Fumane caves combining dental wear analyses and cementochronology”, presented by Alessandra Livraghi for the award of the degree of Doctor, has been carried out under my supervision at the Department of Art History and History of this university.

Tarragona, 1 de setembre del 2022

El/s director/s de la tesi doctoral
El/los director/es de la tesis doctoral
Doctoral Thesis Supervisor/s

Dr. Florent Rivals

Dr. Marco Peresani

To my sister,
To my grandpa,
To my parents.

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Abstract

Neanderthal subsistence strategy has always been a challenging topic in the field of Paleolithic studies. In the last years, the North-east of Italy became more and more relevant in the debate, as the number of investigated deposits grew, and the quality of methodologies improved. As attested by over 20 Middle Palaeolithic multi-layered sites in caves, rockshelters and open air, unearthed and studied recently, the area was well known by Neanderthal groups. Of this large record, evidence pointing for human frequentation during to the Marine Isotopic Stage 4 is documented at a very ephemeral level and makes De Nadale Cave, a single-layered Quina Mousterian dated to 70.2 + 1/-0.9 ka BP, even more significant. In this scenario, De Nadale Cave is a key site to enlarge our knowledge about mobility patterns and subsistence strategies: thanks to the number and to the good preservation of the osteological material, an intensive zooarchaeological analysis was possible.

To broaden the zooarchaeological studies, dental wear analysis and cementochronology were applied to samples from two sites nearby – San Bernardino Cave, on the Berici Hills and Fumane Cave, on the Lessini Mounts – in addition to material yielded by De Nadale Cave.

Herbivore teeth are a valuable source of information for inferring the hunting season of past hunter-gatherers, the spatio-temporal organization of their activities, their socio-economic structure, 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 manuscript, we present the results achieved though the combination of these two high-resolution techniques applied to large and medium-sized herbivore teeth. 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 is addressed 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.

Resum

Les estratègies de subsistència dels neandertals han estat sempre un tema desafiant en el camp dels estudis paleolítics. En els últims anys, el nord-est d'Itàlia s'ha tornat cada vegada més rellevant en el debat, especialment a mesura que el nombre de jaciments investigats i la qualitat de les metodologies han anat creixent i millorant. Com s'ha comprovat a més de 20 jaciments, estudiants recentment, amb importants seqüències estratigràfiques del paleolític mitjà trobats en coves, abrics i també al aire lliure, l'àrea era ben coneguda pels grups neandertals. D'aquest important registre, les proves que apunten a la freqüència humana durant l'estadi isotòpic marí 4 estan documentades a un nivell molt efímer a *De Nadale Cave*, una sola capa de mosterià del tipus La Quina datada fa al voltant de 70.000 anys, fet que parla de la significança d'aquest jaciment. En aquest escenari, *De Nadale Cave* és un lloc clau per ampliar el nostre coneixement sobre els patrons de mobilitat i les estratègies de subsistència: la bona preservació i l'elevat volum de material osteològic, ha permès realitzar un exhaustiu anàlisi zooarqueològic.

Per ampliar els estudis zoològics, es van aplicar els anàlisis de desgast dental i cimentocronologia a mostres de dos jaciments propers - *San Bernardino Cave*, a les muntanyes Berici i la *Fumane Cave*, a les Muntanyes Lessini-, a més del material obtingut a *De Nadale Cave*.

Les dents dels herbívors són una valuosa font d'informació per inferir dades sobre l'estacionalitat de les activitats de caça dels caçadors-recol·lectors del passat, l'organització espai-temporal de les seves activitats, la seva estructura socioeconòmica, i la seva adaptació a la fluctuació estacional dels recursos. S'han dut a terme nombrosos estudis sobre els neandertals a d'Euràsia, però pocs d'ells fan ús de la combinació de diferents tècniques com la cimentocronologia dental i l'anàlisi del desgast de les dents per obtenir informació de la dieta dels ungulats, els paleoambients i el rang temporal dels esdeveniments de mortalitat. En aquest article, presentem els resultats aconseguits a través de la combinació d'aquestes dues tècniques d'alta resolució aplicades a les dents d'herbívors grans i mitjans. Vam combinar les dues metodologies amb l'objectiu de superar qualsevol possible falta d'informació, a causa de l'ús d'un únic mètode. Aquest estudi està dirigit a produir dades que donen suport a la interpretació de l'origen dels dos conjunts arqueofaunistics com a resultat d'esdeveniments de caça estacionals que van tenir lloc principalment a l'hivern. En aquest context geogràfic i mediambiental específic, les nostres dades adquireixen una millor comprensió de les estratègies de subsistència neandertal i els patrons d'ocupació.

Resumen

Las estrategias de subsistencia de los neandertales siempre han sido un tema desafiante en el campo de los estudios paleolíticos. En los últimos años, el noreste de Italia se volvió cada vez más relevante en el debate, a medida que crecía el número de yacimientos investigados y mejoraba la calidad de las metodologías. Como atestiguan más de 20 yacimientos con buenas secuencias estratigráficas del Paleolítico Medio encontrados en cuevas, abrigos rocosos y al aire libre, el área era bien conocida por los grupos neandertales. De este gran registro, la evidencia que apunta a la frecuentación humana durante el estadio isotópico marino 4 está documentada en un nivel muy efímero y hace que *De Nadale Cave*, un Quina Musteriense de una sola capa que data de 70.2 + 1/-0.9 ka BP, sea aún más significativo. En este escenario, *De Nadale Cave* es un sitio clave para ampliar nuestro conocimiento sobre patrones de movilidad y estrategias de subsistencia: gracias al número y a la buena conservación del material osteológico, fue posible un análisis zooarqueológico exhaustivo.

Para ampliar los estudios zooarqueológicos, se aplicaron el análisis de desgaste dental y la cementocronología dental a muestras de dos yacimientos cercanos: *San Bernardino Cave*, en las colinas de Berici y *Fumane Cave*, en los montes Lessini, además del material de *De Nadale Cave*.

Los dientes de herbívoros son una valiosa fuente de información para inferir la temporada de caza de los cazadores-recolectores del pasado, la organización espacio-temporal de sus actividades, su estructura socioeconómica y su adaptación a la fluctuación estacional de los recursos. Se han realizado innumerables estudios sobre los neandertales en Eurasia, pero solo unos pocos se basan en la aplicación de la cementocronología y análisis de desgaste dental combinados para obtener información sobre la paleodieta de los ungulados, los paleoambientes y el rango de tiempo de los eventos de mortalidad. En este artículo, presentamos los resultados obtenidos mediante la combinación de estas dos técnicas de alta resolución aplicadas a dientes de herbívoros de tamaño grande y mediano. Combinamos las dos metodologías con el objetivo de superar cualquier posible falta de información, debido al uso de un solo método. Este estudio está dirigido a producir datos que apoyen la interpretación del origen de los dos conjuntos arqueofaunísticos como resultado de eventos de caza estacional que tuvieron lugar principalmente en invierno. En este contexto geográfico y ambiental específico, nuestros datos obtienen una mejor comprensión de las estrategias de subsistencia y los patrones ocupacionales de los neandertales.

LIST OF PUBLICATIONS

Publications submitted to fulfil the requirements for a cumulative dissertation. Percentage of own contribution to the articles or manuscripts are listed in parentheses (original idea/data collection/data analysis/writing and publication).

Paper 1 (50/100/70/80)

Livraghi A., Fanfarillo G., Dal Colle M., Romandini M., Peresani M., 2021. Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: a study on De Nadale cave, Italy. Quaternary International 586, 24-41. DOI: 10.1016/j.quaint.2019.11.024

Paper 2 (70/100/60/70)

Livraghi A., Rivals F., Rendu W., Peresani M., 2022. Neanderthals' hunting seasonality inferred from combined cementochronology, mesowear, and microwear analysis: case studies from the Alpine foreland in Italy. Archaeological and Anthropological Sciences (2022) 14: 51. DOI: 10.1007/s12520-022-01514-5

Paper 3 (20/50/70/50)

Martellotta E.F., **Livraghi A.,** Delpiano D., Peresani M., 2021. Bone retouchers from the Quina site of De Nadale Cave (Berici Hills, north-eastern Italy). Journal of Archaeological Science: Reports 36, 102864. DOI: 10.1016/j.jasrep.2021.102864

Paper 4 (20/50/60/50)

Terlato, G., **Livraghi A.**, Romandini, M., Peresani, M., 2019. Large bovids on Neanderthal menu: exploitation of *Bison priscus* and *Bos primigenius* in northern Italy. Journal of Archaeological Science: Reports 25, 129-14

1.

INTRODUCTION

1.1 Subsistence strategies and settlement dynamics

In the last 20 years, intensive studies and research have been carried on with the purpose of reconstructing the paleoenvironmental and palaecological contexts of the Neanderthal groups and their mobility patterns. All these efforts lead to several striking achievements in understanding Neanderthal subsistence strategies, mobility, and seasonality. Currently, most of these goals has been achieved thanks to the combination of high-resolution proxies, multidisciplinary approaches and the application of methodologies derived from different fields (e.g., zooarchaeology, lithic technology, stable isotopes, cementum analyses, dental wear analyses and so on).

A large amount of studies demonstrated that Neanderthals were able to cope with the ecological and environmental fluctuations due to the drastic climatic shifts that occurred when they inhabited the Eurasian region (Sánchez Goñi, 2022). 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 changes of the resources (Conard and Prindiville, 2000; Rendu, 2010; Delagnes and Rendu, 2011; Rosell et al., 2012; Chacón et al., 2015). It has been demonstrated that the human groups put in place a huge variety of different subsistence and mobility strategies to adapt to the availability of the resources, depending on the characteristics of the region (e.g. Daujeard and Moncel, 2010; Delagnes and Rendu, 2011; Conard et al., 2012; Jimenez, 2016; Turq et al., 2017; Morin et al., 2019). Archaeological evidence underlined that large and medium-sized ungulates played a fundamental role in Neanderthal’s diet, but it is undeniable that the human groups based they subsistence on a wide spectrum of resources: small game (e.g., Stiner et al., 2000; Hockett and Haws, 2002; Cochard et al., 2012; Carvalho et al., 2018; Romandini et al., 2018b), birds (e.g., Peresani et al., 2011b; Blasco et al., 2016; Laroulandie et al., 2016; Gómez-Olivencia et al., 2018; Romandini et al., 2018b; Blanco et al., 2021; Rufà and Laroulandie, 2021), carnivore (e.g. Auguste, 2003; Petram et al., 2004; Camarós et al., 2017; Gómez-Olivencia et al., 2018) and aquatic resources, including mammals, fishes and molluscs (Zilhão et al., 2020). Moreover, we must consider the vegetal component in Neanderthal's dietary spectrum, in addition to the meaty resource: the large use of vegetable parts, mushrooms, nuts and moss, just to cite some examples (Hardy, 2022).

While in the 80s, Binford (1988) argued that Neanderthals exploited the most common prey in their environments without any selection, in the last years, their great ability to adapt to various environmental constrains and to develop complex hunting strategies became clearer and clearer. For instance, evidence demonstrate that Neanderthal groups practised selective hunting toward a single species that dominates the faunal spectrum (Gaudzinski, 2006; Daujeard, 2008; Rendu, 2010; Niven et al., 2012; Romandini et al., 2012; Daujeard et al., 2019; Ramírez-Pedraza et al., 2020), that they were able to enact mass hunting when the circumstances made it possible (Farizy et al., 1994; Rodríguez-Hidalgo et al., 2017; Gaudzinski-Windheuser et al., 2018; Daujeard et al., 2019) or to kill a large number of individuals at the same time (Farizy et al., 1994; Costamagno et al., 2006). An astonishing example of this complexity comes from the intensive exploitation of reindeer in the record of the Southwest of France. Many studies (Delagnes and Rendu, 2011; Discamps et al., 2011; Niven et al., 2012; Rendu et al., 2019; Rendu, 2022 among others) pointed out how different subsistence strategies were developed during a succession of different cultural events (i.e. Quina Mousterian followed by the Mousterian of Acheulean Tradition and the Discoidal Denticulate Mousterian). Moreover, some sites in the same area have been recognized to have a specific function: Les Pradelles at Marillac-le-Franc was identified as a secondary butchery site (Costamagno et al., 2006; Rendu, 2022), Chez-Pinaud at Jonzac was used as a butchery site linked to a close kill site (Niven et al., 2012) and so on. This contributed to point out that Neanderthals were able to develop a logistic mobility pattern, specifically based on short term occupation sites. The hypothesis behind this statement could be the idea that Neanderthal groups came every year at the same season, to perform the same activities, at the same locations attesting to the existence of an annual schedule of the activities (Costamagno et al., 2006; Delagnes and Rendu, 2011; Rendu et al., 2022).

All this evidence underlines the high dietary flexibility and the great plasticity that characterized the Neanderthal hunting behaviour. Thus, Neanderthals subsistence appears to be extremely complex: the presence of a certain degree of prey selection and scheduling in the activities does not exclude the opportunistic side of their hunting strategies. Moreover, the lack of selection does not imply the inability in organizing a complex social environment in the Neanderthal population (Rendu, 2022).

1.2 Seasonality

Among all the hypotheses and the theses about the great flexibility of the Neanderthals, the debate about how much and in which way their seasonal behaviour induces differences in the faunal assemblages is particularly lively.

At the current state of the art, it is well established that Neanderthal groups were characterized by a high mobility and that they had a behavioural ecology marked by seasonal movements driven by the provisioning of living resources, both vegetal and animal (Lieberman, 1998; Conard and

Prindiville, 2000; Gaudzinski, 2000; Costamagno et al., 2006; Fernândez-Laso et al., 2010; Delagnes and Rendu, 2011). Estimating seasonality and duration of site occupation has always been challenging since the features of deposits themselves don't allow a reliable evaluation of the thickness of each individual accumulation. In the zooarchaeological field, several methods to investigate this aspect of Neanderthals way of living flourished in the last years and allowed researchers to overcome the poor resolution of the traditional age estimation of hunted game by means of tooth eruption and replacement patterns (Aitken, 1974; Mariezkurrena, 1983; D'Errico and Vanhaeren, 2002; Bunn and Pickering, 2010; Gifford-Gonzalez, 2018).

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 (Feranec et al., 2009; Balasse et al., 2012; Julien et al., 2012; Blumenthal et al., 2014), the dental micro- and mesowear analyses (Rivals and Deniaux, 2005; Rivals and Semprebon, 2011; Rivals et al., 2015a; Sánchez-Hernández et al., 2019; Uzunidis, 2020) and the cementochronology technique (Klevezal′ and Kleinenberg, 1969; Klevezal', 1988; Lieberman, 1994; Burke and Castanet, 1995; Rendu, 2007; 2010; Naji et al., 2015; 2016).

Huge steps forward in this field have been made in the last decades when several investigations about seasonality were performed on archaeological material from numerous sites in Europe. Even though dental wear analyses are usually applied to infer palaeoecological aspects, they revealed to be useful to decipher archaeological characteristics of the assemblages. From an archaeological perspective they have been applied to identify intra-site diachronic changes and characterize and estimate the duration of human occupations. Among the most important recent applications of this methodology, notable results were obtained 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), Portel-Ouest level F (MIS 4-3), which was assigned to long-term events of accumulation (Rivals et al., 2015a) 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); in Germany at Salzgitter Lebenstedt (MIS 5–3) and Taubach, where the accumulation of remains corresponds to seasonal (or shorter) events (Gaudzinski and Roebroeks, 2000; Moncel and Rivals, 2011) and at Schöningen 13 II-4 (MIS 9), recognized a longer occupation (Rivals et al., 2015b) and in Spain, at Arago Cave where various types of settlements were identified (Rivals et al., 2009a). Thus, cementum analyses have been successfully applied to several Middle Palaeolithic sites in the southwestern France: Pech-de-l'Azé I (Armand et al., 2001; Rendu et al., 2009), Chez-Pinaud/Jonzac (Niven et al., 2012), La Quina, level 6c (Rendu and Armand, 2009), Les Pradelles and Mauran (Rendu et al., 2012).

Furthermore, the combination of dental wear analyses and cementochronology gave positive results in identifying the season and the extent of human occupation at Arbreda and Teixoneres Caves in the north-eastern Iberian Peninsula (Sánchez-Hernández et al., 2016; 2020) and at Covalejos Cave in the Cantabrian region (Sánchez-Hernández et al., 2019).

In this scenario, a huge gap that involves the Italian peninsula regarding the studies about seasonality. At the current state of the research, Italian sites have been studied with the traditional zooarchaeological approach and lack an intensive investigation about the timing of the human occupation.

1.3 Objectives of the study

This research is a *compendium* of different zooarchaeological studies conducted mainly on the recently discovered Quina Mousterian site of De Nadale Cave. We broaden the scenario including materials from San Bernardino and Fumane Caves, to have a more comprehensive point of view on the Venetian region, in the North-east of Italy. In order to preserve the integrity of the archaeological material, the sample from layers A5+A6 and A9 of Fumane Cave, was selected to perform only the dental wear analyses.

The main objectives of this study are:

1. The acquisition of exhaustive archaeozoological and taphonomic data about the materials recently yielded by De Nadale Cave. A special attention was given to the study of the retouchers, that were found in a great number inside the excavated area. These data help to broaden the current knowledge of the ecology and the subsistence strategies of the human groups that inhabited the region during the Middle Paleolithic.

2. The definition of a specific season during which De Nadale, San Bernardino and Fumane Caves were occupied by Neanderthals and the extent of this occupation. To obtain this we tested the combination of two high-resolution techniques, dental wear analyses and cementochronology, that allows us to overcome a possible lack of information and low-resolution data and enriches the traditional zooarchaeological studies.

3. The comprehension of Neanderthals land use in an area rich in Middle Paleolithic evidence. Such information is still missing for the Italian peninsula and could provide new perspectives on the mobility patterns and the settlement dynamics that interested the region.

2.

ARCHAEOLOGICAL BACKGROUND OF THE SITES

2.1 The regional context

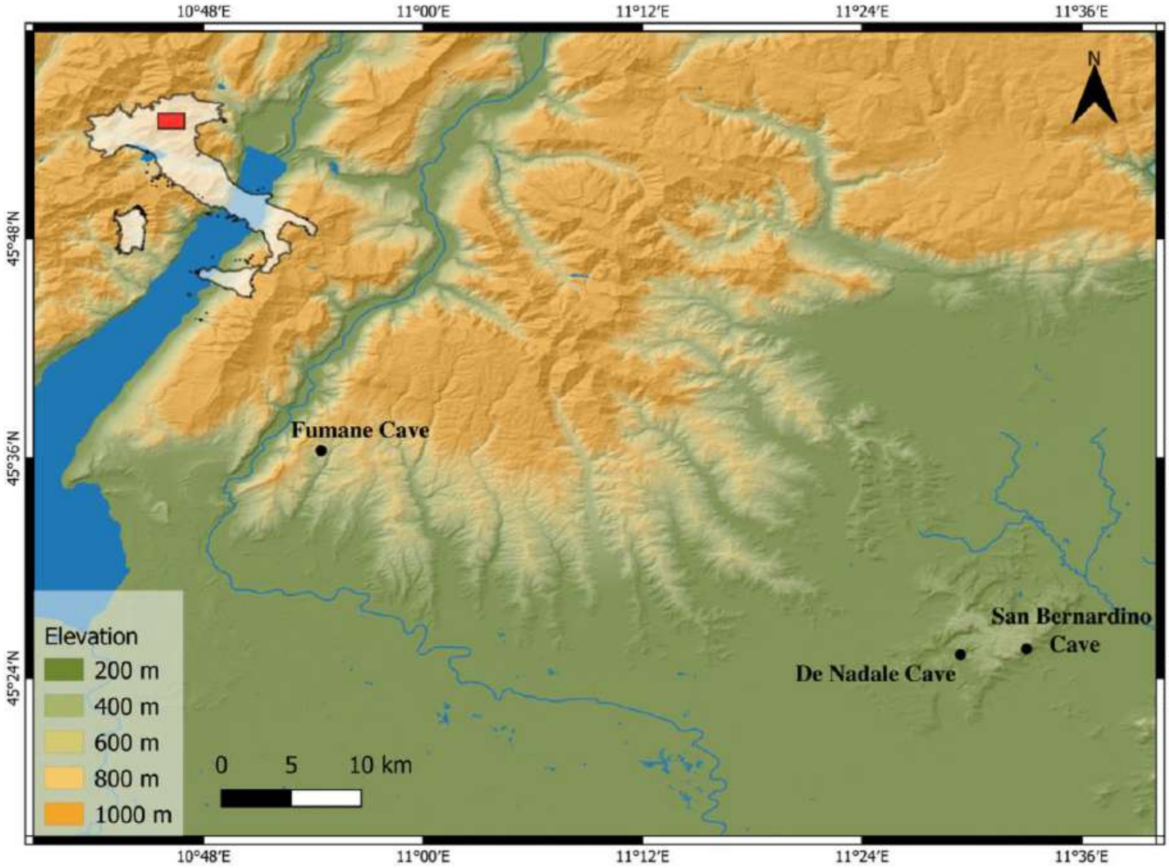


Fig. 1: The geographical location of De Nadale, San Bernardino and Fumane Caves in the north-east of Italy.

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 Lessini fossil karst complex system, where Fumane Cave opens, is located around 60-70 km west of the Berici Hills and it takes the form of a fan-shaped plateau dipping gently to the south towards the alluvial plain of the Adige River. The karst complex is probably datable to the Neogene period and excavated in the Ooliti di San Vigilio carbonate sandstone. The immediate surroundings of the cave are composed of several morpho-tectonic terraces connected to the bottom of the Fumane valley by steep slopes and rock walls that include many caves and shelters. The cave is strategically placed due to its geographic setting, which may have facilitated human penetration to the highlands.

The whole areas 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, 2015; 2001a) used by human groups as part of a settlement system extended to the Euganean Hills, the Alpine foreland, and the southern slope of the Alps.

2.2 De Nadale Cave

De Nadale Cave is a small cavity that opens in the Southern slope of the Berici Hills, at 80 m a.s.l., overlooking the narrow Calto valley, a lower area rich in springs and moist zones. The cave was first reported in 2006 by a collaborator of the University of Ferrara, who found several mammal bones and lithic implements on the surface of reworked sediments resulting from present-day burrowing animals and recent anthropic activities. After the removal of the reworked sediments in 2013, the entrance of a small cavity 8 m wide, almost filled by layered deposits, was discovered. 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 consists of dark brown-grey silt loam with medium-small sized, sub-rounded rocks and it extends on almost entirely the cavity. It yielded a cultural assemblage attributed to the Quina Mousterian (Jéquier et al., 2015; Livraghi et al., 2021) thousands of fragmented bones, charcoals, and a Neanderthal deciduous tooth (Arnaud et al., 2017). In the north-eastern part of the cavity, about 40/50 cm underneath the vault, two concentrations of charcoals and burnt bones (structures 7SI and 7SII) were interpreted as dumping areas or residual hearts. Below Unit 7, Unit 8 is archaeologically sterile, even though a few flaked stones and bones were recovered at the top, close to the boundary with Unit 7. This material has been attributed to Unit 7. Among all the bone fragments recovered, a second lower molar of a large-sized ungulate has been chosen to perform a U/Th dating: it provided a minimum age of 70.2 + 1/-0.9 ka BP (Jéquier et al., 2015).

The technological and typological features of the lithic techno-complex make this industry different from the Mousterian of the rest of the region, especially concerning the method adopted in core reduction, and the type of blanks and retouched tools. The reduction sequence recognized at De Nadale Cave, with the presence of 55 scrapers and invasive retouch (Jéquier et al., 2015), is comparable with Quina assemblages in Italy and south-western France (Bourguignon, 1997; Palma di Cesnola, 2001). Given the absence of lithic raw material in the site nearby, chert was sourced in a district bounded from the eastern side of the Berici Hills and the western side of the Euganean Hills, and the central-western Lessini (20–80 km far from De Nadale).

The anthracological assemblage from SU 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). This result is consistent with the paleoenvironmental and paleoclimatic reconstruction based on small-mammals assemblage from the anthropic layer. The presence of *M. arvalis*, which is the most abundant taxon, and which is currently reported to be more common in open areas and relatively drier regions, identifies a cold climate phase, with a landscape dominated by open woodland formations and open dry meadows. Considering the chronology of the site, this has been associated with 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 bovids (*Bison priscus* and *Bos primigenius*)—dominate the faunal spectrum, both according to NISP and MNI. Smaller ungulates, such as roe deer (*Capreolus capreolus*), cham- ois (*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).

2.3 San Bernardino Cave

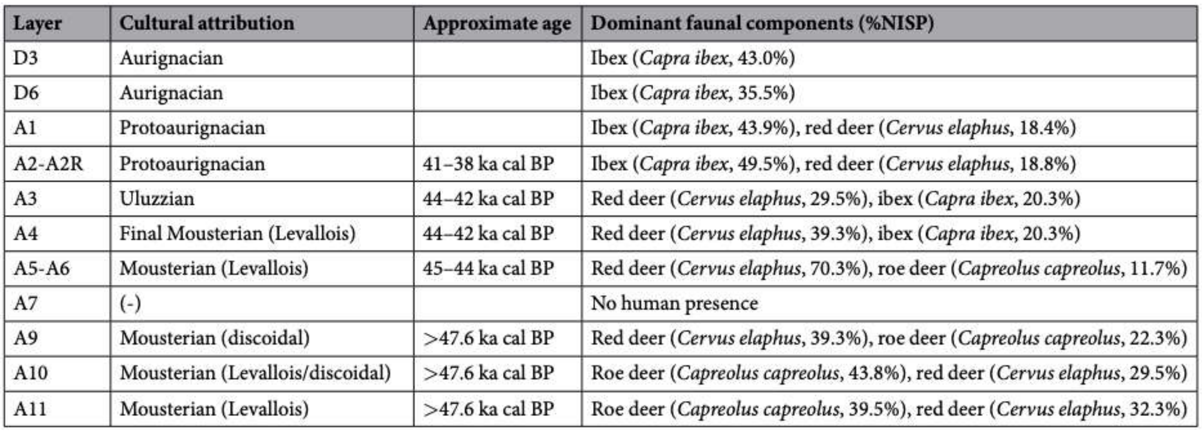
The San Bernardino Cave opens at 135 m a.s.l. Several systematic archaeological excavations were carried out in the second half of the last century and focused on the atrial area: the first began in 1959, while the second stage went on from 1986 to 1994. The excavations unearthed a 4.5-m-thick stratigraphic sequence composed by eight layers spanning from the Late Middle Pleistocene to the Late Pleistocene and containing Mousterian lithic assemblages (Leonardi and Broglio, 1962; Peresani, 1995; Fiore et al., 2004).

Sediment composition and stratigraphy of units from VIII to I identify three main cycles (Cassoli and Tagliacozzo, 1994; López-García et al., 2017; Peresani, 2001a), 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., 2013; 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., 2018b; 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).

2.4 Fumane Cave

Fumane Cave is located in the Monti Lessini Plateau, on the southern slope of the Veneto Pre-Alps in northern Italy. It opens at the base of a rock cliff at an altitude of 350 m a.s.l. and provides a 12 m thick stratigraphic sequence, spanning from the late Middle Paleolithic and the early Upper Paleolithic (macro-units A to D). The anthropogenic deposits consist of several levels and lenses with human occupation features associated with the Mousterian, Uluzzian, and early and late Protoaurignacian (Peresani, 2012; Bertola et al., 2013; Peresani et al., 2016a; Cavallo et al., 2017; Falcucci et al., 2017; Aleo et al., 2021) that are grouped into stratigraphic units labeled, from bottom to top, A13 to A1. Mousterian industries are found in A12-A11, A10, A9, A6-A5, Uluzzian in A4 and A3, and Protoaurignacian in A2 and A1 (Broglio et al., 2006; Peresani et al., 2011a; 2016b; Peresani, 2012) The Aurignacian phase is recorded in the macro-unit D, which includes several layers, embedded in coarse-sandy sediments. Traces of human presence are less dense than in A2–A1; however, hearths and other surface features had been exposed (Broglio et al., 2006). Numerous faunal remains, lithic implements and combustion features attest the human occupation throughout a long-time span. The site also offers unusual finds such as ornamental objects, painted stones, and evidence for the intentional removal of feathers from birds (Broglio et al., 2009; Peresani et al., 2011b; 2013; 2019; Romandini et al., 2016). A whole set of radiocarbon dates, Uranium-Torium dates, and electron spin resonance (ESR) combined dates provides a clear chronological framework for the entire stratigraphy (Higham et al., 2009; Higham, 2011; Douka et al., 2014; Peresani et al., 2017), in addition to paleoecological reconstruction (López-García et al., 2015). More details about the dates are shown in the table (Sinet-Mathiot et al., 2019).



Layer	Cultural attribution	Approximate age	Dominant faunal components (%NISP)
D3	Aurignacian		Ibex (*Capra ibex*, 43.0%)
D6	Aurignacian		Ibex (*Capra ibex*, 35.5%)
A1	Protoaurignacian		Ibex (*Capra ibex*, 43.9%), red deer (*Cervus elaphus*, 18.4%)
A2-A2R	Protoaurignacian	41–38 ka cal BP	Ibex (*Capra ibex*, 49.5%), red deer (*Cervus elaphus*, 18.8%)
A3	Uluzzian	44–42 ka cal BP	Red deer (*Cervus elaphus*, 29.5%), ibex (*Capra ibex*, 20.3%)
A4	Final Mousterian (Levallois)	44–42 ka cal BP	Red deer (*Cervus elaphus*, 39.3%), ibex (*Capra ibex*, 20.3%)
A5-A6	Mousterian (Levallois)	45–44 ka cal BP	Red deer (*Cervus elaphus*, 70.3%), roe deer (*Capreolus capreolus*, 11.7%)
A7	(-)		No human presence
A9	Mousterian (discoidal)	>47.6 ka cal BP	Red deer (*Cervus elaphus*, 39.3%), roe deer (*Capreolus capreolus*, 22.3%)
A10	Mousterian (Levallois/discoidal)	>47.6 ka cal BP	Roe deer (*Capreolus capreolus*, 43.8%), red deer (*Cervus elaphus*, 29.5%)
A11	Mousterian (Levallois)	>47.6 ka cal BP	Roe deer (*Capreolus capreolus*, 39.5%), red deer (*Cervus elaphus*, 32.3%)

Table 1. Fumane stratigraphy, chronological age, and faunal composition (from (Sinet-Mathiot et al., 2019).

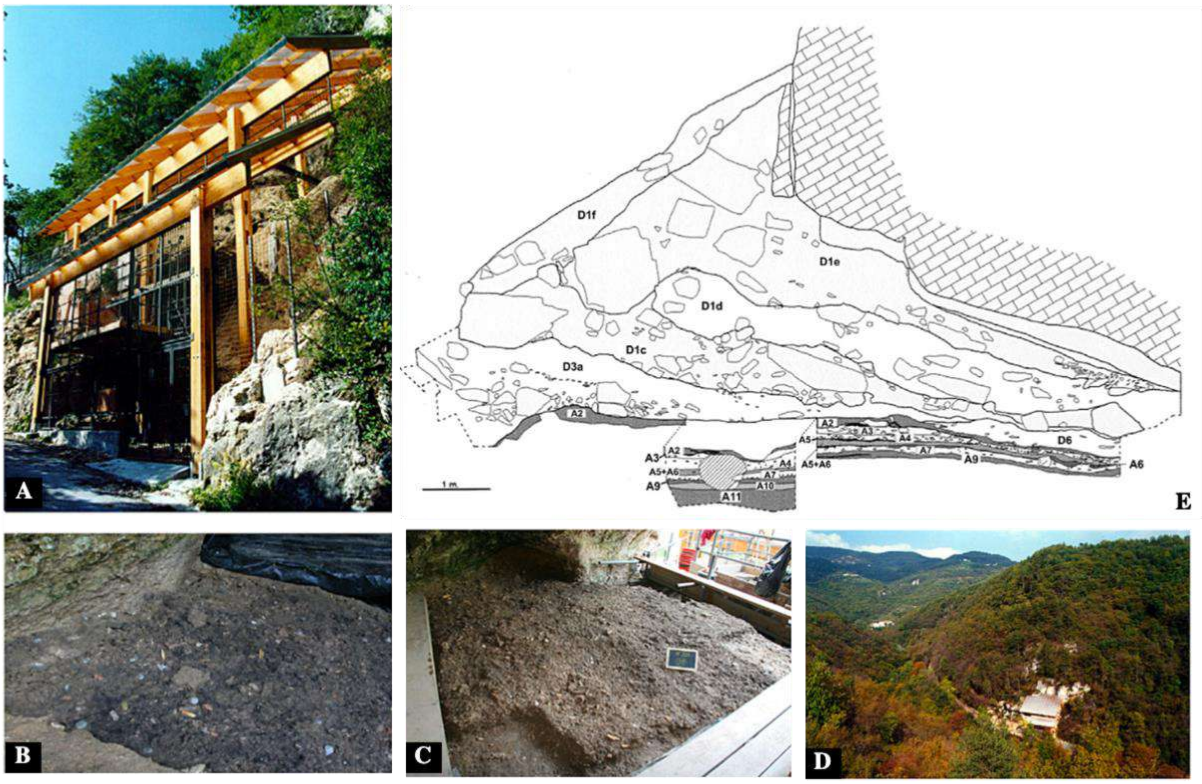


Fig. 2. The entrance of Fumane Cave (A); unit A9 during the 2009 and 2010 excavations (B, C); overview of the cave (D); sketch of sagittal section of the cave with evidence of the late Mousterian (A11-A5), Uluzzian (A4-A3) and earliest Aurignacian layers (A2) (E). (modified from (Romandini et al., 2014).

This work focuses on materials coming from both unit A9 and the stratigraphic complex A5-A6, since they were the only levels that yielded enough teeth to perform the dental wear analyses.

In unit A9 the presence of ungulate is dominant: the most represented taxon is *C. elaphus,* followed by *C. capreolus*. *M. giganteus*, *A. Alces*, *R. Rupicapra*, bovids and *C. ibex* are present, but they are less frequent. Carnivores are also attested but in a lower quantity: among them, the most abundant are bear (*U. spelaeus* and *Urus* sp.), hyena (*C. Crocuta spelaea*) and cave lion (*P. leo spelaea*) (Romandini et al., 2014). Traces of human exploitation have been observed on all the ungulate species recognized and the representation of the anatomical parts contributed to create the hypothesis that Fumane Cave was used as a site where the processing of carcasses was finalized after having been begun at the kill site (Romandini et al., 2014).

In the stratigraphic complex A5-A6, the faunal assemblage includes a rich association of ungulates, carnivores, and birds from diverse environments and climates. The most abundant faunal remains belong to *C. elaphus*, *C. capreolus*, *C. ibex* and *R. rupicapra* whereas, bison, and giant deer are less frequent. Horse and wild boar are rare. All ungulate species, except for horse and wild boar, bear traces of human exploitation. Cave bear, brown bear, fox, and wolf are the most numerous carnivores. The current state of research shows the complex A5-A6 to be unique within the entire stratigraphic sequence due to evidence for attention to the treatment of carnivore carcasses (Romandini et al. 2018). Except for wolves, carnivore remains show butchery marks from skinning and defleshing. This data, together with the scarcity of carnivore gnawing on bones and an elevated number of anthropically modified bones, supports the anthropic nature of the bone accumulation in these units (Peresani et al., 2011a). In addition to the butchery marks on ungulate and carnivore bones, we also report on the discovery of human modifications to some anatomical elements of large raptors and Passeriformes (Peresani et al., 2011b).

3.

MATERIALS AND METHODS

3.1 Zooarchaeological analyses

Traditional zooarchaeological analyses have been carried out for this contribution at De Nadale Cave. 30654 osteological fragments have been unearthed during the seven excavation campaigns, which interested a 19 m^2 area. All the specimens that were at least 5 cm long or identifiable were spatially recorded during the excavations, using an electronic theodolite. Sediment was water-screened using a superimposed mesh from 5 to 0.5 mm and all the bone fragments were recovered after sieving and considered for this study.

In the current state of research, zooarchaeological analyses have been carried out on the whole osteological sample, including bones and teeth recovered in the abovementioned badgers' dens. All of them have been studied and classified from the taxonomical and taphonomical point of view. This study focuses especially on 28088 fragments of animals' bones and teeth that represent the totality of the remains yielded by the ensemble of Units 6base, 7, 8tetto and their interfaces (hereafter Unit 7). They are considered to be archaeologically and stratigraphically affordable, while the rest came from reworked layers and dens filled up with materials mixed to nowadays deposits. These fragments, yielded by reworked layers and dens, are not completely meaningless to the zooarchaeological analysis, considering that their preservation is consistent with the osteological material of the Unit 7 and that the site is characterized by the presence of a single anthropic layer. Evaluating these bone remains is particularly suitable to have a complete estimation of bone retouchers, whose number increases considerably if we include the fragments from reworked layers. Despite not being stratigraphically reliable, there is no doubt about their Mousterian origin.

Taxonomical and anatomical identifications made in this study are based on the complete Alpine fauna reference collection of the Department of Humanities at the University of Ferrara with the help of the well-established literature (Davis, 1987; Lyman, 1994; Reitz and Wing, 2008; France, 2009).

Remains, both identified and those considered unidentifiable on the basis of morphological or size characteristics, have been grouped into five mammal body-size classes, following Bunn et al. (Bunn et al., 1988): I - small (i.e. *Lepus* sp. and other lagomorphs, Mustelidae, *Vulpes vulpes*); II - small-medium (i.e. *Capreolus capreolus*, *Rupicapra rupicapra*, *Canis lupus*); III - medium (i.e. *Capra ibex*, *Sus scrofa)*; IV- medium-large (i.e. *Cervus elaphus*, Ursidae); V- large (i.e. *Megaloceros giganteus*, Bovinae). This partition has been considered more useful to evaluate the faunal assemblage of De Nadale Cave since it underlines the difference in body-size between red deer and giant deer/bovids.

Following the criteria of birth of modern animals, teeth eruption, replacement sequences and dental wear have been used to establish the age at death of the animals, as well as the state of fusion of the epiphysis. Among the ungulates, we considered mainly *Capreolus capreolus* (Aitken, 1974), *Cervus elaphus* (Mariezkurrena, 1983; Hillson, 1986; D'Errico and Vanhaeren, 2002), and bovids (Silver, 1969; Habermehl, 1975; Bunn and Pickering, 2010). In order to avoid distortion in the proportions of age groups in the various units, estimations were also calculated for those remains generally identified as Bovines by considering only the age or the size of the animal not represented in the two categories of the determined taxa (*Bison priscus* and *Bos primigenius*). The collection coming from the paleontological site of Settepolesini di Bondeno (Italy) has been used to give indications about the age of *Megaloceros giganteus* specimens. In this regard, five categories have been identified, following those proposed by Bunn and Pickering (Bunn and Pickering, 2010) and by Marín et al. (Marín et al., 2017): 1) young juvenile (I – 0–5 months; deciduous teeth); 2) subadult juvenile (J – 5–30 months; M3 in eruption); 3) early prime adult (AD I – 30–78 months; complete permanent dentition without wear); 4) late prime adult (AD II – 78–144 months; complete dentition with light wear); 5) old adult or senile (S – > 144 months; permanent dentition with heavy worn).

Concerning the skeletal part profiles, all taxonomically identified specimens, including shaft fragments, were taken into account. NISP (Number of Identified Specimens, (Grayson, 1984) and MNI (Minimum Number of Individuals, (Bökönyi, 1970) indexes were used in order to evaluate species abundance. Estimation of MNI was based on all of the skeletal elements (bones and teeth), even if the most reliable specimens turned out to be the tibia, especially for ungulates, and teeth for carnivores. Minimum Number of Elements (MNE) (Binford, 1981; Klein and Cruz-Uribe, 1984; Stiner, 1994) and fragmentation indexes (Binford, 1981; Brain, 1983; Lyman, 1994) were calculated to evaluate the skeletal representation of different animals and the skeletal survival rate. The following formula was used to calculate the % of survival of anatomical element = (MNE x 100)/(NEE - Number of Expected Elements).

Concerning the taphonomic analyses, samples of bones and of sediments have been selected from Unit 7 to investigate the diagenetic processes with the intent to further contribute to the re- construction of the history of bone taphonomy, the sedimentary context and the modifications occurred (Weiner et al., 1993; Quattropani et al., 1999; Berna et al., 2004; Cohen-Ofri et al., 2006; Karkanas and Goldberg, 2010; Kontopoulos et al., 2019). The main goal of this analysis is to detect the differences in the preservation of bone remains, yielded by two opposite areas of the site. All bone surfaces were evaluated both at macroscopic and at microscopic level: the first examination was effectuated using a hand lens (magnification 10x) under a low-angle light, while the second with a Leica S6D Greenough stereomicroscope with 0.75–70X. Remains coming from the western area of De Nadale Cave appear to be more brownish and with a solid texture, while fragments found in the eastern zone are light-coloured and more fragile. While the reasons for the changing in the preservation status between osteological material found in caves or shelters and remains yielded by open air contexts are well documented, situations in which changes in preservation develop inside the cave, according to the area of the cavity itself (Weiner et al., 1993; Quattropani et al., 1999), are still considerably unknown. The study of this diversity has been carried out observing thin sections from bones and applying Fourier Transform Infrared spectroscopy (hereafter FT-IR) executed at the Department of Chemical and Pharmaceutical Sciences of the University of Ferrara.

Thin sections have been realized on 21 remains which shared common features. Shafts of long bones of large sized animals, without anthropic traces, yielded by distinct areas of the archaeological layer and showing a microscopically different state of preservation were selected. The material has been recognized to be homogeneous (as far as possible) in terms of size: the 21 remains shared a set of dimensional features that make the bones suitable for comparisons (i.e., average length between 4 and 5 cm, average width between 2 and 3 cm and average thickness between 1 and 2 cm. Observations were conducted with Olympus BX 51 microscope. The films of sesquioxide of Fe and Mn were classified according to a scale ranging from 0 to 2: −0 = ab- sent; −1 = present in superficial fissuring; −2 = present inside the assemblage.

FT-IR analyses were carried out on 9 samples, given the substantial homogeneity of the preservation detected on the thin sections. Two soil samples have been added to these remains, from squares Q12 b-e, N11c in order to have a comparison framework of the osteological specimens. The powders extracted from the samples were analysed with a Bruker Vertex 70 in diffuse reflectance, set at 16 scans with the spectra range from 4000 to 400cm-1. The data were interpreted using existing bibliography and the reference collection of FT-IR spectra of standard materials provided by the Kimmel Center for Archaeological Science, Weizmann Institute (http://www.weizmann.ac. il/kimmel-arch/infrared-spectra-library).

In order to identify the nature of bone surface alterations and to distinguish human from animal traces (pits, punctures, scores, fur- rowing, scooping-out, etc.), trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was made to taphonomic literature (Binford, 1981; Brain, 1983; Blumenschine and Selvaggio, 1988;

Capaldo and Blumenschine, 1994; Blumenschine, 1995; Fisher, 1995; Blumenschine et al., 1996; Domìnguez-Rodrigo and Piqueras, 2003; Fernandez-Jalvo and Andrews, 2016). Evidence of anthropic modification has been achieved by considering the type, the position, and the orientation of the cut- marks. Cutmarks have been classified as incisions and scraping marks (Binford, 1981; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983; 1984; Lyman, 2008). An incision is defined as a striation with a linear outline, a V-shaped section and common internal micro striations, while a scraping mark is a shallow sub-parallel cutmark caused by a stone tool dragged transversally along the length of the bone (Shipman and Rose, 1983; 1984; Bromage and Boyde, 1984; Noe-Nygaard, 1989). In order to hypothesize the performed action (skinning, de-fleshing, periosteum removal, etc.), a brief description of the cutmarks was made, taking into account the number of striations, their location and distribution on the bone and their orientation. Chopmarks have also been observed. A chopmark is defined as a broad, relatively short, linear depression that generally has a V-shaped cross section (Fisher, 1995; Lyman, 2008).

Anthropic traces caused during bone breakage for marrow extraction were analysed and divided into two categories: percussion marks and impact flakes. Percussion marks are semi-circular shaped sockets located on the fracture edges with corresponding negative flake scars. Impact flakes refer to positive flakes of the percussion notches derived from the action of breaking the diaphysis (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Blasco et al., 2013; Vettese et al., 2017). Intentional bone breakage to access marrow has been recognized by analysing the shape of the fragmented ends of the shafts themselves (Villa and Mahieu, 1991; Blumenschine, 1995; Fisher, 1995; Outram, 2001; Grunwald, 2016; Coil et al., 2017). According to excavation protocol, non-anthropic traces such as natural post-depositional degradation and animal chewing were identified only on 5 cm long objects - or longer ones - or on those taxonomically relevant.

The degree of combustion was evaluated by employing the methodology developed by the well-established literature; burnt bones have been divided into two different categories: calcined (> 700 °C, grey/ white) and subject to moderate combustion (200–500 °C, black/brown) (Shipman et al., 1984; Stiner and Kuhn, 1995; Théry-Parisot, 2002; Costamagno et al., 2005; Théry-Parisot et al., 2005; Mentzer, 2009).

3.2 Dental wear analyses

The sample analysed in this study is composed of 117 teeth, sorted among the faunal material yielded by the three deposits during the excavations.

The San Bernardino Cave sample is composed of 47 specimens (Table 2) 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.

At De Nadale Cave, 27 teeth coming from Unit 7 (NR: 19) and 13 (NR: 8) were sampled. They have been recognized as belonging to giant deer, red deer, and roe deer, while no bovid specimens were found. We carried out dental wear analysis on 20 molars, 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.

Fumane Cave yielded 43 teeth suitable for the dental wear analyses. For now, we decided not to perform cementochronology on these remains, to preserve them for future analyses. Among these teeth, 22 come from Unit A6 and A5+A6 and 21 from Unit A9. They have been identified as red deer, roe deer, giant deer and bovids. This data is consistent with the faunal spectrum (Cassoli and Tagliacozzo, 1991; Romandini et al., 2014; Peresani et al., 2017).

Taxa	**De Nadale Cave (CN)**			**San Bernardino Cave (SB)**				**Fumane Cave (RF)**		
	7	**13**	**tot.**	**II**	**IV**	**VI**	**tot.**	**A5+A6**	**A9**	**tot.**
Alces alces				3			3			
Megaloceros giganteus	6	5	11	2			2		2	2
Cervus elaphus	8	3	11	15	5		20	14	11	25
Capreolus capreolus	5		5	15	2	1	18	8	7	15
Bovinae				3	1		4		1	1
Total	**19**	**8**	**27**	**38**	**8**	**1**	**47**	**22**	**21**	**43**

Table 2. Detail of the taxa chosen for this study and their stratigraphic provenance.

Among the 117 specimens, 23 out of 25 gave interpretable results when studied with the cementochronology technique and 79 out of 102 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 102 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.

3.2.1 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 cuspids 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., 2018). 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 30 specimens, 9 of which from De Nadale Cave, 10 from San Bernardino Cave and 11 yielded by Fumane Cave.

Following (Fortelius and Solounias, 2000) and (Mihlbachler 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).

3.2.2 Microwear

The microwear technique describes and analyses 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 analysed following the well-established protocol (Solounias and Semprebon, 2002; Semprebon et al., 2004; Rivals et al., 2009c; 2009a; 2009b; 2015a; 2015b; Rivals and Semprebon, 2011; 2012; Sánchez-Hernández et al., 2019; 2020). The occlusal surface of each specimen was cleaned with acetone and then 96% ethanol, and once dry, it is moulded with vinylpolysiloxane, a high-resolution dental silicone. The moulds 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 × 35 magnification with an ocular reticule delimitating a 0.16 mm2 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 significative 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 mm2 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 over- lap partially with the other two categories, being comprised between 20.93 and 70% (Rivals et al., 2009a; 2015a). 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., 2009a; 2015a). Following (Rivals et al., 2015a), 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., 2015a). 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)

3.3 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, 1991b; 1991a; 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, 1991b; 1991a; Lieberman and Meadow, 1992; Lieberman, 1993; 1994; Stutz, 2002b; Gourichon, 2004; Rendu, 2007). 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, 1991b; 1991a; Lieberman and Meadow, 1992; Lieberman, 1993a; 1994; Stutz, 2002b; Gourichon, 2004; Rendu, 2007).

Among the teeth we sampled, 25 (i.e., 12 specimens from San Bernardino Cave and 13 from De Nadale Cave) were analysed with the cementochronology approach, following the well-established protocol for the archaeological application of this method (Saxon and Higham, 1969; Spiess, 1976; Gordon, 1988; Pike-Tay, 1991b; 1991a; Lieberman and Meadow, 1992; Lieberman, 1993a; 1993b; 1994; Burke and Castanet, 1995; Rendu and Armand, 2009).

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 analysed 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 Parmigiani, 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 mould, filled with epoxy resin, and put into a vacuum pump for 12–24 h, in order to remove bubbles and let 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 × 10, × 20, × 40, and × 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, 2002a; 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 sea- son" 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).

4.

RESULT

This thesis consists of four papers.

4.1 Paper 1

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Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: A study on De Nadale cave, Italy

Alessandra Livraghi[a,b], Gabriele Fanfarillo[b], Maurizio Dal Colle[c], Matteo Romandini[b,d], Marco Peresani[b,*]

The first paper of this work investigates Neanderthal hunting behaviour the subsistence strategies at De Nadale Cave, applying the traditional zooarchaeological approach.

Results point out the high predominance of large sized ungulates in the faunal spectrum, with *Megaloceros giganteus*, *Cervus elaphus* and bovids as most abundant species. Other taxa, such as *Capreolus capreolus* and *Rupicapra rupicapra* are present but to a lesser extent. Among carnivores, present but scarce, the most abundant is the bear (both *Ursus spelaeus* and *Ursus* sp.), followed my *Vulpes vulpes* and *Canis lupus*. This scenario fits well with the paleoenvironment reconstruction based on micromammal remains yielded by the site (López-García et al., 2018) and with the chronological framework that dates the anthropic occupation at the onset of the MIS 4. Taphonomical analyses underline the importance of the human hunting activities on the deposit: several shafts bear traces of human exploitation, such as cut marks, percussion marks, scraping traces and so on. All the main steps of the butchering process are recognizable at the site: limb bones, the most abundant skeletal part, have been skinned, disarticulated, defleshed and opened to extract the marrow. The cave also yielded a significative number of bone retouchers used in the lithic Quina production (see below, Paper 3).

This work contributes to shed a new light on the settlement dynamics in the North-east of Italy during the Middle Paleolithic, especially if we consider the scarcity of Quina Mousterian occupation and information about the MIS 4 in the whole peninsula.

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Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: A study on De Nadale cave, Italy

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ABSTRACT

North-eastern Italy was a familiar region for Neanderthal groups, as attested by over 20 Middle Palaeolithic multi-layered sites in caves, rockshelters and at the open, investigated during the last decades. Of this large record, evidence pointing for human frequentation during to the Marine Isotopic Stage 4 is documented at a very ephemeral level. Here we contribute to shed light on a so sparse context through the presentation of De Nadale Cave, a single-layered Quina Mousterian site located in the Berici Hills and dated to 70.2 + 1/-0.9 ka BP. In the following article, zooarchaeological results are presented with important implications in hunting behaviour and subsistence strategies. The scarcity of comparative data from MIS 4 sites in continental and peninsular Italy does not provide hints for evaluating the significance of De Nadale in Neanderthal land-use, rather discussing differences on a diachronic scale with MIS 3 Middle Palaeolithic archaeofaunal assemblages in the same region.

1. Introduction

Reconstructing Neanderthal subsistence strategies is one of the most challenging goals in prehistory and in paleoanthropological studies that researchers have been conducting for decades. This topic has been part of a long-standing argument into how similar or how different Neanderthals were to us (Grayson and Delpech, 2002, 2006; Discamps et al., 2011; Yravedra et al., 2016, among others). A large amount of papers has demonstrated that Neanderthals subsisted primarily on hunting herbivores, possibly complemented by scavenging (Grayson and Delpech, 1994; Stiner, 1994, 2005; Gaudzinski, 1995, 1996; Gaudzinski and Roebroeks, 2000; Speth and Tchernov 1983, 2001, 2007; Burke, 2004; Ready, 2010; Rendu, 2010, among others). Nevertheless, current studies hold that Neanderthals were skilled hunters of large mammals and that they had great behavioural flexibility, allowing them to exploit a wide spectrum of resources. Archaeological evidence attests, for example, the exploitation of marine food resources, including mammals, fishes and molluscs (Stiner, 1994, 2009/2010; Stringer et al., 2008; Colonese et al., 2010; Cortés-Sánchez et al., 2011; Hardy and Moncel, 2011; Nabais and Zilhão, 2019), of small game (Stiner et al., 2000; Hockett and Haws, 2002; Alhaique et al., 2004; Miracle, 2007; Blasco and Fernández Peris, 2012; Cochard et al., 2012; Carvalho et al., 2018; Romandini et al., 2018a; Morin et al., 2019), of birds (Peresani et al., 2011; Finlayson et al., 2012; Romandini et al., 2014b, 2016; Blasco et al., 2016; Laroulandie et al., 2016), and of carnivores (Auguste, 2003; Petram et al., 2004; Camaròs et al., 2017; Romandini et al., 2018b). Several studies on isotopes, dental calculus and dental microwear pointed out the key role of vegetal component in Neanderthal's dietary spectrum, in addition to the meaty component. Some researchers, for instance, have revealed a large use of legumes in Kebara Cave (Lev et al., 2005), grass seed phytoliths in Amud Cave (Madella et al., 2002), starch grains in Shanidar (Henry et al., 2014), mushrooms, nuts and moss in El Sidron Cave (Weyrich et al., 2017) and various plant micro-remains in several specimens of the Mediterranean area (Power et al., 2018).

Despite this recently broadened dietary spectrum, however, the critical component of Neanderthal subsistence was the exploitation of large and medium-sized ungulates (Stiner, 1994; Conard and Prindiville, 2000; Patou-Mathis, 2000; Bocherens et al., 2005; Bocherens, 2009; Gaudzinski-Windheuser and Niven, 2009; Daujeard and Moncel, 2010; Ready, 2010; Discamps et al., 2011; Morin, 2012; Fiorenza et al., 2015; Morin et al., 2016; Marín et al., 2017 among others).

The topic is of crucial importance also in the North of Italy, where

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several studies have been carried out on a zooarchaeological base (Cassoli and Tagliacozzo, 1994a,b; Peresani, 2001, 2015; Alhaique et al., 2004; Fiore et al., 2004; Thun Hohenstein, 2006; Thun Hohenstein and Peretto, 2005; Romandini et al., 2014a; Romandini et al., 2018a-b; Terlato et al., 2019). In order to contribute with further information to these investigations, the following study presents zooarchaeological evidence from De Nadale Cave, a single-layered context in north-eastern Italy. This paper focuses on the taxonomical and taphonomical analysis of a faunal assemblage that dates back to the onset of the MIS 4 (at minimum) and is associated to a Quina lithic assemblage. The De Nadale Cave plays a crucial role in the knowledge of Neanderthal presence in north-eastern Italy since it sheds new light on a poorly known period in this part of Mediterranean Europe.

2. The regional context

The De Nadale cave is located in the Berici Hills area, a karst plateau situated halfway between two similar formations, the Lessini Mounts and the Euganean Hills. The site looks onto the Calto valley, a narrow V-shaped basin where some active water springs are found in its inner zones.

This area in the North-East of Italy, which is part of the Veneto region, is characterized by the presence of three primary geomorphological units. Indeed, its landscape is dominated to the south by the alluvial plains of the two main rivers (the Po and the Adige rivers), to the north from the eastern sector of the pre-Alps (the Lessini mounts) and, to the south-east, by two small sub-alpine massifs (the Berici and the Euganean Hills). The Alpine foreland is a vast alluvial plain that mostly originated during the Middle and Late Pleistocene from the main rivers like the Po, the Adige and the rivers of the Friulan-Venetian plain. While the western region of the Alpine belt includes narrow and deep valleys alternating with summits that can reach 1800–2000 m and steep slopes, the eastern area presents wider and larger basins. This region also includes hills of different origins, such as the Berici Hills and the cone-shaped volcanic reliefs of the Euganean Hills, which are separated by the spreading outwash of the aggrading plain.

The Berici Hills are a karstic plateau at an average elevation of 250 m a.s.l., with a honeycomb of sink-holes and various depressions that delineate an extremely uneven topography with peaks and karstic blocks. The plateau is dissected by depressed systems (e.g., the Fimon, Liona, and Calto valleys) with pocket-valleys where ephemeral streams produced swampy environments and fed historic mills. The slopes are steep all around. To the east, a steep slope with rock cliffs connects the plateau to the alluvial lowlands that were occupied by marshes and swamps during the Pleistocene and earlier phases of the Holocene. To the west, the plateau gently connects to alluvial lowlands originated from the eastern Monti Lessini streams. In the southern eastern area, the Pozzolo depression is a wide trench cutting through the plateau in a NW-SE direction and with an elevation of 150 m. Its ancient karst surface is covered with palaeosols and thick red clayey residual deposits (Sauro, 2002).

This specific geomorphological context has been heavily investigated for the last years and turned out to be extremely rich in evidence dating back to the Middle Palaeolithic: over 20 Mousterian open-air sites, caves or shelters have been discovered (Fig. 1) (Leonardi and Broglio, 1962; Bertola and Peresani, 2000; Peresani, 2001, 2015; Fiore et al., 2004; Duches and Peresani, 2009), with additional sites and findings in the Euganean Hills (Peresani and Perrone, 1999; Duches et al., 2008; Peresani, 2013). Regarding open-air sites – such as, for example, Monticello di Barbarano (Duches and Peresani, 2009), Monte Versa (Peresani, 2000–2001), Gualivone and Monte del Cason (Bertola and Peresani, 2000) – they are attested by only lithic artefacts embedded in pedo-stratigraphic sequences or found dispersed on the surface and they vary in morphological position, distance from lithic sources and techno-typological features of the lithic industries. Caves and shelters, instead, are exclusively set along the eastern side of the Berici Hills, where Broion Cave and Broion Rockshelter (150 m a.s.l.), Paina Cave (335 m a.s.l.), Col de la Stria Cave (365 m a.s.l.) and San Bernardino Caves (135 m a.s.l.) open (Fig. 1). While Paina, Col de la Stria and San Bernardino Minor Caves yielded few artefacts (Bartolomei et al. 1987-88), the San Bernardino Major Cave and the Broion Cave have produced complete evidence. Both of them preserved traces of human occupation across the whole stratigraphic sequence and the lithic industries show to be dominated by the Levallois knapping method (Peresani, 1995-96; Picin et al., 2013), even if different provisioning strategies took place (Peresani and Porraz, 2004).

3. The site

De Nadale Cave is a small cavity that opens in the Southern slope of the Berici Hills, at 80 m a.s.l., overlooking the narrow Calto valley, a lower area rich in springs and moist zones. The cave was first reported in 2006 by a collaborator of the University of Ferrara, who found several mammal bones and lithic implements on the surface of reworked sediments resulting from present-day burrowing animals and recent anthropic activities. After the removal of the reworked sediments in 2013, the entrance of a small cavity 8 m wide, almost filled by layered deposits, was discovered. Six excavation campaigns have been carried out, starting from 2014 until 2017, in order to investigate the deposit preserved at the cave entrance (Jéquier et al., 2015).

The excavations exposed a short stratigraphic sequence, including one single anthropic layer (Unit 7) embedded between sterile levels (Units 6 and 8), lying on a flat pavement coincident with the horizontal bedding of the local carbonate sandstone bedrock.

The original geometry of the Pleistocene deposits and the spatial extension of the stratigraphy are still not easy to determine: ongoing researches are in progress to evaluating the depth of the cavity and the planimetry of the site. However, the field excavations have exposed its most complete section on the west, where a group of Units (3, 6, 7, 8) tilted to an angle of 15° to the north, is visible. Among them, only Unit 7 has been recognized as an anthropic layer: this is the Mousterian archaeological layer and consists of dark brown-grey silt loam with medium-small sized, sub-rounded rocks. This Unit was also disturbed by badger dens, partially emptied during the last two excavations (Units 12, 13, 14, 15 and 16). All these pits were characterized by a circular shape and the almost unique presence of rounded and loose pebbles; among them, a significant number of bone fragments and lithic remains has been recovered, mixed with recent bones and other organic matter. Apart from this, Unit 7 is well preserved and extends into the cave. It has yielded thousands of fragmented bones, flint implements, few tiny fragments of charcoal and a Neanderthal deciduous tooth (Arnaud et al., 2016). In the north-eastern part of the cavity, about 40/50 cm underneath the vault, two concentrations of charcoals and burnt bones (structures 7SI and 7SII, Fig. 2) have been interpreted as dumping areas or residual hearts. Below Unit 7, Unit 8 is archaeologically sterile, even though a few flaked stones and bones were recovered at the top, close to the boundary with Unit 7. This material has been attributed to Unit 7. Among all the bone fragments recovered, a second lower molar of a large-sized ungulate has been chosen to perform a U/Th dating: it provided a minimum age of 70.2 + 1/-0.9 ka BP (Jéquier et al., 2015).

This result is consistent with the paleoenvironmental and paleoclimatic reconstruction based on small-mammals (insectivores, bats and rodents) assemblage from the anthropic layer. The presence of *M. arvalis*, which is the most abundant *taxon,* and which is currently reported to be more common in open areas and relatively drier regions, identifies a cold climate phase, with a landscape dominated by open woodland formations and open dry meadows. Taking into account the chronology of the site, this has been associated with the very beginning of MIS 4 (López-García et al., 2018).

Based on the ecological conditions inferred from the Fimon Lake pollen associations, the Berici area during the transition from MIS 5 to MIS 4 recorded no sharp decrease of Arboreal Pollen %. After a

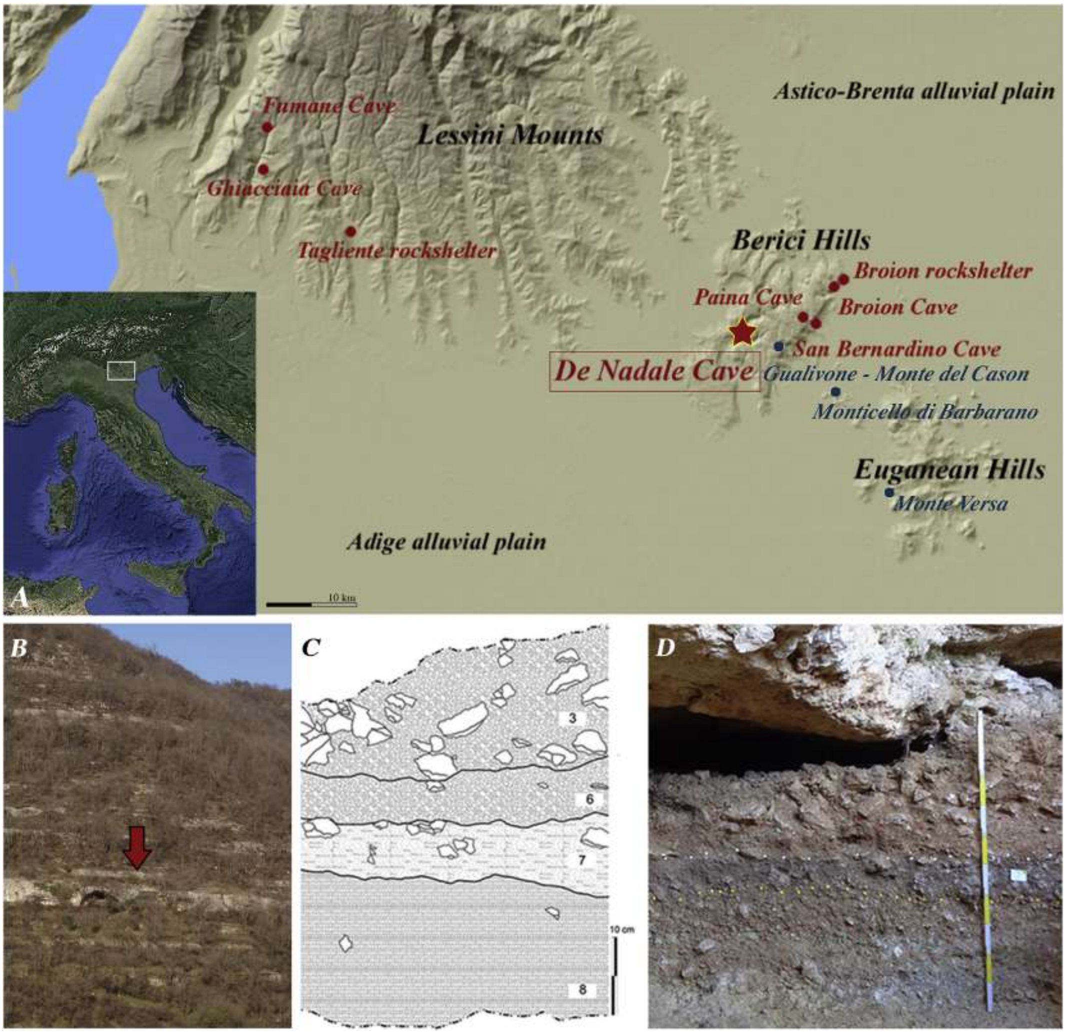

Fig. 1. A sector of the northern Adriatic area with position of De Nadale Cave and Paleolithic sites cited in the text (A – caves and rockshelters in red, open air sites in blue); the location of the De Nadale Cave, at mid-elevation on the southern slope of Monte Spiadi, indicated by the arrow (B); sketch of N section (C - dotted lines show the roof and the bedrock of the cave); the N section showing the archaeological Unit 7 (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

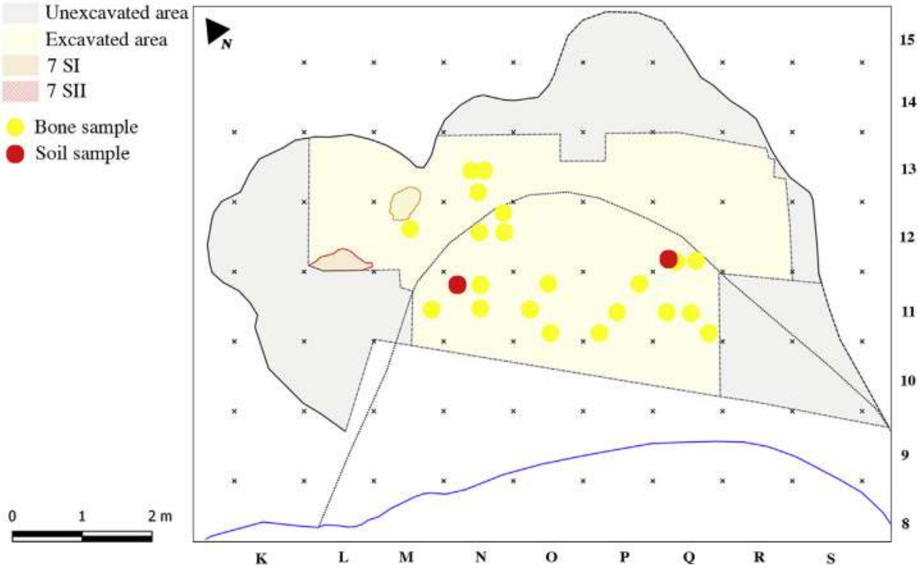

Fig. 2. Plan of the cave with the location of the two possible anthropic structures (modified from Govoni, 2018) and the location of the bones sampled for FT-IR analysis.

moderate decline of *Picea* sp., a mild oscillation enhanced strong expansion of *Betula* sp., *Alnus* sp. and *Tilia* sp. pollen and was followed by a further increase of steppe communities, giving origin to a mosaic of boreal forest and steppe (Pini et al., 2010).

The technological and typological features of the lithic technocomplex make this industry different from the Mousterian of the rest of the region, especially concerning the method adopted in core reduction, and the type of blanks and retouched tools. The reduction sequence recognized at De Nadale Cave, with the presence of 55 scrapers and invasive retouch (Jéquier et al., 2015), is comparable with Quina assemblages in Italy and south-western France (Palma di Cesnola, 2001; Bourguignon, 1997). Given the absence of provisionable lithic raw material in the site nearby, chert was sourced in a district bounded from the eastern side of the Berici Hills and the western side of the Euganean Hills, and the central-western Lessini (20–80 km far from De Nadale).

4. Materials and methods

At De Nadale Cave, 30654 osteological fragments have been unearthed during the seven excavation campaigns, which interested a 19 m^2 area. All the specimens that were at least 5 cm long or identifiable were spatially recorded during the excavations, using an electronic theodolite. Sediment was water-screened using a superimposed mesh from 5 to 0.5 mm and all the bone fragments were recovered after sieving and considered for this study.

In the current state of research, zooarchaeological analyses have been carried out on the whole osteological sample, including bones and teeth recovered in the abovementioned badgers' dens. All of them have been studied and classified from the taxonomical and taphonomical point of view. This paper focuses especially on 28088 fragments of animals' bones and teeth that represent the totality of the remains yielded by the ensemble of Units 6base, 7, 8tetto and their interfaces (hereafter Unit 7). They are considered to be archaeologically and stratigraphically affordable, while the rest came from reworked layers and dens filled up with materials mixed to nowadays deposits. These fragments, yielded by reworked layers and dens, are not completely meaningless to the zooarchaeological analysis, considering that their preservation is consistent with the osteological material of the Unit 7 and that the site is characterized by the presence of a single anthropic layer. Evaluating these bone remains is particularly suitable to have a complete estimation of bone retouchers, whose number increases considerably if we include the fragments from reworked layers. Despite not being stratigraphically reliable, there is no doubt about their Mousterian origin.

Taxonomical and anatomical identifications made in this study are based on the complete Alpine fauna reference collection of the Department of Humanities at the University of Ferrara with the help of the well-established literature (Davis, 1987; Lyman, 1994; Reitz and Wing, 2008; France, 2009).

Remains, both identified and those considered unidentifiable on the basis of morphological or size characteristics, have been grouped into five mammal body-size classes, following Bunn et al. (1988): I - small (i.e. *Lepus* sp. and other lagomorphs, Mustelidae*, Vulpes vulpes*); II - small-medium (i.e. *Capreolus capreolus*, *Rupicapra rupicapra*, *Canis lupus*); III - medium (i.e. *Capra ibex*, *Sus scrofa*); IV- medium-large (i.e. *Cervus elaphus*, Ursidae); V- large (i.e. *Megaloceros giganteus*, Bovinae). This partition has been considered more useful to evaluate the faunal assemblage of De Nadale Cave since it underlines the difference in body-size between red deer and giant deer/bovids.

Following the criteria of birth of modern animals, teeth eruption, replacement sequences and dental wear have been used to establish the age at death of the animals, as well as the state of fusion of the epiphysis. Among the ungulates, we considered mainly *Capreolus capreolus* (Aitken, 1974), *Cervus elaphus* (Mariezkurrena, 1983; Hillson, 1986; D'Errico and Vanhaeren, 2002), and bovids (Habermehl, 1975; Bunn and Pickering, 2010; Silver, 1969). In order to avoid distortion in the proportions of age groups in the various units, estimations were also calculated for those remains generally identified as Bovines by considering only the age or the size of the animal not represented in the two categories of the determined taxa (*Bison priscus* and *Bos primigenius*). The collection coming from the paleontological site of Settepolesini di Bondeno (Italy) has been used to give indications about the age of *Megaloceros giganteus* specimens. In this regard, five categories have been identified, following those proposed by Bunn and Pickering (2010) and by Marí;n et al. (2017): 1) young juvenile (I – 0–5 months; deciduous teeth); 2) subadult juvenile (J – 5–30 months; M3 in eruption); 3) early prime adult (AD I – 30–78 months; complete permanent dentition without wear traces); 4) late prime adult (AD II – 78–144 months; complete dentition with light wear traces); 5) old adult or senile (S – > 144 months; permanent dentition with heavy wear traces). Regarding seasonality, data are too scarce to provide a high-quality interpretation. However, ongoing researches on this topic, carried out by means of the cementochronology and microwear analyses on ungulates' teeth, will provide more specific results that can also be useful to interpret the meaning of the narrow prey spectrum noted at De Nadale Cave.

Concerning the skeletal part profiles, all taxonomically identified specimens, including shaft fragments, were taken into account. NISP (Number of Identified Specimens, Grayson, 1984) and MNI (Minimum Number of Individuals, Bökönyi, 1970) indexes were used in order to evaluate species abundance. Estimation of MNI was based on all of the skeletal elements (bones and teeth), even if the most reliable specimens turned out to be the tibia, especially for ungulates, and teeth for carnivores. Minimum Number of Elements (MNE) (Binford, 1981; Klein and Cruz-Uribe, 1984; Stiner, 1994) and fragmentation indexes (Binford, 1981; Brain, 1981; Lyman, 1994) were calculated to evaluate the skeletal representation of different animals and the skeletal survival rate. The following formula was used to calculate the % of survival of anatomical element = (MNE x 100)/(NEE - number of expected elements).

Concerning the taphonomic analyses, samples of bones and of sediments (Fig. 2) has been selected from Unit 7 to investigate on diagenetic processes with the intent to further contribute to the reconstruction of the history of bone taphonomy, the sedimentary context and the modifications occurred (Quattropani et al., 1999; Weiner et al., 1993; Berna et al., 2004; Cohen – Ofri et al., 2006; Karkanas and Goldberg, 2010; Kontopoulos et al., 2019). The main goal of this analysis is to detect the differences in the preservation of bone remains, yielded by two opposite areas of the site. All bone surfaces were evaluated both at macroscopic and at microscopic level: the first examination was effectuated using a hand lens (magnification 10x) under a low-angle light, while the second with a Leica S6D Greenough stereomicroscope with 0.75–70X. Remains coming from the western area appear to be more brownish and with a solid texture, while fragments found in the eastern zone are light-coloured and more fragile. While the reasons for the changing in the preservation status between osteological material found in caves or shelters and remains yielded by open air contexts are well documented, situations in which changes in preservation develop inside the cave, according to the area of the cavity itself (Quattropani et al., 1999; Weiner et al., 1993), are still considerably unknown. The study of this diversity has been carried out observing thin sections from bones and applying Fourier Transform Infrared spectroscopy (hereafter FT-IR) executed at the Department of Chemical and Pharmaceutical Sciences of the University of Ferrara.

Thin sections have been realized on 21 remains which shared common features. Shafts of long bones of large sized animals, without anthropic traces, yielded by distinct areas of the archaeological layer and showing a microscopically different state of preservation were selected. The material has been recognized to be homogeneous (as far as possible) in terms of size: the 21 remains shared a set of dimensional features that make the bones suitable for comparisons (i.e. average length between 4 and 5 cm, average width between 2 and 3 cm and

Table 1
The faunal assemblage at De Nadale Cave: NISP, %NISP and MNI by age classes. The value written in brackets refers to two adult individuals recognized as generic bovids not distinguishable from the other *B. priscus* or *B. primigenius* adult individuals on the basis of age. Those, therefore, have not been added to the bovids MNI.

Taxa	NISP	*% NISP*	MNI by age classes					MNI
			I	J	AD I	AD II	S	
Canis lupus	3	*0.7*				1		1
Vulpes vulpes	3	*0.7*				1		1
Ursus spelaeus	8	*1.7*		2		1		3
Ursus sp.	18	*3.9*						
Meles meles	1	*0.2*				1		1
Mustelidae	1	*0.2*						
Carnivora undet.	3	*0.7*						
TOTAL Carnivora	**37**	***8.1***						
Sus scrofa	1	*0.2*				1		1
Megaloceros giganteus	126	*27.5*		2	1	4	1	8
Cervus elaphus	127	*27.7*		2	4	2	1	9
Capreolus capreolus	20	*4.4*		2		2		4
Cervidae	59	*12.9*						
Bison priscus	10	*2.2*				3		3
Bos cf. *primigenius*	1	*0.2*				1		1
Bovinae	69	*15.1*		1		(2)		1
Capra ibex	1	*0.2*				1		1
Rupicapra rupicapra	3	*0.7*		1		1		2
Caprinae	4	*0.9*						
Ungulata	1645							
TOTAL Ungulata	**2066**							
TOTAL NISP	**458**	***100.0***						
Small-medium sized mammals	5							
Medium sized mammals	17							
Medium-large sized mammals	22							
Large sized mammals	1285							
Undet. sized mammals	24646							
Total mammals undet.	25975							
Pisces	1							
Aves	9							
TOTAL NR	**28088**							

average thickness between 1 and 2 cm. Observations were conducted with Olympus BX 51 microscope. The films of sesquioxides of Fe and Mn were classified according to a scale ranging from 0 to 2: −0 = absent; −1 = present in superficial fissuring; −2 = present inside the assemblage.

FT-IR analyses were carried out on 9 samples, given the substantial homogeneity of the preservation detected on the thin sections (see section 5.1). Two soil samples have been added to these remains, from squares Q12 b-e, N11c in order to have a comparison framework of the osteological specimens. The powders extracted from the samples were analysed with a Bruker Vertex 70 in diffuse reflectance, set at 16 scans with the spectra range from 4000 to 400cm-1. The data were interpreted using existing bibliography and the reference collection of FT-IR spectra of standard materials provided by the Kimmel Center for Archaeological Science, Weizmann Institute (http://www.weizmann.ac.il/kimmel-arch/infrared-spectra-library).

In order to identify the nature of bone surface alterations and to distinguish human from animal traces (pits, punctures, scores, furrowing, scooping-out, etc.), trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was made to taphonomic literature (Binford, 1981; Brain, 1981; Shipman, 1981; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Blumenschine, 1995; Blumenschine et al., 1996; Fisher, 1995; Domínguez-Rodrigo and Piqueras, 2003; Fernández-Jalvo and Andrews, 2016). Evidence of anthropic modification has been achieved by considering the type, the position and the orientation of the cutmarks. Cutmarks have been classified as incisions and scraping marks (Binford, 1981; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983, 1984; Lyman, 2008). An incision is defined as a striation with a linear outline, a V-shaped section and common internal microstriations, while a scraping mark is a shallow sub-parallel cutmark caused by a stone tool dragged transversally along the length of the bone (Shipman and Rose, 1983, 1984; Bromage and Boyde, 1984; Noe-Nygaard, 1989). In order to hypothesize the performed action (skinning, de-fleshing, periosteum removal, etc.), a brief description of the cutmarks was made, taking into account the number of striations, their location and distribution on the bone and their orientation. Chopmarks have also been observed. A chopmark is defined as a broad, relatively short, linear depression that generally has a V-shaped cross section (Fisher, 1995; Lyman, 2008 among others).

Anthropic traces caused during bone breakage for marrow extraction were analysed and divided into two categories: percussion marks and impact flakes. Percussion marks are semi-circular shaped sockets located on the fracture edges with corresponding negative flake scars. Impact flakes refer to positive flakes of the percussion notches derived from the action of breaking the diaphysis (Blumenschine and Selvaggio, 1988, 1991; Capaldo and Blumenschine, 1994; Blasco et al., 2013; Vettese et al., 2017). Intentional bone breakage to access marrow has been recognized by analysing the shape of the fragmented ends of the shafts themselves (Villa and Mahieu, 1991; Blumenschine, 1995; Fisher, 1995; Outram, 2001; Grunwald, 2016; Coil et al., 2017). According to excavation protocol, non-anthropic traces such as natural post-depositional degradation and animal chewing were identified only on 5 cm long objects - or longer ones - or on those taxonomically relevant.

The degree of combustion was evaluated by employing the methodology developed by the well-established literature; burnt bones have been divided into two different categories: calcined (> 700 °C, grey/white) and subject to moderate combustion (200–500 °C, black/brown) (Shipman et al., 1984; Stiner et al., 1995; Théry-Parisot, 2002; Théry-Parisot et al., 2005; Costamagno et al., 2005; Mentzer, 2009).

5. Results

In Unit 7 of De Nadale Cave, 28088 bone fragments have been unearthed. Within the analysed sample, it has been possible to identify 2103 remains of mammal species, 1 remain of fish and 9 remains of avifauna, which correspond to 46 individuals, from 13 taxonomic groups (Table 1).

5.1. General taphonomic observations

In general, an excellent preservation of the osteological material has been observed. The most common post-depositional modification is the presence of manganese stains that affect the bones surface in a high proportion: 43.5% of the fragments present this kind of oxide. Degradation due to root-etching is attested in a lower, but still significant, rate (33.1%). The percentage of carbonate concretions is quite relevant (18.6%) and the osteological shafts showing that alteration are plentiful; they have been found mainly along the boundary of the inner part of the cave, close to the walls, where dripping and water percolation are abundant. Trampling traces (16.4%) are common and can be associated with the rocky composition of the sediment. Some shafts show micro fissures from weathering and/or weathering cracks (13.6%), rare exfoliations (1.5%), chemical corrosion (2.6%) or roundings (0.8%).

Observations of the thin sections (Fig. 3) reveal that the bone tissue is well preserved. The Haversian systems are clearly recognizable and not shattered in most of the cases. This result is consistent with the scarcity and doubtful presence of fluoride carbonate detected by FT-IR

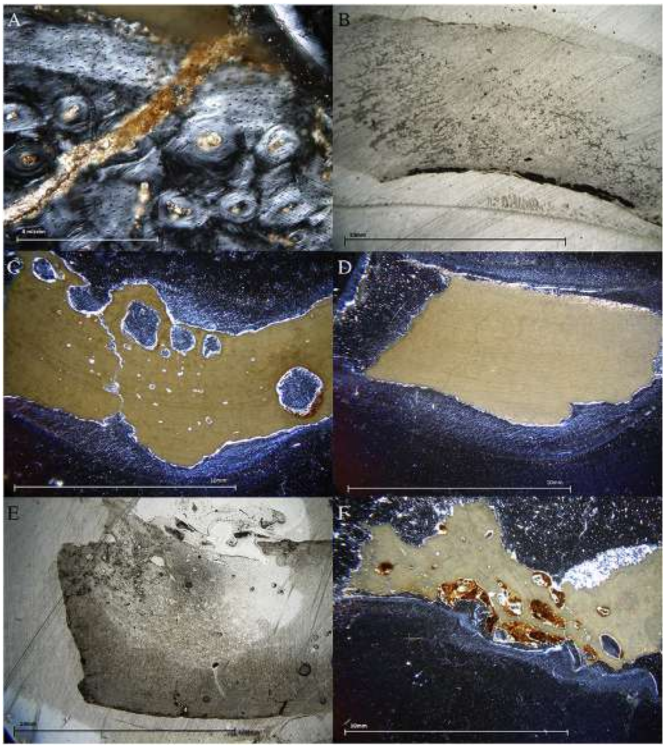

Fig. 3. Micrographs from bone thin sections: presence of Fe and Mn (XPL - 200X) (A); (B) tunnelling due to fungi attack (PPL - 12.5X) (B); trace of fissuration (XPL - 12.5X) (C); presence of Mn and Fe 0 (D) (XPL - 12.5X); the presence of Mn and Fe 1 (PPL – 12.5X) (E); the presence of Mn e Fe 2 (XPL – 12.5X) (F).

analyses confirming the low degree of diagenesis and structural modifications in which these faunal specimens have been incurred and the great abundance of carbonate hydroxyapatite. Bone trabeculae, where present, are filled by infiltrations of Fe–Mn sesquioxides. These characteristics are equally distributed among the sample (Fig. 4). Fe 0 appears in almost all the specimens. Fe 1 appears well distributed like Fe 2. Mn 0 is present and well distributed among the various parts, while Mn 1 and 2 appear more present in the N-M squares. It is important to note that the Mn 0 is always in association with the Fe 0, the Mn 1 always with the Fe 1, and the Mn 2 always with the Fe 2. Fe 1 and 2 are not always associated with Mn of type 1 and 2. This could explain the different coloration of the faunistic finds in the two zones: in fact, in the area N–W the bones appear more yellow/ochre coloured. The presence of iron not linked to the presence of manganese indicates that the deposit underwent substantial fluctuations in terms of humidity. This is, probably, linked to the repeated cycles of humidity that may have affected the deposition of manganese.

Finally, a fissuration trace is present only in N11e, perhaps attributable to frost-thaw. Tunnelling traces due to fungi are present on three samples located in squares Q and O. This is associated with the presence of oxides: microorganisms such as bacteria and fungi can cause the precipitation of oxides that accumulate on the findings if affected by oxidants conditions. However, microbiotic activity could be stimulated even in the presence of large quantities of organic matter (Courty et al., 1989).

FT – IR spectroscopic analysis of bones reveals that peaks around 2900cm-1 indicate the presence of CH2 and-CH3 groups (Fig. 5, A – B). The range of vibrations from 1350cm to 1 to 1500cm-1 due to the functional-CO group, relates to the presence of carbonates, and those between 900cm-1 and 1200cm-1 that can be attributed to PO-groups, confirms the presence of phosphates. More specifically, it would be carbonate hydroxyapatite (Dahillite), confirmed by the key peaks for its recognition at 1414cm-1 and 872cm-1 and from the peak to 565cm-1 higher than that at 603cm-1 (Weiner, 2010).

In soil samples (Fig. 5CandD), in 1350cm-1 - 1500cm-1 range, there is the presence of –CO groups, calcium carbonate. In 900cm-1 - 1200cm-1 range phosphates, -PO groups. It is also possible to identify the clay's typology. Peaks at 3622cm-1, 914cm-1, 778cm-1, 472cm-1 suggests presence of Montmorillonite's minerals and peaks at 3695cm-1, 540cm-1 presence of Kaolinite. Organic matter is identified with the peaks at 1737cm-1, –COOH groups, that indicates humus' presence and 1615cm-1 peaks, referred to Amide I, collagen. Organic fraction, possibly related to roots in the soil, seems to be confirmed by the -CH3 e -CH2 groups, identified at 2930cm-1 e 2850cm-1 peaks.

This context presents clays that tend to form a typically acid

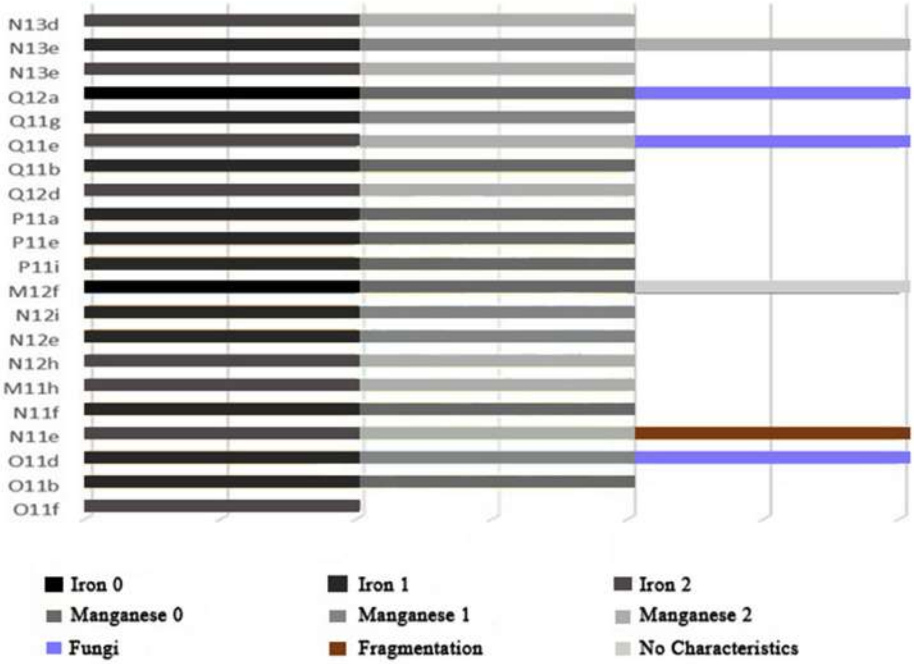

Fig. 4. Most relevant features observed on the bone thin sections from layer 7 listed in accordance with the grid system.

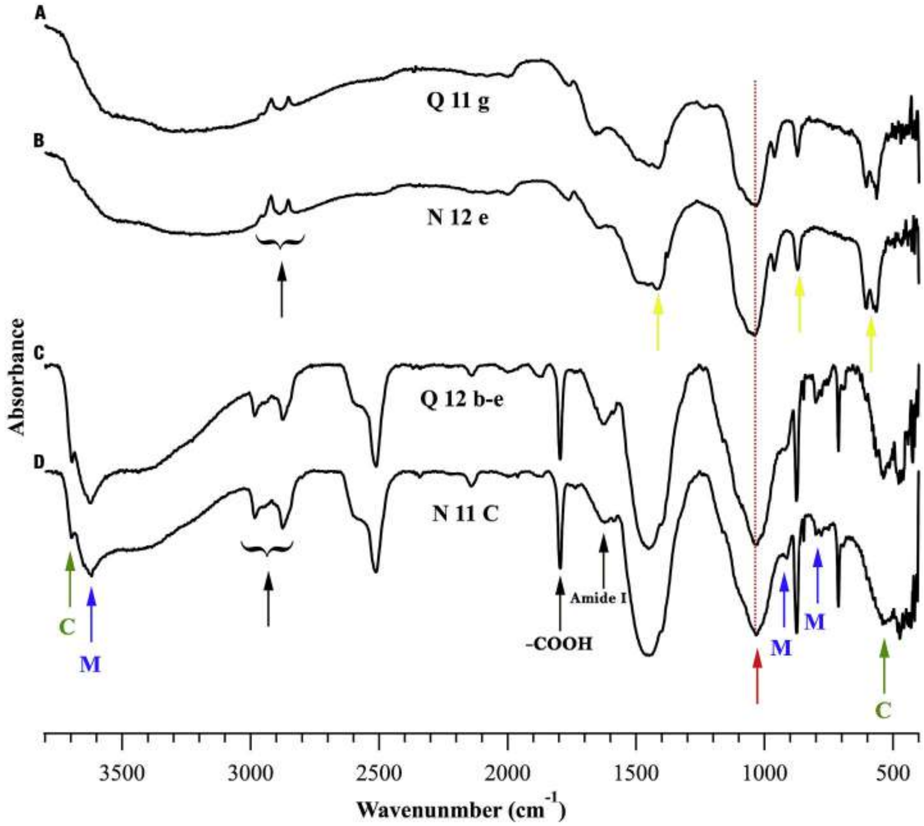

Fig. 5. FT-IR spectra of bone samples (A–B) and soil samples (C–D) from layer 7. Bones: sq. 11g and 12e showing peaks of Carbonate - idroxiapatite (Dahillite, yellow), –CO group (1350 cm^{-1} – 1500 cm^{-1} range), -PO group (red), -CH2/-CH3 groups (black, around 2900 cm^{-1}). Soil: sq. Q12b-e and N11c showing additional peaks of Montmorillonite (M), Caolinite (C), organic matters (-COOH/Amide I). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

situation with, however, the presence of calcium carbonates and phosphates in significant quantities that, conversely, certify alkaline/sub-alkaline contexts. In fact, phosphates can react with clays. This tends to happen in acidic conditions: clays lose a sheet of tetrahedrons, becoming structurally more similar to Kaolinite, and more stable forms of phosphates tend to form (Weiner, 2010). This would explain the quantitatively minor presence of Kaolinite in the soil and the abundance of carbonate hydroxylapatite.

5.2. *Composition of the assemblage*

Among the 2103 mammals remains, the 21.8% (NISP: 458) has been identified both at an anatomical and at a specific level, while the 78.2% has been recognized as generic Ungulata (NR: 1644) or Carnivora (NR: 3). 25975 fragments have been categorised as generic mammals and sorted into the abovementioned body-size classes (Table 1) since no other more specific identification was possible. Considering the totality of the osteological fragments (NR: 28088), only the 1.6% (NISP: 458) of the whole sample has been recognized at a precise taxonomical and anatomical level. This is due to the high rates of breakage (the 87.5% of the remains are smaller than 2 cm) and combustion (49.6%).

At De Nadale Cave, red deer (*Cervus elaphus*) and giant deer (*Megaloceros giganteus*) are the most represented species, according to NISP and MNI (Fig. 6). Large bovids (*Bison priscus; Bos primigenius* and Bovines) are also abundant according to the MNI, although the NISP for them is considerably lower than for other taxa. Other 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 also rare and they have been identified as belonging to cave bear (*Ursus spelaeus*) and other non-identifiable bear species, wolf (*Canis lupus*), fox (*Vulpes vulpes*) and badger (*Meles meles*).

Bones grouped into body-size categories display the same tendency as the one observed in the taxonomic representation: elements of the large-sized carcasses (NR: 1285) are the most frequent even if the possibility or underrepresentation of the other categories is to be taken into account. This is due to the high fragmentation of the assemblage that makes the recognition of the body-size class not always possible, as proved by the unidentified size fragments (NR: 24646, 89.2%). Cervids' remains follow the same tendency: all the 59 fragments have been recognized as belonging to the medium-large and large-sized animals' category (IV/V, following Bunn et al., 1988).

5.3. *Age estimation and Minimum Number of Individuals*

Concerning age distribution (Table 1), the predominance of late prime adults is evident, although the proportion of juvenile individuals is also substantial.

For red deer, the combination of dental wear data and the state of epiphyseal fusion in the post-cranial skeleton shows that nearly all age classes are represented. Among the 9 individuals, at least, recognized in the faunal assemblage, two are subadult juveniles (5–30 months), four are early prime adults (30–78 months), two are late prime adults (78–144 months), and one is an old adult (more than 144 months) (Table 1). Regarding giant deer age distribution, the pattern is similar but slightly shifted to the late prime adult category: among the 8 individuals, two are subadult juveniles, one is an early prime adult, four are late prime adults and one is an old adult.

On the other hand, the age distribution trend is different considering *Ursus spelaeus* that shows a slight predominance of younger on adult individuals. Nevertheless, the presence of infants and very young animals is remarkable and can lead to interesting future hypotheses about the seasonality and the timing of the occupation of both humans and carnivores. In this regard, important hypotheses can be inferred by the presence of a fragmented radius belonged to a foetal individual of a large-sized herbivore.

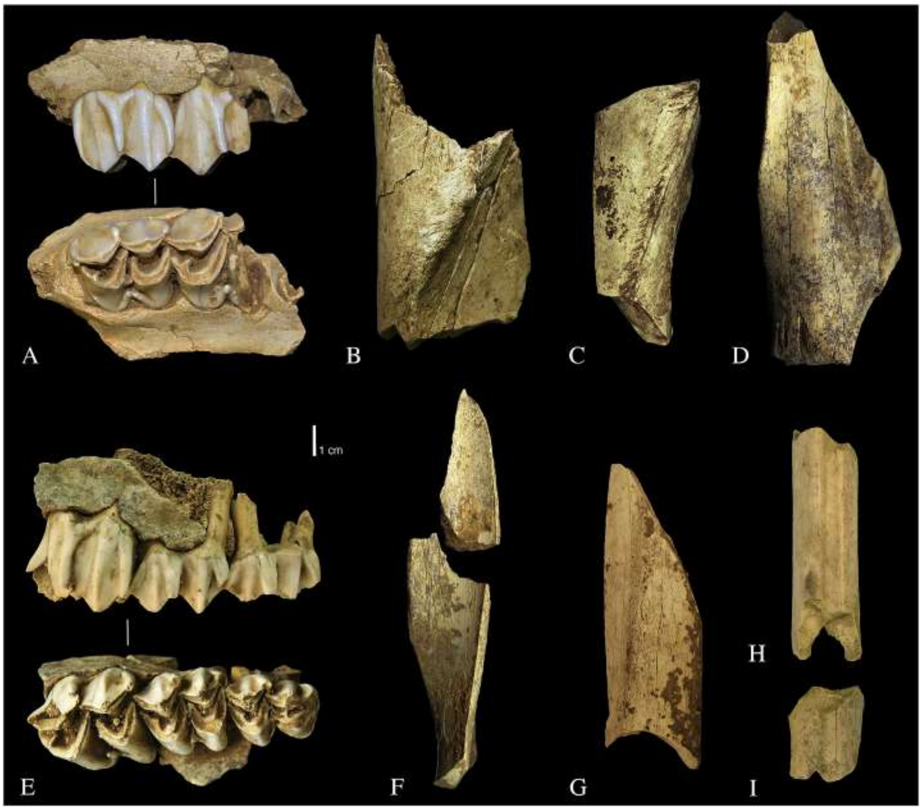

Fig. 6. Bone shafts from Unit 7. *Megaloceros giganteus*: right maxilla and teeth (A), left humeri (B, C) and right radius (D); *Cervus elaphus*: right maxilla and teeth (E), left tibia with a post-depositional fracture (F), left tibia (G) and metatarsals (H, I).

5.4. *Carnivore, rodent and human modifications*

Bone modifications caused by carnivores or rodents are scarce: the first is attested on the 0.3% of the total number of remains and the latter on the 0.1%. Pits, scores and gnawing toothmarks on the diaphysis of large-sized animals are the main identified alterations. Regarding the shape and the dimension of these carnivore toothmarks, they seem to indicate that the main non-human predator that acted on the assemblage might be a medium-large/large-sized carnivore, with a dimension spanning from the one of a wolf to the one of a bear.

The incidence of burnt fragments, which represents almost the half of the total remains (39.4% are burnt and 10.2% are calcined), is elevated: within this group, 79.5% were subject to moderate combustion while 20.5% were calcined.

Among the whole assemblage, anthropic modifications caused by butchering have affected only ungulates (Table 2, Fig. 7). The butchering sequence is complete: 5% of all the recovered shafts bear anthropogenic modifications due to defleshing, skinning, marrow extraction activities, etc. This percentage grows if we consider only the determined fragments (63.7%). Cutmarked bones are frequent in the assemblage: most of these human traces are incisions (63.1%), although scraping marks related to periosteum removal activity and chop marks were identified (16.7%). The incisions are usually located on the bone shafts and they are either longitudinal or oblique. This kind of cutmarks are mainly caused by defleshing, even if some of them, located on cranial fragments and ribs suggest skinning and removal of viscera. Removal of fat and periosteum is documented from scraping marks. On the other hand, chop marks, which are few, are associated with disarticulation and dismembering processes or tendons removal.

Diagnostic elements of anthropogenic breakage have been noted and documented on several faunal remains (Table 2, Fig. 7). Percussion marks, which are often associated with cutmarks, and impact flakes are the most represented. The faunal assemblage from De Nadale Cave is characterized by oblique, curved and smooth fractures, which indicate that the bones were mainly broken green. The result of this activity, carried on in order to extract marrow for an alimentary purpose, is a quite highly fragmented assemblage.

In the whole Unit 7, the amount (NR: 156) of shaft fragments that were used as retouchers to produce flint tools, is significant. Punctiform traces, linear impressions, retouch-induced incisions and notches related to this purpose were found mainly on bone fragments characterized by substantial weight and thickness, such as shafts identified as belonged to large sized herbivore (red deer, giant deer and bovids) (Jéquier et al., 2018; Terlato et al., 2019). The same situation has been noted regarding unidentified remains: 87 retouchers was determined as large-sized Ungulata (Table 2). Additionally, it is important to underline that the quantity of retouchers increases significantly if we add the remains yielded by the reworked units (interpreted as dens): in total 224 bone shafts have been recognized as implements used in the retouching phase of the lithic *chaine opératoire*.

5.5. *Skeletal part representation*

Considered as a whole, the assemblage is dominated by fragmented shafts and teeth, while epiphyses and spongy tissue are under-represented (Table 3). Ungulates skeleton, altogether, show the predominance of the limbs over the bones of the axial skeleton. The general trend is characterized by a significative presence of the long bones of the hindlimbs (tibia, femur and metatarsal in particular) and of the forelimbs (humerus, radius and metacarpals), followed by the paw bones (tarsals and carpals, phalanges and sesamoids), which are very scarce. In general, cranium fragments are present but rare and predominantly represented by isolated teeth and parts of the maxilla. The trunk and the spinal column are nearly absent.

A more detailed analysis can be carried out on the most frequent species, red deer, giant deer and bovids (Table 4, Fig. 8). Both red deer

Table 2
Ungulates with a list of butchering marks, thermal alterations and carnivore marks. CM: cut-marks; PM: percussion marks; CM + PM: cut-marks + percussion marks; IF: impact flakes; CM + IF: cut-marks + impact flakes; Tot. BM: Total butchering marks; %BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks. Percentages of butchering marks are calculated on the total NR for each taxon and on the total NR analysed in this paper.

Taxa	NR	CM	PM	CM + PM	IF	CM + IF	Tot. BM	% BM	R	B	C	GM
Sus scrofa	1	1					1	*100.0*				
Megaloceros giganteus	126	40	14	23	1		78	*61.9*	17	3	1	8
Cervus elaphus	127	55	9	13	2	1	80	*63.0*	27	6		4
Capreolus capreolus	20	2					2	*10.0*		1	1	
Cervidae	59	19	3	4	2	1	29	*49.2*	4			
Bison priscus	10	1	2	3			6	*60.0*				1
Bos cf. *primigenius*	1	1					1	*100.0*	1			
Bovinae	69	20	8	9			37	*53.6*	14			7
Capra ibex	1											1
Rupicapra rupicapra	3									1		
Caprinae	4	1					1	*25.0*				
Ungulata	1645	643	50	51	247	40	1031	*62.7*	86	448	58	61
Mammals undet.	25975	98	1	1	44	1	145	*0.6*	7	10622	2084	6
TOTAL	**28088**	**881**	**87**	**104**	**296**	**43**	**1411**	***5.0***	**156**	**11081**	**2144**	**88**

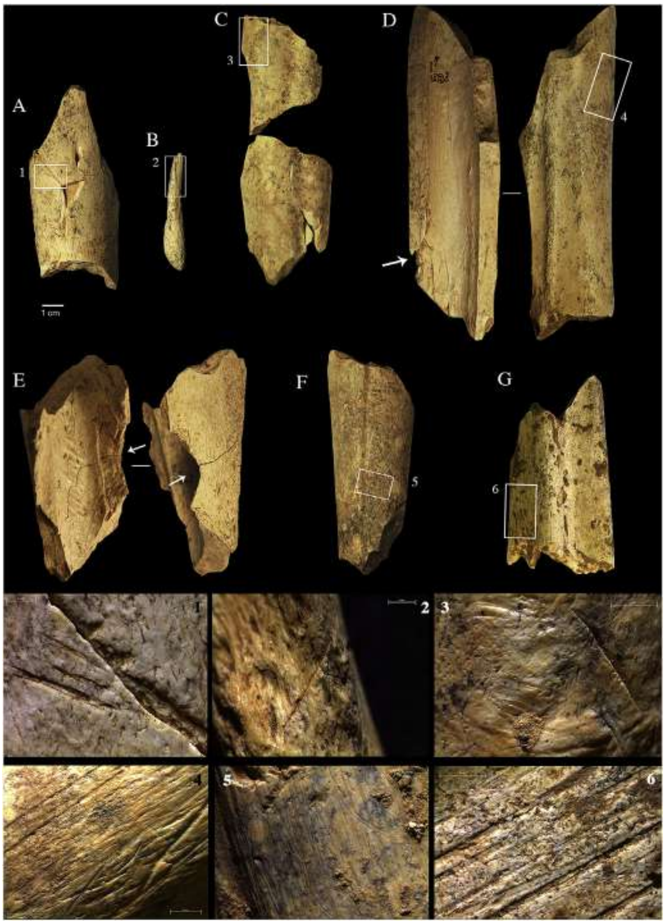

Fig. 7. Cutmarks and impact marks impressed on some of the recovered specimens, with closeups. *Cervus elaphus*: left femur (A, 1) and false metacarpal (B, 2); Bovinae: metacarpal (C, 3) and left tibia (D, 4); *Megaloceros giganteus*: left humerus (E), metacarpal (F, 5) and metatarsal (G, 6). Arrows indicate the impact marks.

Table 3
NR and % of diaphysis, epiphysis + spongy bone and unidentified elements, both burnt or calcined and unburnt.

	Unburnt		Burnt + Calcined	
	NR	%	NR	%
diaphysis	13660	*96.6*	13819	*99.1*
epiphysis + spongy bones	179	*1.3*	88	*0.6*
other elements + unidentified	306	2.1	36	*0.3*
TOTAL	**14145**	***100.0***	**13943**	***100.0***

and giant deer have been exploited in a similar way: the MNE shows a clear predominance of the limbs over the bones of the axial skeleton (Table 6). As shown by the survival rate values, in fact, the percentage of ribs, vertebrae and sternum elements that has been found in the assemblage, is meagre, both for *C. elaphus* (1.1%) and for *M. giganteus* (0.5%). The absence of the atlas and the axis is also remarkable, because these bones may have been still connected either with the cranium or with the rest of the spine when the head was disarticulated from the body. This trend is evident not only for red deer and giant deer, which are represented mainly by fragments of long bones shafts, but it becomes even more pronounced in the case of bison, aurochs, and remains identified as Bovines (Table 3). A similarly differential representation was also noted for medium-sized ungulates such as roe deer and chamois, which are missing ribs, vertebrae, and fragments of spongy tissue.

Much higher are the values for limb bones, among which tibia and metatarsal are always the most represented elements. Some differences can also be detected between forelimbs and hindlimbs representation. This issue is noticeable as regards the skeletal part representation of red deer (hindlimbs survival rate stands at 46.3%, while the same value for forelimbs stands at 15.1%) and the discrepancy is still present if we compare these values for giant deer (26% for hindlimbs and 21.9% for forelimbs), even if the trend is not so pronounced. Moreover, no carpals and just one tarsal of *M. giganteus* have been detected, while phalanxes are underrepresented (skeletal survival rates stand at 3.2% for red deer and 3.9% for giant deer). Cranial elements are more frequent for *M. giganteus* (%surv. rate: 16.7%) than for *C. elaphus* (%surv. rate: 7.4%), but they are not even close to the values of limbs.

The skeletal part representation of bovines' carcasses is to take into account to complete this scenario. Although the site did not yielded a number of remains sufficiently representative to calculate the skeletal survival rate, the frequency pattern of skeletal elements is close to the one of red deer and giant deer: hindlimbs turned out to be more present than forelimbs and, in general, limbs are more common than axial skeleton specimens (Terlato et al., 2019).

Table 4
MNE (Minimum Number Elements), NEE (Number Expected Elements), skeletal survival rate and fragmentation index of *Cervus elaphus*, *Megaloceros giganteus* and large bovids (*Bos primigenius*, *Bison priscus* and Bovines).

	Cervus elaphus					*Megaloceros giganteus*					Bovidae			
	NISP	MNE	NEE	*Skeletal surv. Rate (%)*	*Fragm. Index MNE/NISP*	NISP	MNE	NEE	*Skeletal surv. Rate (%)*	*Fragm. Index MNE/NISP*	NISP	MNE	NEE	*Fragm. Index MNE/ NISP*
Cranium	1	1	9	*11.1*	*1.0*	4	1	8	*12.5*	*0.3*	2	1	5	*0.5*
Hemimandible	1	1	18	*5.6*	*1.0*	4	3	16	*18.8*	*0.8*	4	3	10	*0.8*
Tooth	10					8								
Total cranium	**12**	**2**	**27**	***7.4***	***0.2***	**16**	**4**	**24**	***16.7***	***0.3***	**6**	**4**	**15**	***0.7***
Vertebra	2	2	225	*0.9*	*1.0*									
Rib	5	3	234	*1.3*	*0.6*	1	1	208	*0.5*	*1.0*				
Sternum											2	1	5	*0.5*
Total axial skeleton	**7**	**5**	**459**	***1.1***	***0.7***	**1**	**1**	**208**	***0.5***	***1.0***	**2**	**1**	**5**	***0.5***
Scapula	3	3	18	*16.7*	*1.0*	3	2	16	*12.5*	*0.7*	2	2	10	*1.0*
Humerus	12	6	18	*33.3*	*0.5*	8	6	16	*37.5*	*0.8*	6	5	10	*0.8*
Radius/Ulna	1	1	18	*5.6*	*1.0*	1	1	16	*6.3*	*1.0*	1	1	10	*1.0*
Radius	5	2	18	*11.1*	*0.4*	15	6	16	*37.5*	*0.4*	8	6	10	*0.8*
Ulna						1	1	16	*6.3*	*1.0*	2	2	10	*1.0*
Metacarpal	13	6	18	*33.3*	*0.5*	11	5	16	*31.3*	*0.5*	2	1	10	*0.5*
Metacarpal rudim.	1	1	36	*2.8*	*1.0*									
Total forelimb	**35**	**19**	**126**	***15.1***	***0.5***	**39**	**21**	**96**	***21.9***	***0.5***	**21**	**17**	**60**	***0.8***
Coxal											1	1	5	*1.0*
Femur	11	5	18	*27.8*	*0.5*	12	6	16	*37.5*	*0.5*	4	4	10	*1.0*
Tibia	39	12	18	*66.7*	*0.3*	23	9	16	*56.3*	*0.4*	27	7	10	*0.3*
Tarsals						1	1	48	*2.1*	*1.0*				
Metatarsal	14	8	18	*44.4*	*0.6*	23	9	16	*56.3*	*0.4*	9	5	10	*0.6*
Total hindlimb	**64**	**25**	**54**	***46.3***	***0.4***	**59**	**25**	**96**	***26.0***	***0.4***	**41**	17	**35**	***0.4***
Metapodials	5	3			*0.6*	3	2			*0.7*	5	4		*0.8*
First phal.	2	2	72	*2.8*	*1.0*	1	1	64	*1.6*	*1.0*				
Second phal.	1	1	72	*1.4*	*1.0*	3	3	64	*4.7*	*1.0*	3	2	40	*0.7*
Third phal.											2	2	40	*1.0*
First phal. rudim.	1	1	72	*1.4*	*1.0*	2	2	64	*3.1*	*1.0*				
Second phal. rudim.						1	1	64	*1.6*	*1.0*				
Third phal. rudim.														
Sesamoid						1	1			*1.0*				
Total undet. limb	**9**	**7**	**216**	***3.2***	***0.8***	**11**	**10**	**256**	***3.9***	***0.9***	**10**	**8**	**80**	***0.8***
TOTAL	**127**	**58**	**882**	***6.6***	***0.5***	**126**	**61**	**680**	***9.0***	***0.5***	**80**	**47**	**195**	***0.6***

5.6. Carcass processing

Traces of human exploitation have been recognized on bones belonged to all the species recovered at De Nadale Cave. In particular, from the few cranial elements to the more abundant limbs, the large-sized ungulates (red deer, giant deer and large bovids) show different phases of carcass processing, which were carried out more consistently compared to smaller animals (ibex, chamois, roe deer and wild boar). No traces have been observed on carnivores' remains.

Despite the non-homogeneous presence of skeletal portions, the exploitation of the prey is attested on the whole carcass (Fig. 9): as shown in Tables 5–7, all anatomical districts bear traces of human activities, both for dietary and non-nutritional purposes.

Cut-marks (NR: 1028; 3.7% of the total NR) due to the use of lithic implements are the most common human traces: they are usually repeated and insisting on a particular area and they are generally the result of attached soft tissue (muscles, tendons, ligaments and so on) removal activity. The same marks on cranial or appendicular elements suggest skinning. Longitudinal and parallel scrapings (NR: 149; 0.5% of the total NR) on shafts point out that the periosteum has been removed to clean the bone from residual meat and to achieve greater control over breakage. At De Nadale cave, this kind of marks is more commonly found on metapodial, tibia and femur.

Bone breakage activity that enables marrow recovery is also linked to the presence of a series of percussion marks that includes chopmarks, percussion pits, spiral fractures and impact flakes. They have been found primarily on bones that are long, thick, and resistant to trauma, such as distal tibias and humeri, metapodials and, in some cases, femurs. Among all the remains, 339 impact flakes (1.2%) and 191 conchoidal flake scars have been found, some still carrying visible chopmarks on the cortical surface. Of the huge amount of fragmented bone shafts, over 200 have been used like retouchers, giving peculiarity to the De Nadale Cave in the Middle Palaeolithic of the north of Italy (Jéquier et al., 2012, 2013; 2018).

6. Discussion

The faunal assemblage of De Nadale Quina context expresses some zooarchaeological features that allow researchers to state its anthropogenic nature: there are dominant taxa, most of the fragments can be referred to adult individuals, there is a great abundance of limb and cranial bones compared to the axial elements, etc. In addition to that, the high number of cutmarks and intentional bone breakages for marrow recovering and the use of shafts as retouchers are related to a primary and immediate access to the ungulates and an intensive exploitation of the carcasses (Binford, 1981; Bunn, 1986, 1989; Blumenschine, 1988; Domínquez-Rodrigo, 1999; Gaudzinski and Roebroeks, 2000). On the other hand, features produced by carnivores (pits, scores, digested bones, etc. but also deciduous teeth of other juvenile specimens) have been detected among the fragments, although the percentage of these traces is not enough substantial to indicate the presence of a den or other evidence that can support hypothesize the action of natural agents for the deposition of the osteological material. In addition to this, the relevant quantity of burnt and calcined fragments can further underline the human origin of this deposit.

The amount of data recovered during the excavations and inferred from the zooarchaeological analysis provides hints to shed light on the ecology and the subsistence strategies of the Quina Neanderthals in the

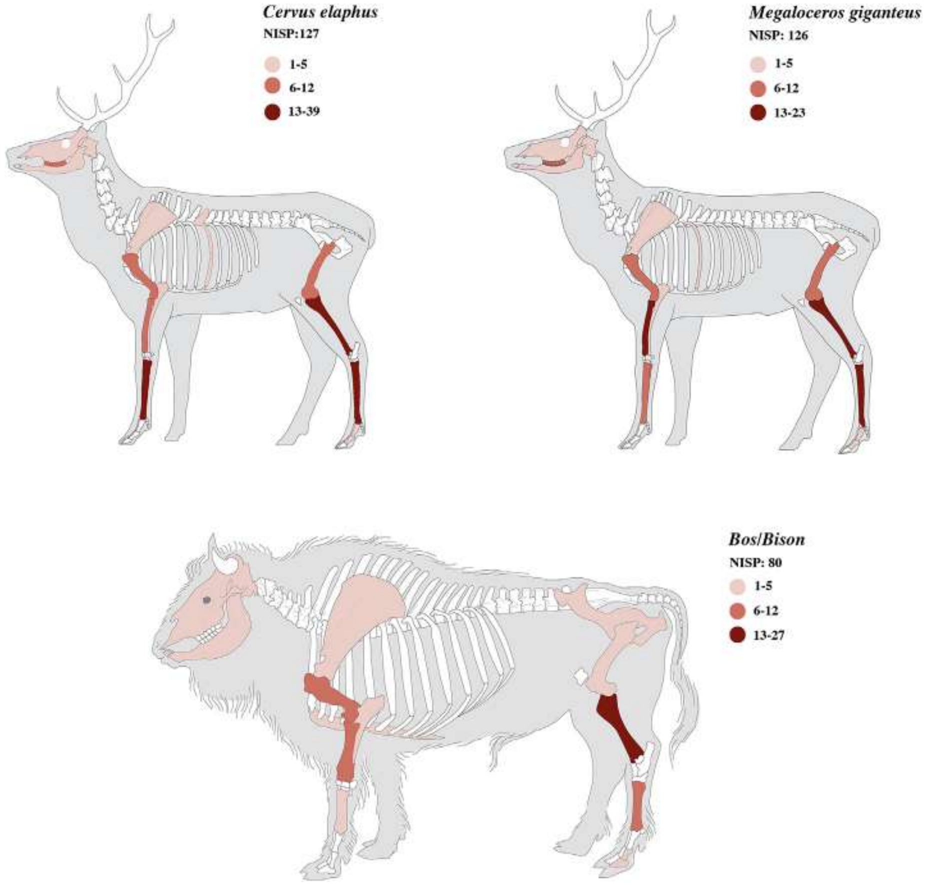

Fig. 8. Frequency of skeletal elements of the three main taxa, *Cervus elaphus*, *Megaloceros giganteus* and large bovids (*Bos primigenius*, *Bison priscus* and Bovinae).

Table 5
Number of anatomical elements of *Cervus elaphus* with anthropic modifications and carnivore marks. CM: cut-marks; PM: percussion marks; CM + PM: cut-marks + percussion marks; IF: impact flakes; CM + IF: cut-marks + impact flakes; Tot. BM: Total butchering marks; % BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks.

	NISP	CM	PM	CM + PM	IF	CM + IF	Tot. BM	*% BM*	R	B	GM
Cranium	1										
Hemimandible	1	1					1	*100.0*			
Tooth	10										
Total cranium	**12**	**1**					**1**	***8.3***			
Vertebra	2		1				1	*50.0*			
Rib	5	2					2	*40.0*	1		
Total axial skeleton	**7**	**2**	**1**				**3**	***42.9***	**1**		
Scapula	3	2					2	*66.7*	1		
Humerus	12	5	2	1	1		9	*75.0*	1		1
Radius/Ulna	1	1					1	*100.0*			
Radius	5	4		1			5	*100.0*	2		
Metacarpal	13	4	1	3			8	*61.5*	5	1	
Metacarpal rudim.	1	1					1	*100.0*			
Total forelimb	**35**	**17**	**3**	**5**	**1**		**26**	***74.3***	**9**	**1**	**1**
Coxal											
Femur	11	6		4			10	*90.9*	5	1	
Patella											
Tibia	39	15	4	3	1		23	*59.0*	8	2	2
Metatarsal	14	9	1	1		1	12	*85.7*	3	2	
Total hindlimb	**64**	**30**	**5**	**8**	**1**	**1**	**45**	***70.3***	**16**	**5**	**2**
Metapodials	5	4					4	*80.0*	1		
First phal.	2										1
Second phal.	1	1					1	*100.0*			
First phal. rudim.	1										
Total undet. limb	**9**	**5**					**5**	***55.6***	**1**		**1**
TOTAL	**127**	**55**	**9**	**13**	**2**	**1**	**80**	***63.0***	**27**	**6**	**4**

Table 6
Number of anatomical elements of *Megaloceros giganteus* with anthropic modifications and carnivore marks. CM: cut-marks; PM: percussion marks; CM + PM: cut-marks + percussion marks; IF: impact flakes; CM + IF: cut-marks + impact flakes; Tot. BM: Total butchering marks; % BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks.

	NISP	CM	PM	CM + PM	IF	Tot. BM	*% BM*	R	B	GM
Cranium	4			1		1	*25.0*			1
Hemimandible	4	2				2	*50.0*			
Tooth	8									
Total cranium	**16**	**2**		**1**		**3**	***18.8***			
Rib	1	1				1	*100.0*			
Total axial skeleton	**1**	**1**				**1**	***100.0***			
Scapula	3	3				3	*100.0*			1
Humerus	8	2	1	4		7	*87.5*	1		
Radius/Ulna	1	1				1	*100.0*	1		
Radius	15	6		5		11	*73.3*	1	1	1
Ulna	1		1			1	*100.0*			
Carpals										
Metacarpal	11	4	2	3		9	*81.8*	5		3
Metacarpal rudim.										
Total forelimb	**39**	**16**	**4**	**12**		**32**	***82.1***	**8**	**1**	**5**
Coxal										
Femur	12	4	2	2		8	*66.7*	2		1
Patella										
Tibia	23	7	4	5		16	*69.6*	4	1	
Tarsals	1									
Metatarsal	23	6	4	3		13	*56.5*	2		1
Total hindlimb	**59**	**17**	**10**	**10**		**37**	***62.7***	**8**	**1**	**2**
Metapodials	3	2			1	3	*100.0*	1		
First phal.	1									
Second phal.	3	1				1	*33.3*			
Third phal.										
First phal. rudim.	2	1				1	*50.0*			
Second phal. rudim.	1									
Sesamoid	1									
Total undet. limb	**11**	**4**			**1**	**5**	***45.5***	**1**		
TOTAL	**126**	**40**	**14**	**23**	**1**	**78**	***61.9***	**17**	**2**	**7**

North-east of Italy. Moreover, they can propose a framework for models of mobility from comparisons with few but significant indicators from Western Europe.

6.1. Paleoecological implications

The De Nadale Cave is located at the centre of the Berici Hills, a physical landscape positioned between the wide Po plain to the south and the Alpine mountain range to the north. Therefore, it opens on a tributary of a long valley cut (Val Liona) at a position dominating the valley bottoms and in proximity of the wide plateau above. This favourable location could have been suitable to control the movements of grazing large herbivores, such as auroch and bison, giant deer and red deer, also attracted from water springs and bodies located at the valley bottoms.

The faunal spectrum resulting from the zooarchaeological analysis is consistent with an environment characterized by open woodland formation and open dry meadows. The presence of *Megaloceros giganteus* and *Cervus elaphus* and large bovids enhances this hypothesis. Following Vislobokova (2012) and van der Made (2006, 2010) the ecogenesis of the genus *Megaloceros* shows that the giant deer may have been a mixed feeder living in an open woodland or shrub environment since morphometric features typical of grazers are poorly pronounced (Chritz et al., 2009; Immel et al., 2015). *M. giganteus* seems to have preferred grass-shrub vegetation and open woodland with larch, spruce, pine and birch trees (Stuart et al., 2004). Moreover, red deer is actually a ubiquitous species and its ecological niche can be considered overlapping with the giant deer's one. These animals are highly adaptable and thrive in a variety of habitats. They prefer, nowadays, an interspersed environment including meadows, grasslands with fragmented forested areas and brushy zones (Geist, 1998; Clutton-Brock, 1982). The presence of large bovids completes the scenario: paleoenvironmental evidence suggests that, like the extant American bison, *Bison priscus* favoured extensive dry meadows and steppe grasslands (Brugal et al., 1999; Julien et al., 2012; Massilani et al., 2016). On the contrary, *Bos primigenius* inhabited a forested, fluvio-lacustrine, and marshy areas, even if the fossil record suggests that the aurochs could probably adapt to colder and drier climate conditions, at least to a certain extreme (Brugal, 1985; van Vuure, 2002, 2005; Vercoutère and Guérin, 2010).

These data fit well with a recent study on small mammals (López-García et al., 2018) which highlights the presence of *Microtus arvalis* that is currently reported to be common in open areas and relatively drier regions of northern Italy (Amori et al., 2008). In addition to that, *Chionomys nivalis* and *Microtus agrestis*, which can be found nowadays at over 1000 m of elevation in the Veneto region (Bon et al., 1996), are indicators of harsh climatic conditions prevailing at the time when the formation of Unit 7 took place. This analysis agrees with the Italian terrestrial pollen sequences from Fimon Lake (Pini et al., 2010) and Azzano Decimo core in Friuli (Pini et al., 2009), revealing for MIS 4 a mosaic of open forest and steppe with a predominance of *Pinus-Picea* and an abundance of *Betula* and herbaceous plants.

6.2. Skeletal representation: human choice or matter of conservancy?

As the results of this study show, at De Nadale cave the frequency of axial elements is low. The almost total lack of these elements cannot be ascribed to a differential preservation process caused by post-depositional events, even considering that differences in bone diagenesis have been observed as a function of local physical and chemical sedimentary conditions and that parts of the vertebrae and ribs could not have been identified at a taxonomic level and they were consequently sorted into body-size categories.

Based on the skeletal part representation of all ungulates, it is reasonable to assume that the treatment of the carcasses did not take place

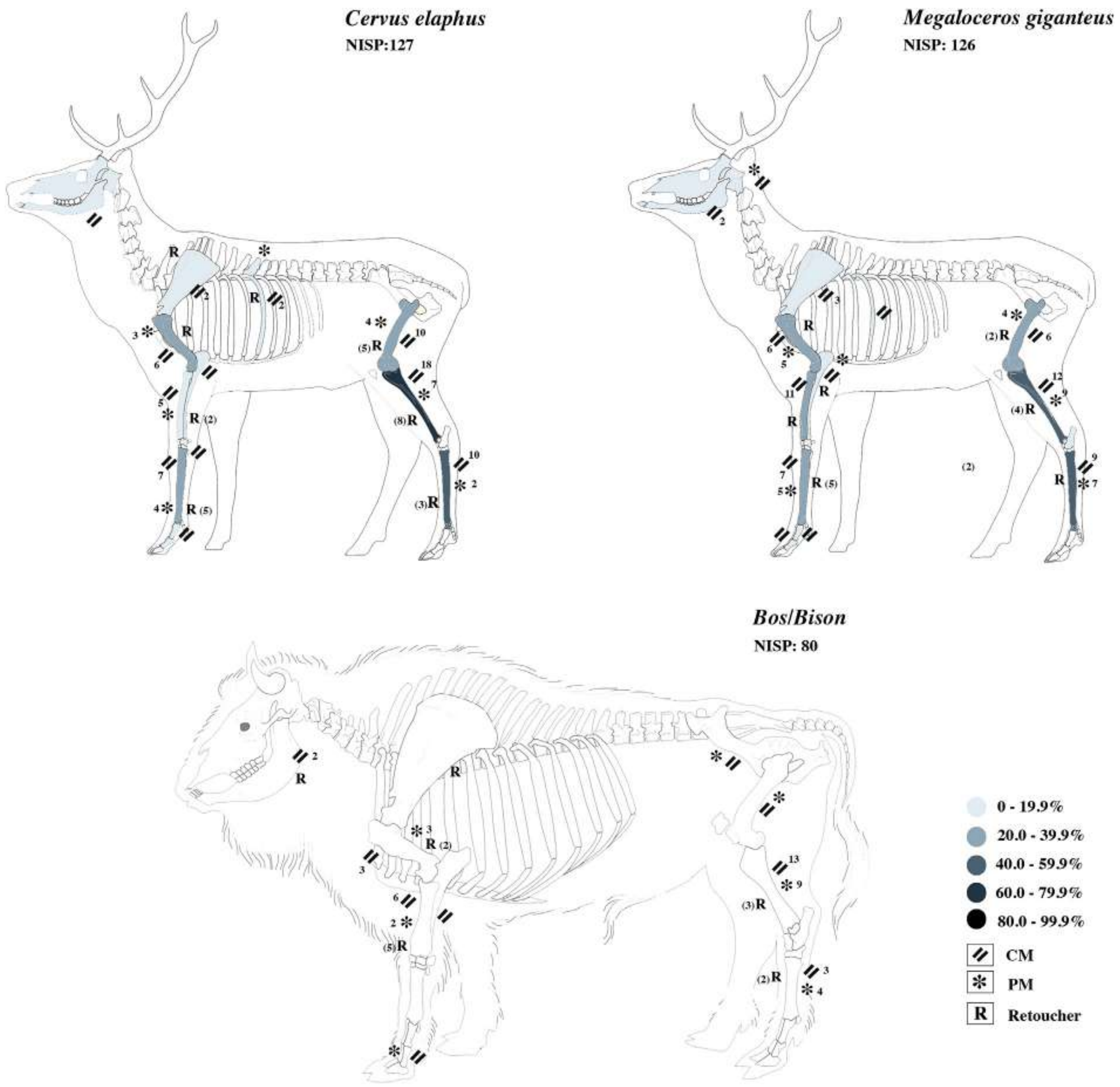

Fig. 9. Skeletal survival rate and distribution of the anthropic modifications on the skeletal elements of *Cervus elaphus* and *Megaloceros giganteus*. Distribution of the anthropic traces on the skeletal elements of large bovids (*Bos primigenius*, *Bison priscus* and Bovinae).

in the cave but presumably at the kill site. Only selected parts of the animal were transported to the cave, increasing the difference between the amount of useful anatomical elements recovered in the cave and those of "low caloric utility" (Binford, 1978a, 1978b; 1982; Metcalfe and Jones, 1988). From the data recovered, it is inferable that at least one complete carcass has been brought into the site, but the general trend was to introduce preferably the quarters.

According to several naturalistic studies (Blumenschine, 1988) and experimental works (Marean and Spencer, 1991; Marean et al., 1992) hominids and carnivores are the primary agents that lead to this situation, in which vertebrae, ribs and epiphyses of long bones are scarcely present. Considering the scarcity of the features attributable to carnivores (pits, scores and so on), the bias in the skeletal profiles observed in Unit 7 could be interpreted as a consequence of the anthropic differential transport of skeletal parts, comparably to other Middle Palaeolithic assemblages – Kobeh Cave (Marean and Kim, 1988), Kujin (Marean and Cleghorn, 2003), Level J at Abric Romaní (Rosell et al., 2011), Les Pradelles (Costamagno et al., 2006), Salzgitter-Lebenstedt (Gaudzinski and Roebroeks, 2000) among others. If the entire animals were carried to the site, numerous ribs, vertebrae and spongy tissue remains should be found. This transport choice could have had several advantages from the cost-effectiveness point of view: only skeletal parts with high nutritive values (meat and marrow), easy to transport and advantageous in terms of nutritional gain, were introduced in the site, with a consequential optimisation of energy costs (Rosell et al., 2011). Once the animal has been dismembered, in fact, limbs are easy to transport while the axial trunk is heavier and prevents the hunter from moving freely. Moreover, once the back muscles and the viscera have been removed, the thoracic skeleton results completely useless (at least for alimentary purpose) and could be left on place (Oliver, 1993).

However, this hypothesis alone cannot explain the absence of epiphyses of long bones and spongy element, such as vertebrae, ribs and articular short bones. The well-established presence of longitudinal and oblique scraping marks and cut marks on diaphysis suggests that limb bones were entire when they were introduced into the cave and they lose their epiphyses after defleshing (Domínquez-Rodrigo, 1999). In addition to that, another possibility could be found in the anthropic processing and consumption patterns: epiphyses contain fat and grease that have a great nutritional utility and that can be extracted by heating the bones. For this purpose, the epiphysis must be separated from the

Table 7
Number of anatomical elements of Bovinae with anthropic modifications and carnivore marks. CM: cut-marks; PM: percussion marks; CM + PM: cut-marks + percussion marks; IF: impact flakes; CM + IF: cut-marks + impact flakes; Tot. BM: Total butchering marks; % BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks.

	NISP	CM	PM	CM + PM	Tot. BM	*% BM*	R	GM
Cranium	2							
Hemimandible	4	2			2	*50.0*	1	1
Total cranium	**6**	**2**			**2**	*33.3*	**1**	**1**
Rib (stern)	2							
Total axial skeleton	**2**							
Scapula	2						1	
Humerus	6	1	1	2	4	*66.7*	2	
Radius/Ulna	1							
Radius	8	4		2	6	*75.0*	5	1
Ulna	2	1			1	*50.0*		
Metacarpal	2							
Total forelimb	**21**	**6**	**1**	**4**	**11**	***52.4***	**8**	**1**
Coxal	1			1	1	*100.0*		
Femur	4	1	1		2	*50.0*		1
Tibia	27	9	5	4	18	*66.7*	3	3
Metatarsal	9	1	2	2	5	*55.6*	2	1
Total hindlimb	**41**	**11**	**8**	**7**	**26**	***63.4***	**5**	**5**
Metapodials	5	2		1	3	*60.0*	1	
Second phal.	3	1	1		2	*66.7*		1
Third phal.	2							
Total undet. limb	**10**	**3**	**1**	**1**	**5**	***50.0***	**1**	**1**
TOTAL	**80**	**22**	**10**	**12**	**44**	***55.0***	**15**	**8**

diaphysis and crushed. The result of this activity is a systematic breakage that fits well with the high percentage of fragments less than 2 cm long and that has been recognized in other Middle Palaeolithic sites such as Abric Romaní (Rosell et al., 2011), Les Pradelles (Costamagno et al., 2006, 2017) and Grotte du Noisetier (Costamagno, 2013). A similar hypothesis can be made about spongy elements, although difficult to prove archaeologically (Daujeard, 2008; Costamagno, 2013; Speth, 2015; Morin and Soulier, 2017), as it has been observed in other Palaeolithic sites such as Roc de Marsal (Castel et al., 2017) and Abri du Maras (Daujeard et al., 2017) among the others. These data fit well also with the high rate of burnt and calcined bone fragments recovered at the site which can be linked to an intense use of bone material as a fuel, such as attested by Costamagno et al. (2005).

6.3. *A deliberate economic strategy or a purely "ecological" specialization?*

As the taxonomic data demonstrate, the majority of animal remains brought onto the site was from species inhabiting lowlands, valley bottoms and plateaux. At De Nadale cave the meat income was based mainly on cervids and bovids and this subsistence strategy seems not to reflect the probable natural association of species around the cave. This evidence of targeted exploitation of large-sized/medium-large-sized prey types, which may have had lower encounter rates than medium/small-medium-sized ones (ibex, wild boar, roe deer and chamois) or perhaps they might have been disregarded on occasion if the hunters' success rates were too low (Bird et al., 2009), is remarkable. At the current state of research, it is still unclear to what extent this difference in the faunal spectrum can be linked to significantly diverse environmental conditions, or to differences in the season of occupation or to a deliberate subsistence choice, possibly related to techno-cultural features of the human groups. Further analyses, concerning, for example, seasonality, paleoenvironment and faunal niche, on De Nadale cave itself and on other possibly MIS 4 Middle Palaeolithic sites, would be fundamental to frame the situation. Nowadays, there are no sites in the North of Italy that yielded deposits dated or clearly referable to the MIS 4. A dominance of middle-sized ungulates (red deer and ibex) has been preliminarily recorded at Fumane Cave Unit BR11 (Fiore et al., 2004), chronologically positioned at the end of MIS 4 unless this chronometric set will be confirmed from a new dating programme. Additional MIS 4 archaeofaunal assemblages from Tagliente Rockhelter, Ghiacciaia Cave and San Bernardino Cave require further chronological refinements and in-depth analyses to assess consistency in the range of medium-large or medium-sized ungulates represented (Cassoli and Tagliacozzo, 1994b; Bertola et al., 1999; Fiore et al., 2004; Thun Hohenstein, 2004). Moreover, extensive studies have been carried out on the faunal assemblage of Unit A9 of Fumane Cave (Romandini et al., 2014a), which, however, dates to MIS 3 and cannot be directly compared with the case of De Nadale Cave. Anyway, the Unit A9 points out a different situation: medium-sized cervids, *Cervus elaphus* and *Capreolus capreolus*, were the primary meat income resources, in association with *Capra ibex* and *Rupicapra rupicapra*, exploited to a lesser extent. Bovids, *Megaloceros giganteus*, *Alces alces* and *Sus scrofa* are also present but in a less significant quantity.

Without specific comparisons, speculating about the faunal spectrum noted at De Nadale, is difficult and reckless. Moreover, the discrimination between "faunal specialization as a deliberate economic strategy" and "purely 'ecological' specialization" (Mellars, 2004) is uncertain using only archaeological information and the debate about a monospecific hunting strategy adopted by Neanderthals is still lively (David and Enloe, 1993; Mellars, 2004; Costamagno et al., 2006; Delagnes and Rendu, 2011).

Even if the De Nadale Cave has been occupied probably at the onset of a cold period, it is likely that the prey catchment zone around the site, which probably included the nearby Val Liona and Pozzolo plateau, would have provided species other than giant deer, red deer and bovids. Thus, the narrow species focus that characterizes the assemblage may reflect a particular hunting pattern, which is still not well known in Italy. However, evidences of this specialized diet have been found, in the south-east of Italy, at the Oscurusciuto Rockshelter with its dominance of *Bos Primigenius* in Unit 4 (Boscato et al., 2011), at the Santa Croce Cave with the exclusive representation of *Bos primigenius* and *Equus ferus* (Boscato et al., 2010) and at the Cavallo Cave Unit F with the association of *Bos primigenius*, *Cervus elaphus* and *Equus ferus* (Boscato and Crezzini, 2006). Regarding the North-eastern part of Italy, a particular pattern is the one recognized at Rio Secco Cave where anthropically modified bear bones abound in the levels 5top+7 and 5 + 8 (Romandini et al., 2018b). Although the directionality in hunting behavior in Neanderthal context has always stimulated controversy, a large number of deposits, however, have been interpreted as probable accumulation resulting from specialized hunting. Narrow animal spectrum or even monospecific-based diet have been revealed at numerous Middle Paleolithic sites in different regions, for example, in the Zagros Mountains at Kobeh (Marean and Kim, 1998), in the Caucasus at Il'skaya I (Hoffecker et al., 1991), in Western Europe at Mauran (Girard and David, 1982; Farizy et al., 1994), La Borde (Jaubert et al., 1990), Coudoulous I (Mellars, 1996; Jaubert et al., 2005), Le Roc (Mellars, 1996), Jonzac (Niven et al., 2012) and Les Pradelles (Costamagno et al., 2006; Rendu et al., 2012) and in Central Europe at Wallertheim (Gaudzinski, 1995) and, Salzgitter Lebenstedt (Gaudzinski and Roebroeks, 2000; Gaudzinski, 2006) and Neumark-Nord (Gaudzinski-Windheuser et al., 2018).

7. Conclusions

The targeting of a limited spectra of games is not a novelty in Neanderthal dietary habits as some of the above-mentioned studies demonstrate, although it requires additional evidence to overcome the patchiness of this record in western Eurasia. De Nadale assumes here specific relevance in that it contributes to shed light on hunting behavior at the onset of MIS4 in a regional context where the data available are still embryonal for reconstructing human ecology and land-use. The estimation of the territory covered by the Neanderthals settled at De Nadale remains to be implemented with major detail after the chert provisioning strategies adopted for stone tools equipment will be inferred from the on-going petroarchaeological investigation of the lithic assemblage. Comparably to the other sites distributed on the southern slope of the prealpine mountain range, the position of the cave remains unfavourable for catching knappable stones at the short distance range and stimulates inquiries on the comparison of a set of scales in human land-use with their different encounter rates.

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4.2 Paper 2

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Large bovids on the Neanderthal menu: Exploitation of *Bison priscus* and *Bos primigenius* in northeastern Italy

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The aim of this study is to discuss the contribution of large bovids to Neanderthal subsistence in northern Italy and the conditions that might have affected the presence or absence of these animals during MIS 4 and MIS 3. This paper focuses on the presence of bovids at De Nadale Cave, San Bernardino Cave (Unit II) and Fumane Cave (Units A5+A6 and A9). It has been shown here that *Bison priscus* and *Bos primigenius* were an important resource for different groups of Middle Palaeolithic hunters that lived across a wide territory of northern Italy, although they were commonly not the most exploited species. Furthermore, they were present and, in some cases, hunted in a variety of landscapes, influenced by the behaviour of the species themselves. A significant set of evidence shows that Neanderthals were able to face environmental and topographical constraints and change over time by adapting their hunting behaviour, technological lithic system, and mobility. Results underline intense exploitation of the bovids resource at all the sites taken into consideration. This scenario could be due to different factors: other resources may have been available during the year (e.g., cervids) and may have been more abundant in the surrounding areas or may have been easier to hunt; seasonality may have been one of the factors that made Neanderthals hunt specific animals at certain time of the year; there may have been a cultural aspect related to the Quina techno-complex, etc.

In this paper, we contributed to the results bringing the data about the bovids exploitation at De Nadale Cave and implementing the discussion with the comparisons with a Quina Mousterian site.

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ABSTRACT

In northern Italy, Fumane Cave (Lessini Mountains -Verona), San Bernardino Cave, and De Nadale Cave (Berici Hills - Vicenza) provide data to interpret the exploitation dynamics of the Pleistocene's large bovids *Bos primigenius* and *Bison priscus* between 70 and 42 ky BP. Through the taphonomic study of bone assemblages, we have attempted to reconstruct the strategies, methods, and butchery practices in the exploitation of these game animals adopted by different cultural groups of Middle Palaeolithic hunters. Therefore, Neanderthal hunting behaviour has been examined using different proxies such as the choice of anatomical parts, selective transport of elements, prey selection, and age estimation. Results suggest bovines were an important subsistence resource in some cases, even if they were not the most exploited taxa in others, indicating differences and similarities depending on the context across the Italian peninsula. These results highlight additional aspects of Neanderthal landscape use and hunting strategies.

1. Introduction

One of the most controversial issues in the understanding of human evolution is the debate over Neanderthal ecology, subsistence strategies, and diet (Gaudzinski-Windheuser and Roebroeks, 2011; Morin et al., 2016; Ready, 2010, 2013). In recent years, several approaches, among them faunal and taphonomic analysis (Brugal et al., 1999; Gaudzinski-Windheuser and Kindler, 2012; Germonpré et al., 2014; Jaubert and Brugal, 1990; Patou-Mathis, 2000; Romandini et al., 2018a, 2018b), dental microwear patterns (Harvati et al., 2013; Pérez-Pérez et al., 2003), tooth calculus analysis (Henry et al., 2014; Weyrich et al., 2017), lithic use-wear and residue analysis (Hardy and Moncel, 2011), and the investigation of stable carbon and nitrogen isotopes of bone and tooth collagen (Bocherens et al., 2005; Bocherens, 2009; Richards and Trinkaus, 2009; Wißing et al., 2016), as well as the contextualisation of the overall archaeological record have vastly improved our knowledge of food acquisition and exploitation and thus subsistence strategies by Neanderthals. Among all the different methods, there is common agreement that Neanderthal subsistence strategies show great flexibility in foraging systems, with adaptations to different environments and variation across the faunal spectrum depending on species availability (Blasco and Fernández Peris, 2009, 2012; Blasco et al., 2013; Costamagno et al., 2006; Finlayson et al., 2012; Fiore et al., 2016; Gaudzinski, 2006; Romandini et al., 2018a, 2018b). In general, the core meat sources of Neanderthals were medium-sized and large herbivores like cervids, equids and large bovids. Hunting practices focused on large-sized prey increased with the introduction of *Levallois* technology, a new knapping method that was not a simple modification in flake production, but was part of relevant behavioural changes (Gaudzinski, 2006). Neanderthal subsistence tactics inferred from many archaeological sites in Europe comprised long-term and seasonal exploitation strategies. Within cave and open-air sites, which were regularly used for their abundance of biotic resources, some hunting locations were selected to take advantage of animal routes or seasonal migration, which indicates planning for the future (Mellars, 1996).

Some of the best evidence of Neanderthal subsistence tactics and hunting practices of large herbivores come from the zooarchaeological studies of bovines: *Bison priscus* and *Bos primigenius*. The study of several bone assemblages suggests that bovines were an important source of subsistence for Middle Palaeolithic hunters. Large accumulations of butchered carcasses have been recovered in western-central Europe, at La Quina (Chase, 1999; Rendu and Armand, 2009), Mauran (David et al., 1994; David and Fosse, 1999; Rendu et al., 2012), Coudoulous

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(Jaubert et al., 2005), La Borde (Jaubert et al., 1990), Biache-Saint-Vaast (Auguste, 1995), Hénin-sur-Cojeul (Marcy et al., 1993), Wallertheim (Gaudzinski, 1995, 1996), Il'skaja (Hoffecker et al., 1991), and Mezmaiskaja Cave (Baryshnikov et al., 1996). A group of these sites provides evidence that Neanderthal groups used favourable landscape topography, such as cliffs, swamps or gorges to drive and trap the herds. The planned and systematic exploitation and in some cases the selection of individuals, also suggest the existence of repeated collaboration and organization between hunters (Rendu et al., 2012).

The situation differs in southern Europe, where the faunal spectrum is more varied (e.g. Brugal and Valente, 2007; Garralda et al., 2014; Miracle, 2005; Morin and Soulier, 2017a; Panagopoulou et al., 2004; Rosell et al., 2012; Starkovich, 2017; Starkovich et al., 2018; Zilhão et al., 2010) and specialized hunting behaviours that focus on particular species such as large bovids are variable, as noted in Italian peninsula. Faunal assemblages from sites in southern Italy (Grotta di Santa Croce, Riparo l'Oscurusciuto, and Grotta del Cavallo) are characterized by the predominance of *Bos primigenius* (Boscato and Crezzini, 2006, 2012; Boscato et al., 2011; Villa et al., 2009).

In northern Italy, Neanderthals exploited large bovids as well (Romandini et al., 2014), but not as intensively. Cervids and caprinae are commonly well-represented, while bovines are scarcely documented (Cassoli and Tagliacozzo, 1994; Fiore et al., 2004; Moroni et al., 2018; Peresani et al., 2014; Sala, 1990; Thun-Hohenstein and Peretto, 2005; Valensi and Psathi, 2004). Thus, several questions revolve around the exploitation of bovines in the Middle Palaeolithic. Why were *Bison priscus* and *Bos primigenius* not frequently exploited? Was the exploitation of these animals influenced by site topography or, rather, by the animals' seasonality? Could the climate have affected the availability of these resources? Could the technological systems adopted by different Neanderthal groups (e.g. Quina or *Levallois*) have influenced the exploitation of these animals? In order to answer these questions, the analysis presented here focuses on three sites in northern Italy, Fumane cave (Grotta di Fumane), San Bernardino cave (Grotta Maggiore di San Bernardino) and De Nadale cave (Grotta De Nadale), which preserve taxonomic and taphonomic data on several distinct human occupations. The aim of this work is to assess the condition that might have affected the presence or absence of *Bison priscus* and *Bos primigenius*, and to better understand their exploitation in the late Middle Palaeolithic, during Marine Isotope Stages (MIS) 4-3, on the southern foothill of the Eastern Alps. To this end, we use ethological information (ecology and behaviour) from fossil evidence and through analogy of living representatives to infer the size and social composition of the herds. With such information, we attempt to contribute to interpretations of Neanderthal hunting and subsistence strategies.

1.1. *Bison ethology*

The Eurasian steppe bison, *Bison priscus* (Bojanus, 1827), disappeared from the fossil record around 10–12 ky ago, although it seems to have survived until the mid-Holocene in Siberia (Boeskorov et al., 2016; Kirillova et al., 2015). It was a formidable animal with long horns and robust legs over 2 meter long at the withers and reached a total length of > 2.7 m. The reconstruction of its ecology and ethology must be inferred from fossil evidence and through analogy with its closest living relatives, the American bison, *Bison bison* (Linnaeus, 1758), and European bison or wisent, *Bison bonasus* (Linnaeus, 1758). As a genus, they are ecologically flexible: American bison are primarily grazers of wooded steppe mosaics, while wisents now occupy deciduous and mixed forest, the areas to which they were introduced. However, recent studies suggest that the European bison was not necessarily a forest specialist (Bocherens et al., 2015; Kerley et al., 2012; Kowalczyk et al., 2015). *B. priscus* was adapted to forest-steppe and steppe ecosystems and is considered indicative of open environments (Brugal et al., 1999). Paleoenvironmental evidence suggests that, like *B. bison*, *B. priscus* was more of a grazer than *B. bonasus*, which is a mixed feeder (Bocherens et al., 2015; Massilani et al., 2016). The diet of *B. priscus* included typical steppe and grassland (C_3) vegetation and lichens (Bocherens et al., 2015; Julien et al., 2012) but probably did not totally exclude woody vegetation, since some individuals, such as the bison bull mummy “Blue Babe” from Alaska, had 7% of woody material among the plant fragments trapped in its dentition (Guthrie, 1990). However, the structure of the neck and hump of the fossil species indicates that they held their heads higher, which might be a result of the adaptation to grazing taller and sparser grasses (Guthrie, 1990). All living bisons are gregarious, the size and structure of the herds varies according to age, sex, season, resources, habitat and environment (Meagher, 1986, 1989; Plumb et al., 2009; Krasińska and Krasiński, 2013). Available resources condition herd size; for example, North American average group size can be as low as ~11–20 bison during winter, increases to ~200 in summer, and reaches a maximum of ~1000 during the rut season in June and September (White et al., 2016). The *B. bonasus* average group size is environment-dependent. Typically, groups consist on average of ~8–13 individuals in different populations. Sometimes, European bison forage in open areas (mown or mountain meadows and deforested grassland glades) and form larger groups, of ~23 individuals. In all populations bulls are often found in pairs, though more than half of males lead a solitary life (Krasińska and Krasiński, 2013). Bison herds may be sedentary or seasonally migratory; movements are altitudinal or directional. There are no historical data on seasonal migrations of lowland European bison; however, seasonal movements are observed in the forest-field landscape in Poland and also altitudinal seasonal movements related to weather condition and snow cover are observed in mountain areas (Krasińska and Krasiński, 2013). In the closely related American plains, seasonal movements of bison were observed with distances as long as 250 km (Meagher, 1986). Bison forage discontinuously on open bottomlands and lower adjacent slopes, but their routes sometimes traverse forest areas and steep slopes (Meagher, 1989). Bison have poor vision but can detect movement up to 1.5 km. Their hearing and olfactory senses are highly developed, and they rely on them heavily to detect danger. They can smell humans 500 m away, and upon sensing danger, can run at speeds reaching up to 60 km/h (Fuller, 1960; Krasnokutsky, 1996). Juveniles and young bisons may act unpredictably and run in other directions, but the adults will try to adjust their path accordingly. If the herd encounters an obstacle, the lead animals will veer sharply, but if the momentum of the herd is too great, it might plough forward into further danger and over cliffs (Krasnokutsky, 1996).

1.2. *Aurochs ethology*

The aurochs, *Bos primigenius* (Bojanus, 1827), became extinct during the 17th century. Any estimate of its social, behavioural ecology and morphology must therefore rely on historical reports, baseline data from extant species of wild cattle, and images from Lascaux, Chauvet, Altamira, and Romito caves (van Vuure, 2002). From these sources, the height of the withers has been estimated between 160 and 180 cm for the bull, and around 150 cm for the cow. Their horns grew outside from the skull then curved forward (in an angle of ca. 60° with the forehead) and inward (towards each other) (van Vuure, 2002, 2005).

As studies indicate (Von Koenigswald, 2007), *Bos primigenius* was an interglacial animal. European specimens would withdraw to the Mediterranean area during cold periods and expand to the north during warmer periods (Von Koenigswald, 2007). Fossil records, in western Europe (Brugal, 1985) and in some parts of Asia, which show the presence of both *Bos primigenius* and *Bison priscus* in the same sites, suggest that aurochs were probably adapted to colder and drier climatic conditions, at least to a certain extent (van Vuure, 2002). *B. primigenius* was a grazer or intermediate feeder, feeding mainly on grasses and graminoids, supplemented with forbs, leaves and branches of trees and bushes (van Vuure, 2002, 2005). According to palynological data, research on fossil insects, and historical accounts, the habitat that aurochs occupied in Europe was characterized by closed forests, fluvio-lacustrine environments, and marshy areas (van Vuure, 2002, 2005). In general, *Bos primigenius*'s behaviour was similar to the rest of the Bovini tribe; aurochs tended to separate into cow (or mixed) herds, bull herds, and solitary bulls. Bulls only joined cow herds during the rut season (between August–September), and most calves were born at the end of spring.

2. The north Italian context

2.1. The pre-alpine fringe and subalpine area of the southeastern Alps. Physical and ecological setting from MIS 4 to MIS 3

Along the southern slope of the Alps, the pre-alpine mountain range and the sub-alpine zones succeed one another, forming a discontinuous series of short chains and mountain groups from the Lago Maggiore to Istria. This region encompasses a 40 km-wide mountain belt that is oriented west to east in its western-middle sector and progressively turns to the north in the eastern transect. The landscape of the Eastern Pre-Alps is composed of limestone massifs and high, karstic plateaus 1000–1200 m above sea level (a.s.l.), with summits that rise above 2000 m. This is interspersed with gorges, large river valleys, and wide basins that host important glacial alpine lakes. Of these high plateaus, the Monti Lessini is a fan-shaped karstic plateau that dips gently to the south towards the alluvial plain of the Adige River, and is characterized to the north by summits that reach 1500–1600 m. It is bounded to the west by the Adige Valley, a long and deep cut that connects the inner Alpine region with the Po Plain. The Monti Lessini is characterized by tectonic terraces connected to the bottom of the stream valleys by steep slopes and rock walls that include caves and shelters. At the eastern end, the Trieste karstic plateau forms a typical flat landscape that extends at a low elevation to the Sava and Danube basins. The subalpine zone of the Eastern Pre-Alps comprises hills of different origins, such as the pre-MIS2 glacial moraines south of Garda Lake, the Monti Berici plateau, and the Colli Euganei cone-shaped hills. The latter two groups are isolated from the alluvial plain. The Alpine foreland is a large alluvial plain that mostly originated during the Middle and Late Pleistocene from the major rivers, including the Po, Adige and the rivers of the Friulian-Venetian Plain (Mozzi, 2005). The Berici Hills are a karstic plateau of special interest for our investigation. At an average elevation of 250 m a.s.l., the plateau contains a honeycomb of sinkholes and various depressions that delineate an extremely uneven topography with peaks and karstic blocks that are affected by surface dissolution. The plateau is dissected by depressed systems (e.g., the Fimon, Liona, and Calto valleys) with pocket-valleys where ephemeral streams produced swampy environments and fed historic mills. The slopes are steep all around. To the east, a steep slope with rock cliffs connects the plateau to the alluvial lowlands that were occupied by marshes and swamps during the Pleistocene and earlier phases of the Holocene. In the southern eastern area, the Pozzolo depression is a wide trench cutting through the plateau in a NW-SE direction and with an elevation of 150 m at both the SE and NW ends. It is the relict segment of an old valley that was cut by a river during the first uplifting phases of this morpho-unit. The ancient karst surface is covered with palaeosols and thick red clayey residual deposits (Sauro, 2002).

For long parts of the Late Pleistocene, the eastern Italian Alps were a physical and ecological barrier due to the presence of ice fields and alpine glaciers formed during the cold stages, while temperate vegetation was only partially restored during the warmest interstadials. The morphological and sedimentary evolution of this part of the Po Valley and the shoreline displacements that occurred during this period have been assessed in several works (Antonioli, 2012; Fontana et al., 2008; Mozzi, 2005; Zecchin et al., 2008). After the last interglacial, the sudden lowering of sea-levels at the beginning of the glaciation triggered erosion of the near-shore sediments and the incision of the lower reaches of the rivers, probably affecting the entire Venetian foreland as well as the Alpine and Berici foothills (Monegato et al., 2011). In the 65,000 years that span from MIS5d to MIS3, no signs of fluvioglacial or significant aggradation have been recorded: rivers flowed within stable trenched paths, and relatively low sedimentation rates (Monegato et al., 2011) in both lacustrine and alluvial successions indicate water table stability. Persistent afforestation with some temperate trees, notably *Tilia* and *Abies*, have been recorded throughout the entire early and middle part of the last glaciation, with only moderate forest withdrawals during early Dansgaard-Oeschger events (Pini et al., 2010). The first part of MIS3 records a prevailing zonal vegetation on the plain that includes open birch-conifer forests, xerophytic scrubs and steppe, and phases of contracting conifer forests and expanding steppic communities alternating with mixed conifer (*Pinus* and *Picea*) – Betula forests (Pini et al., 2009). Soil formation affected aeolian deposits (Zerboni et al., 2015). During a late phase of this period (about 38.2 ± 1.45 ky cal BP according to Pini et al., 2010) aggradation of the alluvial fans in the western Venetian Plain occurred, in coincidence with the establishment of long-lasting marshes in the Friulian-Venetian Plain (Fontana et al., 2008).

2.2. Fumane Cave

Fumane Cave is located at 350 m a.s.l. (Fig. 1) and has provided a dated sequence spanning from MIS 5 to MIS 2 (López-García et al., 2015). The Middle and Upper Palaeolithic deposits consist of numerous thin to very thin parallel levels and lenses grouped into stratigraphic units labelled from A13 to A1 (from bottom to top). The Mousterian levels are characterized by lithic and faunal remains densely scattered on the living floors, as is the case in units A11, A10, A9 and A6 (Peresani, 2012; Peresani et al., 2011b). Cherts in A12-A11, A10V, A10, and A6–A5 were exploited mostly through *Levallois* technology (Peresani, 2012). The focus of this paper is the stratigraphic complexes unit A8–A9 and unit A5–A6, dated to 47.6–45 and 44.8–42.2 ky cal BP, respectively (Higham et al., 2009; Peresani et al., 2008). Of these units, layer A6 in particular has provided evidence of a structured use of the living space, covering the entire entrance area (Peresani et al., 2011a). Over 40 combustion features and dumps of combustion debris are associated with zones used for *Levallois* manufacture, tool shaping and curation, ungulate butchery, and the treatment of hides and furs. The faunal assemblage includes a rich association of ungulates, carnivores, and birds from diverse environments and climates. Notably, unit A9 with Discoid technology is ecologically analogous to A5–A6 (Romandini et al., 2014), where the most abundant faunal remains are red deer, ibex, and roe deer, whereas chamois, bison, and giant deer are less frequent. Moose, horse, and wild boar are rare (Table 1). All ungulate species, with the exception of horse and wild boar, bear traces of human exploitation. Tibias, femurs and metapodials, radii and humeri from Cervids (red deer, roe deer, and very large specimens of giant deer or moose), and to a lesser extent from other ungulates, were used as retouchers (Jéquier et al., 2012, 2018). Fox, wolf, brown bear, and cave bear are the most numerous carnivores (Table 1). Except for wolves, carnivore remains show butchery marks from skinning and defleshing (Romandini et al., 2018a, 2018b). The elevated number of cut marks, compared to the scarcity of carnivore gnawing on bones, supports the anthropogenic nature of bone accumulation in these units. In addition to the butchery marks on ungulate and carnivore bones, we also report on the discovery of human modifications to some anatomical elements of large raptors and Passeriformes (Peresani et al., 2011a; Fiore et al., 2016; Romandini et al., 2016).

2.3. San Bernardino Cave

The cave opens on the eastern slope of the Berici plateau (Vicenza), 135 m a.s.l., west of the alluvial plain of the Bacchiglione River (Fig. 1). In a 4 m thick stratigraphic sequence, eight lithological units and three main paleoclimatic cycles have been identified, shifting from temperate

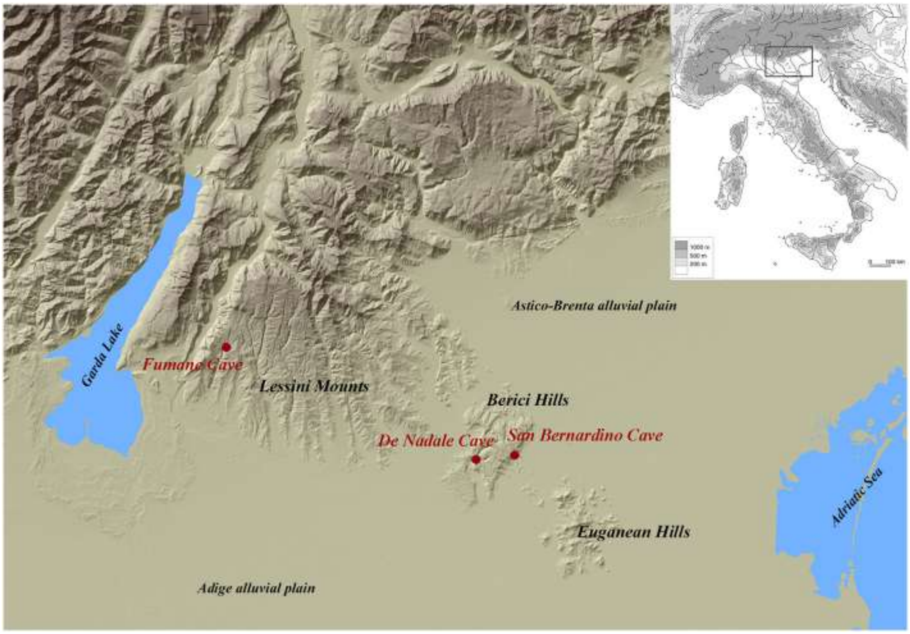

Fig. 1. Geographical location of cave sites.

Table 1
Mammal NISP and NISP% from Fumane Cave (FC – unit A8–A9 and A5–A6), San Bernardino Cave (SB – unit II) and De Nadale Cave (CN – units 6–8).

Taxa	FC – unit A8–A9		FC – unit A5–A6		SB – unit II		CN – units 6–8	
	NISP	NISP%	NISP	NISP%	NISP	NISP%	NISP	NISP%
Lepus sp.			1	0.1	3	0.3		
Marmota marmota	4	0.2	1	0.1	16	1.8		
Castor fiber					25	3		
Total Lagomorpha and Rodentia	4	0.2	2	0.1	44	5.1		
Canis lupus	4	0.2	11	0.3	3	0.3	3	0.2
Vulpes vulpes	4	0.2	46	1.5	7	0.8	2	0.1
Vulpes/Alopex			3	0.1				
Ursus arctos	2	0.1	9	0.3	1	0.1		
Ursus spelaeus	5	0.3	4	0.1	84	9.7	11	0.6
Ursus sp.	3	0.2	22	0.7	38	4.5	16	0.9
Martes sp.					1	0.1		
Mustela putorius					2	0.2		
Mustela nivalis			1	0.1				
Crocuta crocuta	1	0.1						
Felix silvestris					1	0.1		
Linx linx					6	0.7		
Panthera pardus					1	0.1		
Panthera leo	1	0.1						
Carnivora indet.	13	0.7	17	0.5			3	0.2
Total Carnivora	33	1.9	113	3.6	144	16.6	35	1.9
Sus scrofa	2	0.1	2	0.1	29	3.4	1	0.1
Megaloceros giganteus	65	3.9	38	1.3	4	0.4	105	5.6
Alces alces	11	0.6	5	0.2	24	2.8		
Alces/Megaloceros					31	3.6		
Cervus elaphus	391	23.3	1392	44.8	81	9.3	105	5.6
Capreolus capreolus	215	12.9	230	7.4	149	17.2	17	0.9
Cervidae indet.	134	8	167	5.3	56	6.5	54	2.9
Bison priscus	6	0.3	4	0.1			10	0.5
Bos primigenius	6	0.3			1	0.1	1	0.1
Bos/Bison	29	1.7	28	0.9	20	2.3	70	3.8
Capra ibex	42	2.6	84	2.7	1	0.1	1	0.1
Rupicapra rupicapra	54	3.2	87	2.8	24	2.8	3	0.2
Caprinae indet.	15	1	19	0.7	8	1	2	0.1
Stephanorinus sp.					1	0.1		
Ungulata indet.	671	40	932	30	248	28.7	1455	78.2
Total Ungulata	1641	97.9	2988	96.3	677	78.3	1824	98.1
Total NISP	1678		3103		865		1859	
Total Indeterminate	81,090		168,161		3354		22,288	
Total NR	82,768		171,264		4219		24,147	

to dry cool conditions and dating from the Middle-Late Pleistocene (cycle 1) to the Late Pleistocene (cycles 2–3) (Cassoli and Tagliacozzo, 1994; López-García et al., 2017; Peresani, 2001). Unit II, the focus of this paper, was dug over 20 sqm and its thickness ranges up to 40 cm. It records humid climatic conditions, the expansion of woodlands (Cassoli and Tagliacozzo, 1994; López-García et al., 2017), and an increase in the rate of accumulation of anthropogenic remains with respect to the underling units, as suggested from the frequency of faunal remains, lithic artefacts, and hearths. The most abundant ungulate remains belong to roe deer, red deer, moose, wild boar, and bovines (Table 1), while cave bear is the most numerous carnivore (Romandini et al., 2018b). Taphonomic analyses on large ungulate bone surfaces from the main part of the sequence have revealed traces of disarticulation, defleshing, intentional shaft fracturing, and the use of bone fragments as retouchers. Evidence of carnivore activity is scarce.

2.4. De Nadale Cave

De Nadale Cave is a small cavity located at 80 m a.s.l., in the southern slope of the Berici (Fig. 1). It opens on the Calto Valley, a narrow V-shaped fluvio-karstic canyon-type valley with active water springs in its inner zones. The hydrographic drainage system of this area features the initial segment of the Liona Valley with the confluence of other incisions currently supplied by springs from the north and the west, where they are limited by the Pozzolo suspended valley. The geometry and nature of the lowest Calto Valley deposits are unknown, but it is probable that this depressed area (about 55 m a.s.l.) was characterized by moist or swampy environments with peaty deposits in the past, comparable to what is known along the Val Liona.

Field investigations started in 2013 and are still in progress. Under a superficial and reworked layer, a 2 m thick stratigraphic sequence has been unearthed during the last three campaigns. Although ten stratigraphic units have been identified in this sequence, only one (unit 7) can be recognized as archaeological. This unit contains several osteological remains and lithic implements attributed to the Quina method. Uranium-series (U−Th) dating, performed on an herbivore maxillary fragment, provided a minimum age of 70.2 + 1/−0.9 ky BP (Jéquier et al., 2015). The faunal assemblage (Table 1) reveals that the most abundant species are the giant deer and the red deer, followed by large-sized bovines. Chamois and roe deer have also been identified, but in lower numbers. Carnivores are scarcely present: among them, the most common is the bear (*Ursus* sp.; *Ursus spelaeus*), while wolf and fox are represented by 3 fragments each. A taphonomic analysis indicates an excellent preservation of the osteological remains: nearly half of the total amount of bones preserves butchering marks, including scraping and cut marks, impact notches and spiral fractures on the surface of several bone shafts. Furthermore, the large number of pieces with retouch damage is exceptional. This association of taxa, in addition to the ecological data based on the micromammal assemblage, reflects a cold climatic context in a landscape dominated by open woodlands and open dry meadows, which, taking into account the chronology of the site, could be related to the onset of MIS 4 (López-García et al., 2018). Moreover, the importance of large-sized cervids and aurochs in the faunal assemblage supports this interpretation and suggests the presence of a swampy area with water sources (Jéquier et al., 2015).

3. Materials and methods

The bones examined in this study were discovered in the last 30 years of excavations using dry and wet sieving. Zooarchaeological and taphonomic analyses were performed on 175 bovine bones. Taxonomic and skeletal identifications are based on the complete alpine fauna reference collection of the Department of Humanities at the University of Ferrara and, for more problematic cases, in the Quaternary Paleontology and Zooarchaeology Laboratory of the Ethnographic-Prehistoric National Museum “L. Pigorini” (Rome, Italy). For the identification of the remains described here, the publications of Sala (1986) and Martin (1987) were used. Potentially burnt bones were determined by combustion grade level following the criteria described by Stiner et al. (1995). Microscopic analyses of bone surfaces were carried out using a Leica S6D Greenough stereomicroscope with 0.75–70× magnification range for capturing images. In order to identify the nature of surface alterations and to distinguish human from animal damage, trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was made to well-established taphonomic literature (Fernández-Jalvo and Andrews, 2016). Sex and age at time of death were determined by dental wear and by the state of epiphyseal fusion (Habermehl, 1975; Bunn and Pickering, 2010; Silver, 1969). In order to evaluate species abundance, the following methods were used: number of identified specimens (NISP) (Grayson, 1984), minimum number of elements (MNE) (Klein and Cruz-Uribe, 1984; Stiner, 1994), and minimum number of individuals (MNI) (Bökönyi, 1970). Estimating MNI was difficult due to the high degree fragmentation, which mostly involves the long bones and some teeth. As those bones and teeth were frequently cracked into several fragments, it was not always possible to compare the different elements. In order to avoid distortion in the proportions of age groups in the various units, estimations were also calculated for those remains generally determined as *Bos/Bison* by considering only the age or the size of the animal not represented in the two categories of the determined taxa (*Bison priscus* and *Bos primigenius*). To estimate age at death, we used dental wear and the state of epiphyses fusion, as well as the proportions between thickness and growth of crests of femur and tibia. Combustion degree was distinguished between moderate (200–500 °C, black/brown) and elevated with calcination (> 700 °C, grey/white). Cut-marks were classified as incisions, like skinning marks, defleshing marks, and scrapes (Potts and Shipman, 1981; Shipman and Rose, 1984). Intentional bone breakage to access marrow was documented by diagnostic criteria like percussion marks/notches and impact flakes, and positive flakes of the percussion marks (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Pickering and Egeland, 2006; Villa and Mahieu, 1991). Traces left by carnivores were identified as deep punctures in the cortical bone surface, concentrated on the articular ends of the bones, as well as pits and scores with U-shaped striations. These results were compared to data from Fisher (1995), Selvaggio and Wilder (2001), Domínguez-Rodrigo and Piqueras (2003).

4. Results

The bovine bone assemblage, subdivided by anatomical element in craniocaudal order, shows that entire carcasses are not completely represented. In particular, the cranial remains (maxilla, hemimandible, horn, and teeth) and the axial skeleton (ribs and vertebra) are rarely represented. The stilopodium (humerus/femur), zeugopodium (radius-ulna/tibia-fibula), and metapodium (metacarpal/metatarsal) are well represented in all three sites, which contrasts with the low number of limb extremities (Table 2; Fig. 2).

In an osteological context it is difficult to distinguish between the two genera *Bos* and *Bison*, due to the great ambiguity of many of their anatomical elements as well as the high fragmentation of the remains. Due to these factors, most of the remains from the three sites were generically assigned to the category *Bos/Bison*, which is also the case at many other contemporaneous sites. Overall, despite the small number of diagnostic remains, the *Bison priscus* was found at Fumane and De Nadale (n = 10 respectively) and *Bos primigenius* was recovered from all three sites (n = 6 in Fumane Cave, n = 1 in San Bernardino and n = 1 in De Nadale).

Table 2
Anatomical elements of *Bovinae* (*Bison priscus*, *Bos primigenius*, and *Bos/Bison*); NISP and MNI.

	FC – unit A8–A9	FC – unitA5–A6	SB – unit II	CN – units 6–8
Cranium	2	6	1	2
Hemimandible	2	2	2	4
Tooth indet.	2			
Hyoid				
Total cranium	6	8	3	6
Atlas-axis				
Vertebra			1	
Rib	1		1	
Sternum				2
Total trunk	1		2	2
Scapula			1	2
Humerus		2		6
Radius		1	2	9
Ulna	1	1		2
Carpals				
Metacarpal		2		2
Total frontal limb	1	6	3	21
Coxal	1		1	1
Femur	3	3	2	4
Tibia	14	8	3	28
Tarsals			2	
Metatarsal	7		1	9
Total hind limb	25	11	9	42
Metapodial				5
First phalanx		2	3	
Second phalanx	2	3		3
Third phalanx				2
Sesamoid	3		1	
Total indet. limb	5	5	4	10
Indet.	3	2		
Total	41	32	21	81
MNI	6	4	2	7

4.1. Taphonomy

4.1.1. Fumane Cave

Among the natural taphonomic processes that have affected the surface of the studied bovine bones from units A8–A9 and A5–A6 (NISP 73), root modifications were the most common, affecting 30% of the bones. In some cases, root etching was associated with the presence of manganese stains. Concretions were found on many bones (26%), probably due to their immediate proximity to the cave wall. Carnivore damage is very rare, found on only 3 *Bos/Bison* bones. In both units, several remains (56% and 46.8%, respectively) show traces of butchery (Table 3; Figs. 2, 3). These are observed as isolated cuts or cuts in a series, testifying to short- and medium-length gestures. Percussion marks (PM) on long bones for the extraction of marrow account for 13% and 46.6% of the total bovine remains with modifications (Table 3), and are in some cases associated with cut-marks (CM). It should, however, be clarified that for certain anatomical elements where the bone is less protected from the muscular tissue, cut-marks may indicate the recovery of skin or disarticulation (Table 3; Fig. 3). Cut-marks found on a fragmentary left mandible with deciduous dentition, as well as a few phalanges, sesamoids, and metapodials, demonstrate defleshing and in some cases, disarticulation. The defleshing and detachment of muscle mass is evident: sixteen tibiae from different individuals, three femurs, two humerus and two radii preserve cut marks. Five bones from A8–A9 (12.1%) and one from A5–A6 show traces of thermal alteration. In two cases, a *Bos primigenius* metatarsal (A9 SVI.2) and a radius of *Bison priscus* (A5 SIII) were associated with combustion features (Fig. 3F). So far, the only seasonal indication of human use of the site is limited to the A8–A9 unit, where a fragment of an infant *Bison priscus* (right mandible with attached premolar deciduous teeth) had evidence of skinning (Fig. 3A_1). This suggests that the animal was hunted between spring and summer. Five bone shafts (2 *Bison priscus* and 3 *Bos/Bison*) were used as hammers for retouching flint artifacts. The retouchers were manufactured from metapodials, femurs, and tibia, most of them cut-marked (Table 4; Figs. 2, 6A_1).

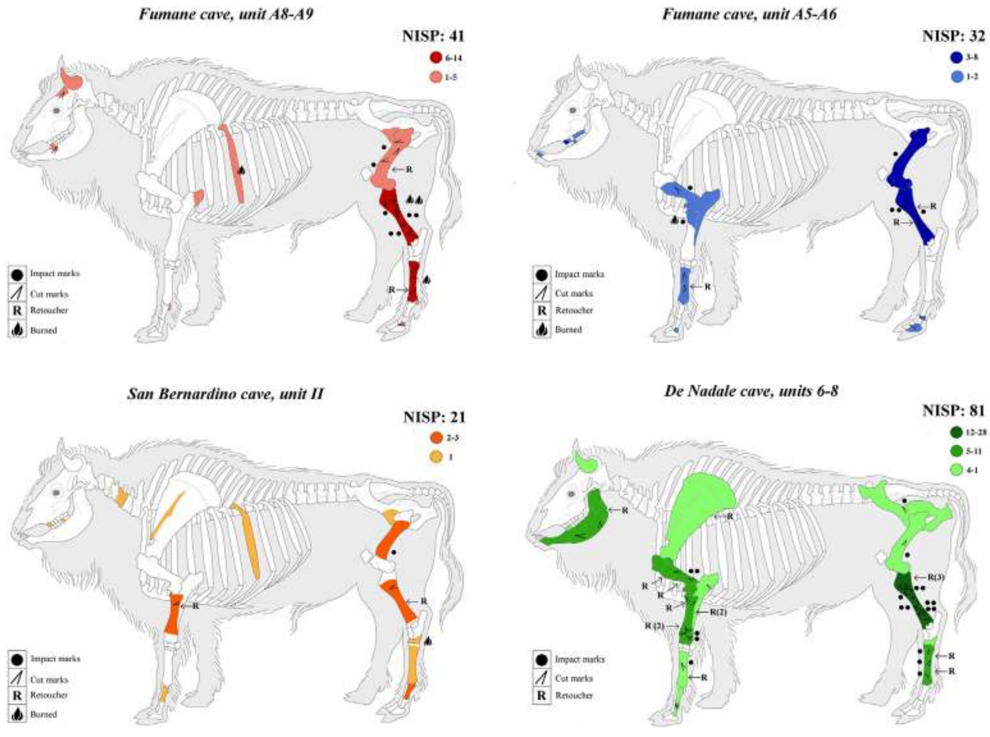

Fig. 2. Frequency of skeletal elements of the *Bovinae* (*Bison priscus*, *Bos primigenius*, and *Bos/Bison*) and distribution of butchery marks.

Table 3
Number of anatomical elements of *Bovinae* with anthropogenic modifications and carnivore marks; CM cut-marks, PM percussion marks, CM + PM cut-marks + percussion marks, BM butchery marks, R retoucher, B burned, GM gnaw marks.

	Bovinae - FC unit A8–A9								Bovinae - FC unit A5–A6								Bovinae - SB unit II								Bovinae - CN units 6–8							
	NISP	CM	PM	CM + PM	TOT. BM	R	B	GM	NISP	CM	PM	CM + PM	TOT. BM	R	B	GM	NISP	CM	PM	CM + PM	TOT. BM	R	B	GM	NISP	CM	PM	CM + PM	TOT. BM	R	B	GM
Cranium	2	1			1				6								1								2							
Hemimandible	2	1			1				2								2								4	2			2	1		1
Tooth indet.	2																															
Total cranium	6	2			2				8								3								6	2			2	1		1
Vertebra																	1															
Rib	1						1										1															
Clavicle																									2							
Total trunk	1						1										2								2							
Scapula																	1								2					1		
Humerus									2	1	1		2												6	1	1	2	4	2		
Radius									1		1		1		1		2	1			1	1			9	4		2	6	5		1
Ulna	1								1																2	1			1			
Carpals																																
Metacarpal									2	2			2	1											2							
Total frontal limb	1								6	3	2		5	1	1		3	1			1	1			21	6	1	4	11	8		1
Coxal	1																1								1			1	1			1
Femur	3	1		2	3	1		1	3		1		1				2		1		1				4	1	1		2			
Tibia	14	4	2	5	11		2	1	8	1	2	2	5	2			3	1			1	1			28	9	5	4	18	3		3
Tarsals																	2						1									
Metatarsal	7	2	1	1	4	1	1	1									1								9	1	2	2	5	2		1
Total hind limb	25	7	3	8	18	2	3	3	11	1	3	2	6	2			9	1	1		2	1	1		42	11	8	7	26	5		5
Metapodial																									5	2		1	3	1		
First phalanx									2	1			1				3															
Second phalanx	2	1			1				3	1			1												3	1	1		2			1
Third phalanx																									2							
Sesamoid	3	1			1												1															
Total indet. limb	5	2			2				5	2			2				4								10	3	1	1	5	1		1
Indet.	3	1			1		1		2		2		2																			
Total	41	12	3	8	23	2	5	3	32	6	7	2	15	3	1		21	2	1		3	2	1		81	22	10	12	44	15		8
MNI	6								4								2								7							

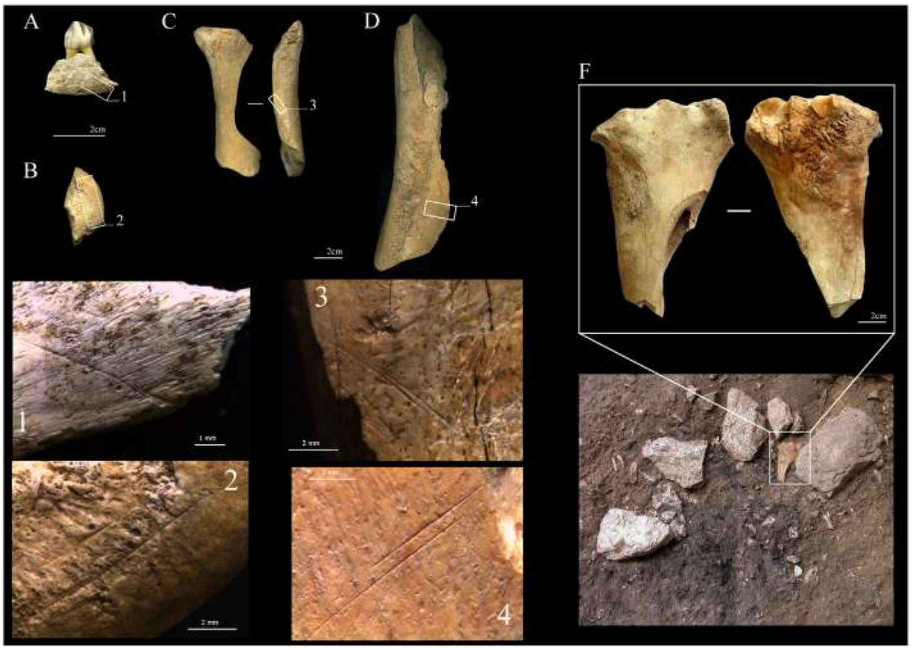

Fig. 3. Fumane Cave (unit A8–A9 and unit A5–A6), localization and details of anthropogenic traces: A) right mandible with premolar deciduous teeth of *Bison priscus*, with traces on buccal side (1 – close-up of *striae*); B) distal portion of second phalanx of *Bos/Bison* with traces (2); C) right metacarpal of *Bos/Bison* with traces on lateral portion (3); D) right tibia of *Bos primigenius* with traces on diaphysis (4); F) Combustion structure (A5 SIII) and associated radio of *Bison priscus*.

4.1.2. San Bernardino Cave

Among the natural taphonomical processes that have affected the bovine remains (NISP 21), manganese coatings and roots had the biggest impact, modifying the bone surface of 38% and 26% of the assemblage, respectively. No traces attributable to carnivores were found in this assemblage. The bovine remains with traces of butchering marks are scarce (Table 3; Figs. 2, 4), and include only one radius and one tibia. The documented activities probably relate to defleshing and the detachment of muscle mass. Percussion marks are visible only on the diaphysis of a femur (Table 3; Fig. 4B), which presents two relatively large percussion grooves, one of which covered most of the cortical surface. Two retouchers were present (Table 4, Figs. 2, 6B_2), made from a radius and tibia of generic *Bos/Bison*. Cut-marks on the dorsal face of the radius (defleshing) were noted in association with the area used for retouching.

4.1.3. De Nadale Cave

Taphonomic analysis suggests that the most common bone surface modifications are due to manganese staining and root etching. Manganese stains have been detected on 47 bovine bones (56.6%), while root modifications are present on 52 remains (62.6%). Trampling also affected several remains, as it has been recognized on 38 bone shafts (47.8%). Carnivore gnawing is rare: 8 of the 81 (9.8%) bone fragments show pits and tooth marks. Butchering marks are abundant: 44 fragments (54.3%) show anthropogenic modifications related to defleshing, skinning, and marrow extraction activities. Moreover, 22 remains are cut marked (27%), 10 have percussion marks (12.3%), and 12 bone fragments (14.8%) have both (Table 3; Figs. 2, 5). The presence of cut marks on a second phalanx and on two fragmented mandibles reflects skinning activities; the same traces detected on three fragments of humerus, six radii, one ulna, one coxal, one femur, thirteen tibias, three metatarsals, and three generic metapodial, suggest defleshing and muscle mass removal. Furthermore, there are some large, deep scrape marks on two tibia shafts, on a metatarsal and on two mandibles, pointing to the removal of the periosteum. On one of the mandible fragments, these traces seem to be linked to the retouch damage. Percussion marks have been observed on three humerus diaphyses, two radii, one coxal bone, one femur, nine tibias, four metatarsals, one generic metapodials, and one second phalanx, attesting to the intentional fragmentation of the long bones to extract marrow (Fig. 5A and D). In total, there are 15 bone retouchers (Figs. 2, 6C_3; D_4–5): one mandible, one scapula, two humeri, five radii, three tibias, three metatarsals and one generic metapodial. Of these 15 bone tools, 12 are also cut-marked and 8 have percussion marks for marrow extraction.

4.2. Age and minimum number of individual estimation

Data from Fumane indicate the presence of individuals of almost all ages, with a small preference towards adults (Table 4). In A8–A9 specifically, MNI indicates at least 6 bovines (2 *Bison priscus*; 2 *Bos primigenius* and 2 *Bos/Bison*): *Bison priscus*-1 infant (> of 1 month); 1 generic adult; *Bos primigenius*-2 generic adults of different ages; *Bos/Bison*-1

Table 4
NISP and MNI divided by age of *Bison priscus*, *Bos primigenius*, and *Bos/Bison*.

	FC – unit A8–A9						FC – unit A5–A6					SB – unit II				CN – units 6–8				
Taxa	NISP	MNI by age				Total MNI	NISP	MNI by age			Total MNI	NISP	MNI by age		Total MNI	NISP	MNI by age			Total MNI
		I	Y-A	A	S			Y	A	S			Y	A			I	Y	A	
Bison priscus	6	1		1		2	4		2	1	3					10			4	4
Bos primigenius	6			2		2						1		1	1	1			1	1
Bos/Bison	29		1	*1*	1	2(*1*)	28	1	*3*	*1*	1(*4*)	20	1	*2*	1(*2*)	70	1	1	*3*	2(*3*)
TOT.	41	1	1	3	1	6	32	1	2	1	4	21	1	1	2	81	1	1	5	7

Italic numbers represent the MNI by age of *Bos/Bison* not considered in the total because already represented in the two categories of determinate taxa (*Bison priscus* and *Bos primigenius*).

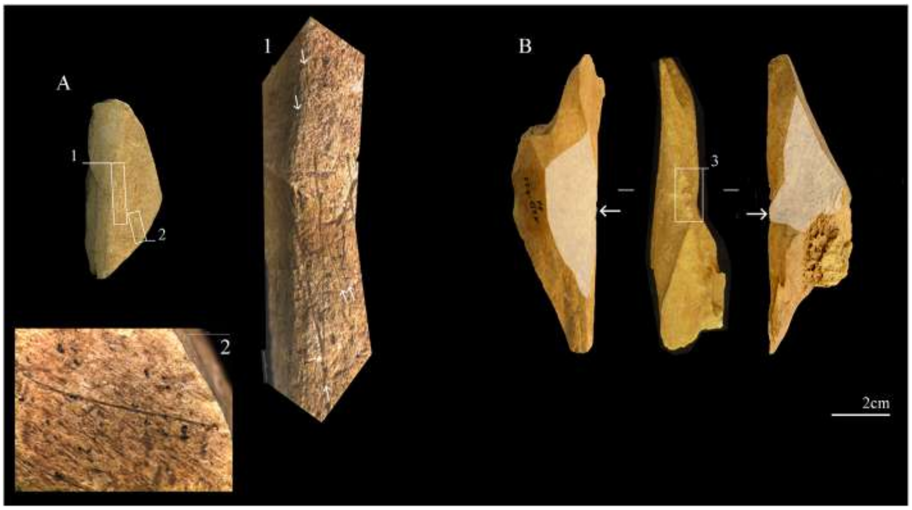

Fig. 4. San Bernardino Cave, localization and details of anthropogenic traces: A) tibia of *Bos/Bison* with traces on diaphysis (1–2); B) femur of *Bos/Bison* with percussion marks (3) and percussion notch.

young adult; 1 senile. To date, in A5–A6 an MNI of 4 bovines has been estimated (3 *Bison priscus*; 1 *Bos/Bison*): *Bison priscus*-2 generic adults; 1 senile; *Bos/Bison*-1 young (< 24 months).

At San Bernardino, a combination of young and adult individuals is noted, while infant and senile individuals are absent. An MNI of 2 bovines was estimated (1 *Bos primigenius* and 3 *Bos/Bison*): *Bos primigenius*-1 generic adult; *Bos/Bison*-1 young (12–24 months).

All ages are present at the De Nadale, with a clear predominance of adults. The bovine remains can be ascribed to seven individuals (4 *Bison priscus*, 1 *Bos primigenius* and 2 *Bos/Bison*), at least: *Bison priscus*-4 generic adults; *Bos primigenius*-1 generic adult; *Bos/Bison*-1 infant and 1 young. The presence of a *Bos/Bison* fetus establishes that the occupation of the site occurred mostly between spring and summer.

5. Discussion

In the all three bone assemblages, it was not possible to distinguish between *Bison priscus* or *Bos primigenius* for all remains, due to their high fragmentation rate and similarities of many anatomical elements. The taxonomy of large bovids is traditionally based on cranial and horn characteristics (Breda et al., 2010), but a number of authors (Martin, 1987; Sala, 1986; Sher, 1997) have shown that well-established characteristics can also be used to identify some of the postcranial skeletal elements to taxon. Taphonomic analyses have provided evidence of human exploitation of large bovids for meat and other resources. Butchering marks are abundant: 38 NISP (52.0%) in Fumane A9–A5, 3 (14.3%) at San Bernardino and 44 (54.3%) at De Nadale provide evidence of defleshing and marrow extraction (Table 3). In most of the examined cases, the low number of axial skeleton elements induces us to hypothesize that Neanderthals intentionally preferred certain anatomical elements (front and hind limb) over others (skulls and mandibulae, which are represented in small numbers). This selection likely took place directly at the kill site in order to facilitate the transport of the highly valued body elements to the sites, while body parts with low economic value would have been left behind (Marín et al., 2017). Such decisions are influenced by various factors including the body sizes of prey, distance to the site, weather, topography, the number of hunters involved, the cost of carcass processing and transporting, as well as the competition with other carnivores (Bunn et al., 1988; Monahan, 1998; Schoville and Otárola-Castillo, 2014). Furthermore, considering the potential weight of these animals, which in some cases were considerably bigger than their modern descendants, it makes sense that the

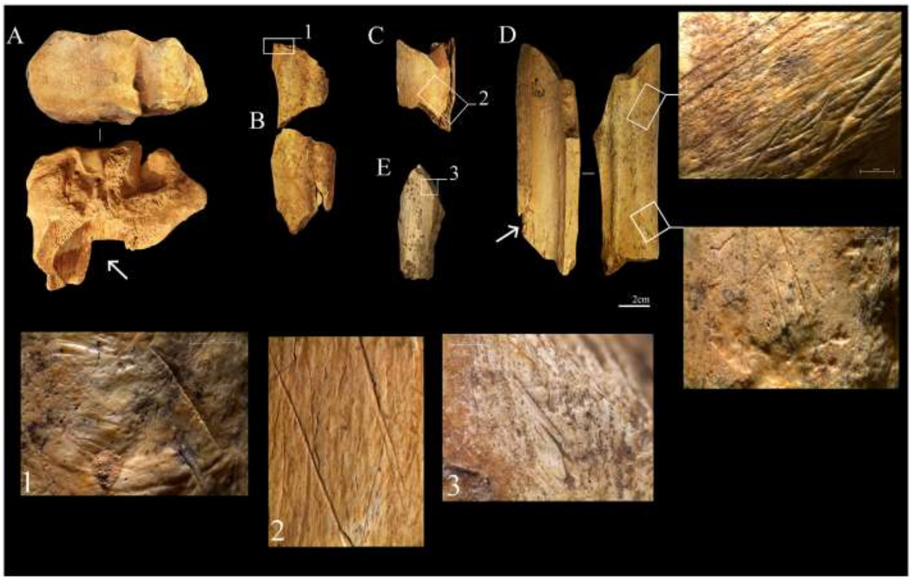

Fig. 5. De Nadale Cave, localization and details of anthropogenic traces: A) right radius *of Bos/Bison*, with percussion marks (white arrow); B) metacarpal of *Bos/Bison* with traces on dorsal face (1 – close-up of *striae*); C) rib of Bos/Bison with traces (2); D) left tibia of *Bison priscus* with traces on diaphysis and percussion marks (white arrow); E) tibia of *Bos/Bison* with cut-marks (3).

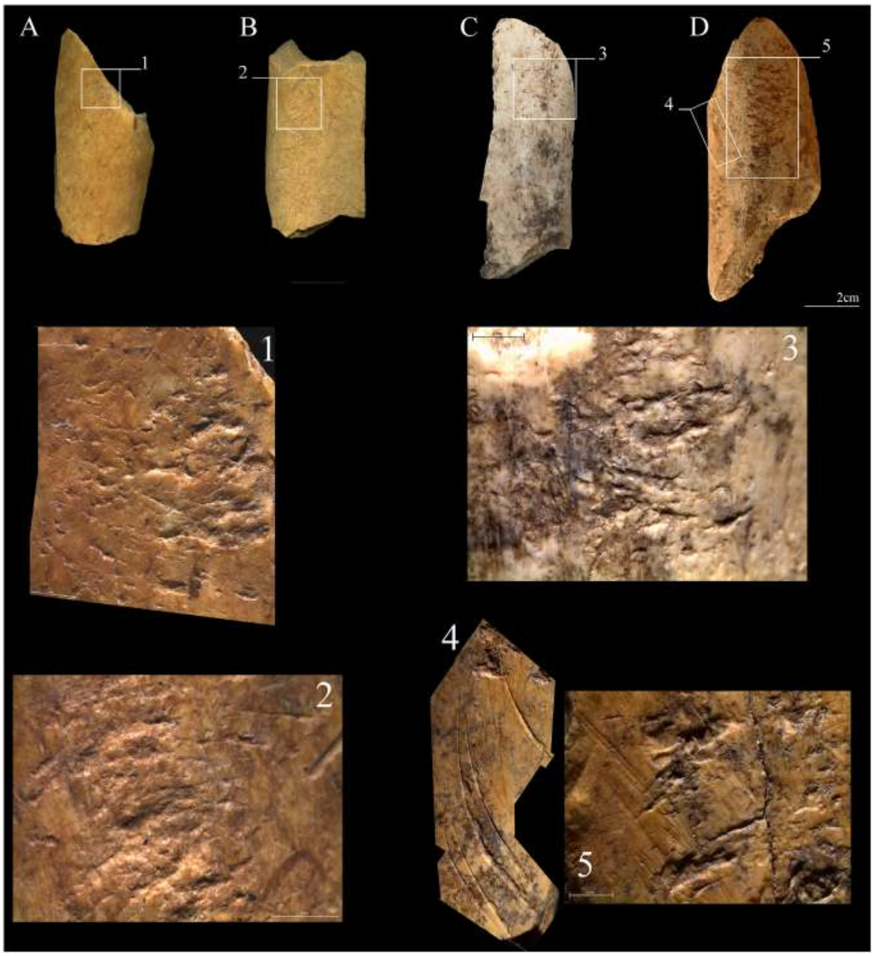

Fig. 6. *Bovinae* bone retouchers from Fumane Cave (A), San Bernardino Cave (B) and De Nadale Cave (C–D). A) femur of *Bison priscus* with pits produced during knapping (1); B) tibia of *Bos/Bison* with close-up of area used like retoucher (2); C) scapula of *Bos/Bison* with close-up on the areas used for retouching stone artifacts (3); D) left humerus of *Bos/Bison* with cut-marks (4) and pits produced during knapping on diaphysis (5).

first steps of butchering would have occurred at the kill site. The presence of elements of relatively poor nutritional value like the few skull and mandible fragments at Fumane and De Nadale might correlate to the transport of the complete carcass from the kill site. The latter should be located a short distance from the settlement, as the skull has the greatest decrease in probability of transport as a function of increasing distance (Schoville and Otárola-Castillo, 2014). However, the almost complete absence of low survival elements (vertebrae and ribs) with carpals and tarsals may be due in part to multiple attrition processes generated by Neanderthals, the action of carnivores, and post-depositional agents. A further reduction could result from the intensive treatment of these anatomical parts by boiling (Morin and Soulier, 2017b) or from their use as fuel. On the other hand, the absence of axial bones does not occur with the same incidence in these assemblages, so their presence, although rare, indicates that at some point carcasses were introduced into the caves intact.

Based on these observations, it seems that the anatomical representation may be related to the sum of different carcass transport patterns, where the size of the animal was one of a few determining factors. Fetal bones at De Nadale are indicative of at least one pregnant female that was brought to the cave in its entirety. The age at death of both species suggests a lack of individual selection. The presence of two infant remains from Fumane and De Nadale indicates that hunting occurred between spring and summer, the period when bovids disperse into small, highly mobile groups (counting only a few individuals in some cases) and give birth (Rendu and Armand, 2009). The rarity of available data and the low number of individuals do not support further considerations about age at death.

Our data and analyses thus indicate that large bovids were hunted in the Middle Palaeolithic of northern Italy but were not specially targeted by Neanderthals as their main prey. A similar situation has been observed in this region where variable evidence of large bovid exploitation by humans has been recorded, even if it is in some cases ephemeral, like at Riparo Tagliente (Thun-Hohenstein and Peretto, 2005). Large bovids are also found at Grotta della Ghiacciaia in the Lessini Mountains, despite the limited investigation carried out at the site (Bertola et al., 1999), Grotta del Broion (Peresani and Porraz, 2004) and Grotta di Paina (Gurioli et al., 2006) in the Berici Hills (however, these two caves preserve only ephemeral traces of human occupation). In the Fumane, San Bernardino, and De Nadale bone assemblages the ratios of large bovid remains to other ungulates are −1:0.02, 1:0.05, 1:0.3 respectively. One reason for this is that other resources were available during the year (e.g. cervids), and may have been more abundant in the surrounding areas or may have been easier to hunt (Delagnes and Rendu, 2011). In general, hunting and related activities are largely reflected among ungulates relative to their taxonomic abundance and the ecological conditions found in the proximity of each specific site. This shifted with climatic oscillations during the Late Pleistocene (Fiore et al., 2004). Red and roe deer were mainly targeted, with the occasional hunting of chamois and ibex (Fiore et al., 2004; Romandini et al., 2014) and the limited exploitation of giant deer, elk and, very rarely, wild boar. Nevertheless, De Nadale partly diverges from this pattern in that it demonstrates that predation was mostly focused on large herbivores like giant deer, red-deer and bovids. As the faunal spectrum

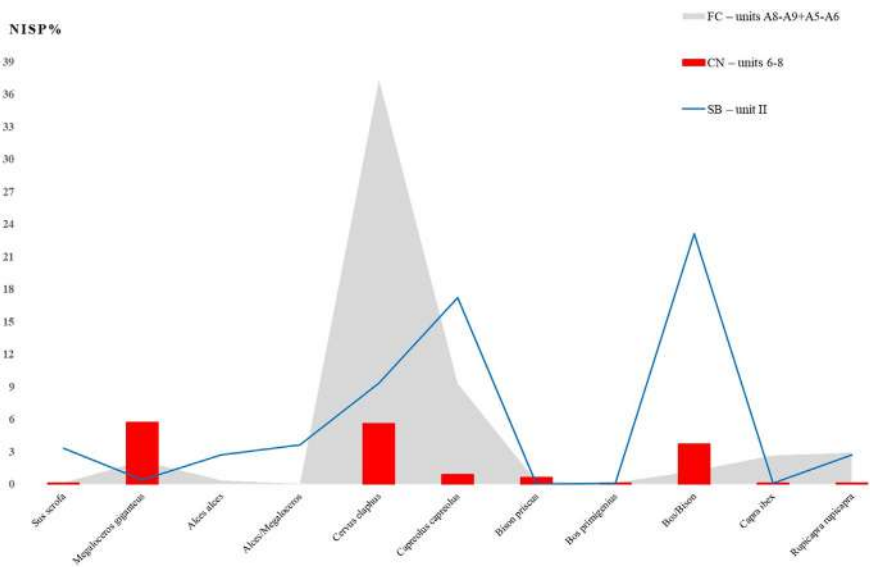

Fig. 7. NISP % of ungulates from Fumane Cave, San Bernardino Cave and De Nadale Cave.

suggests (Fig. 7), even if other medium sized prey – roe deer, chamois and ibex – were encountered near the surroundings, hunting seems to have focused on large sized ungulates. This aspect is highlighted by the NISP and the MNI indices, which are higher for bovids and giant deer when compared to other taxa. Moreover, over half of the total amount of large sized ungulates bears human traces produced from butchering and the exploitation of the shafts as retouchers for shaping stone tools. While the broad game spectrum possibly reflects the ecological variability around the cave, with the co-existence of open landscapes on the Berici plateau and the presence of springs at the bottom of the Calto Valley, the predominance of large sized taxa might be linked to a specific hunting behaviour, related to the mobility of Neanderthal groups. In addition to this, cultural and technological differences might have played a major role in the intense exploitation of these animals.

During MIS 4–3 in northeast Italy, large bovids were present across a wide territory including the lowest mountain ranges, and the karst plateau and alluvial plains of the Po, Adige, and the rivers of the Friulian-Venetian plain (Fig. 8). Bovid remains (*Bison priscus*, *Bos primigenius* and *Bos/Bison*) are reported in Late Pleistocene deposits (Fig. 8: Bon et al., 1991; Breda and Gallini, 2001; Cassoli and Tagliacozzo, 1994; Sala, 1990; Sami and Ghezzo, 2015) and both species are often found in association within the same site, for instance at the Quinzano quarries and Grotta Tilde (Bon et al., 1991; Cassoli and Tagliacozzo, 1994). This suggests the existence of different ecological conditions, from dense forests with wetlands and small streams, ecologically more attractive to *Bos primigenius*, to hilly grasslands and plains, populated by bison. According to this distribution, could topography have influenced the hunting of both animals in relation to the structure of the settlement system in the area? What is certain is that the Fumane, San Bernardino, and De Nadale caves are located in a

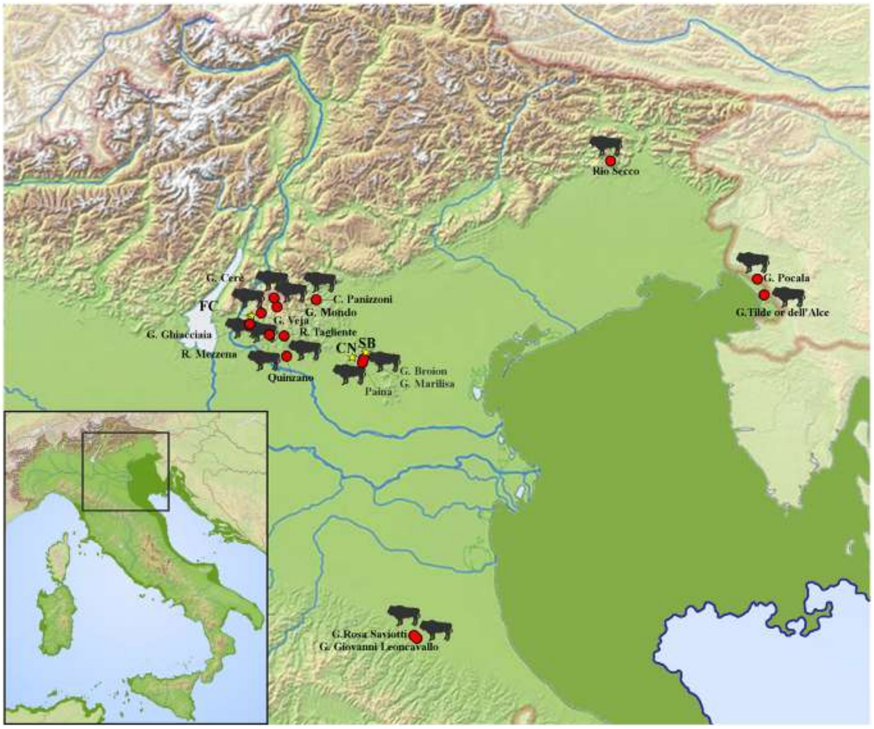

Fig. 8. Localization of *Bovinae* remains (*Bison priscus*, *Bos primigenius* and *Bos/Bison*) in northern Italy during MIS 4–3, including the sites of this work (yellow star). Sea level 70 m below the present-day coastline (courtesy by S. Ricci, University of Siena. Based on the global sea-level curve by Waelbroeck et al. (2002), but lacking estimation of post-MIS 3 sedimentary thickness and eustatic magnitude). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

region that included large bovid habitats; however, the exploitation of these resources could effectively have been influenced by the physical landscape of the site's surroundings. Fumane Cave was situated on a steep slope in proximity to one of the flat ridges of the Monti Lessini, a fan-shaped high plateau gently raising from the Adige alluvial plain, dissected by large valleys that converge at higher elevation on the plateau. Herds of animals may have migrated seasonally along these ridges to and from the alluvial plain. Similarly, the location of De Nadale must have played a fundamental role in the acquisition of certain preys. The excellent view and the strategic location on the Calto Valley would have allowed hunters to easily monitor herd movements. This situation may explain the presence of entire carcasses at the site. At the same time, the location of the sites in an ecologically varied landscape should have favoured access to a spectrum of resources. These considerations lead us to question if the selection and hunting of certain kinds of prey could have been influenced by other factors, such as climate or seasonality. Climatic conditions fail to explain this phenomenon for San Bernardino and Fumane, which both date to the first part of MIS 3, demonstrated by the presence of the same resources in the region. De Nadale Cave provides a different pattern. A study of its micromammal assemblage (López-García et al., 2018) shows that it was likely surrounded by open woodland and open-dry habitats, probably at the onset of MIS 4, which may explain the higher incidence of bovids when compared to the MIS 3 evidence from San Bernardino and Fumane caves. An increase in bison populations during MIS 4 in Western Europe was previously suggested by Delpech (1999) on the base of zooarchaeological data.

It has also been considered that seasonality may have been one of the factors that made Neanderthals hunt specific animals at certain time of the year, thus exploiting the less migratory and more predictable animals such as bovines in some periods. However, studies on seasonality are still incomplete; therefore, a more detailed analysis based on cementochronology or isotopes, similar to those undertaken for some European sites (Bocherens et al., 2015; Julien et al., 2012; Lieberman, 1994; Naji et al., 2015; Niven et al., 2012; Rendu, 2010; Rendu and Armand, 2009; Rendu et al., 2012) is necessary to provide further information.

Culture is often considered an important factor in explaining the variability of Neanderthal subsistence patterns. Of the most common techno-typological systems adopted to fulfill mobility patterns, the Quina Mousterian is traditionally considered as the expression of a highly mobile technological system related to hunting strategies focused on predictable seasonal displacements of gregarious and migratory prey. This is the case of many regions of Europe where the acquisition of migrating large ungulates was largely related to reindeer hunting (Delagnes and Rendu, 2011) and where a specific site was repeatedly settled for the exploitation of this particular taxon in accordance with a year-round pattern. However, the Quina system is not exclusively correlated to the targeted exploitation of reindeer herds. Although found in fewer numbers, western European sites indicate that bovids were largely exploited as well. This is the case of Mas-Viel and Sous-les-Vignes caves in Dordogne, France, both dated to the first half of MIS 3 and for this reason recording the persistence of the Quina Mousterian longer than MIS 4 (Turq et al., 1999). To these two sites, which show a relatively important reliance on large bovids, we add Axlor Cave (Cantabria, Spain), where the Quina Mousterian dates to beyond the limit of the radiocarbon method (Rios-Garaizar, 2017).

6. Conclusion

Bovids were exploited at various times during the Late Middle Palaeolithic of Europe (Jaubert et al., 1990; Martinez Moreno, 1999; Turner, 1999) according to the ecological contexts and mobility patterns of these large herbivores. Sites at the rim of the northern Adriatic Plain during MIS 4 and MIS 3 confirm that bison and aurochs were targeted by Neanderthals but at the same time indicate a different scenario in relation to faunal and human movements. The mobility patterns of large bovids in this wide and flat land are still unknown, due to the lack of MIS 4 and MIS 3 faunal assemblages between the northern and the southern edge of the Po plain, and to the still incomplete data on seasonality, isotope compositions, and other sources for inferring dietary patterns. Although the northern Adriatic Plain was more extended than it is today, it still did not support seasonal movements of bovid herds at a large scale, unlike less constrained landscapes in western Eurasia. The possibility that large herbivores did not show extensive mobility patterns is furtherly enhanced by the ecological conditions of MIS 4, which never reached the level of the arctic open-landscapes of Western and Northern Europe, thus providing a sustainable biomass to maintain local subsistence patterns and the adaptation of hominins bearers of the Quina techno-typological system.

The aim of this study was to discuss the contribution of large bovids to Neanderthal subsistence in northern Italy and the conditions that might have affected the presence or absence of these animals during MIS 4 and MIS 3. It has been shown here that *Bison priscus* and *Bos primigenius* were an important resource for different groups of Middle Palaeolithic hunters that lived across a wide territory of northern Italy, although they were not the most commonly exploited animals. Furthermore, they were present and, in some cases, hunted in a variety of landscapes, influenced by the behaviour of the species themselves. A significant set of evidence shows that Neanderthals were able to face environmental and topographical constraints and change over time by adapting their hunting behaviour, technological lithic system, and mobility.

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4.3 Paper 3

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Bone retouchers from the Mousterian Quina site of De Nadale Cave (Berici Hills, north-eastern Italy)

Eva Francesca Martellotta [a,b,c], Alessandra Livraghi [b,c], Davide Delpiano [c], Marco Peresani [c,d,e,*]

This paper focuses on the analysis of 335 retouchers yielded by De Nadale Cave. The taxonomically species-level determination is in line with the general faunal spectrum recognized at the site: *Megaloceros giganteus*, *Cervus elaphus* and large bovids (*Bos/Bison* and *Bison priscus*) are the most represented taxa.

Long bones are the most selected specimens, in particular tibiae, followed by radii, femurs, metacarpals and metatarsals. Peculiar anatomical portions used as retouchers are seven broken ribs, three fragments of mandible (one still bearing teeth) and two fragments of scapula. Regarding skeletal parts or taxa, no precise choice of was recognized but the thickness and the weight must have played a fundamental role in the selection of the material.

Anthropic traces due to butchering activities, always located underneath the retouch stigmata, are observed on 82% of retouchers. Among them, cut marks are the mostly frequent registered. Some shafts present impact notches and few of them have been recognized as impact flakes. In many cases the shafts bear more than one functional area overlapping.

We contributed to this paper focusing on the taxonomical identification and the taphonomical analyses.

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ABSTRACT

Bone retouchers are present in the human toolkit throughout the Lower and Middle Palaeolithic and appear in many contexts across Europe, sometimes in association with heavily retouched stone tools. Here we present the complete assemblage of bone retouchers recovered in the Mousterian Quina site of De Nadale Cave in the north of Italy dated to the onset of MIS 4. The results show that this assemblage is consistent – both in morphological and technological features - with bone retouchers recovered in the rest of Europe. The predominance of cervid and bovid limb bones is observed, and the study of the retouch-induced stigmata reveals intense modification of the lithic industry carried out on-site. This analysis contributes to our understanding of Neanderthal cultural and economic choices in the Quina complex in Europe.

1. Introduction

Retouchers are among the most ancient bone tools in existence. They have been recovered in several important sites in Europe, starting from the Lower Palaeolithic, at Gran Dolina TD10-1 (Rosell et al., 2011, 2015), Bolomor Cave and Qesem Cave (Blasco et al., 2013; Rosell et al., 2015, 2018) and Schöningen (Julien et al., 2015) among others. These tools became widespread during the Middle Palaeolithic in Eurasia (Mallye et al., 2012; Mozota Holgueras, 2012; Abrams et al., 2014; Daujeard et al., 2014, 2018; Costamagno et al., 2018; Doyon et al., 2018; Neruda and Lázničková-Galetová, 2018; Turner et al., 2020, among others). In the north of Italy, the focus region of this paper, Tagliente Shelter and Ghiacciaia Cave (Bertola et al., 1999; Thun Hohenstein et al., 2018), Rio Secco Cave (Peresani et al., 2014; Romandini et al., 2018), Fumane Cave (Jéquier et al., 2012, 2013, 2018; Martellotta et al., 2020) and San Bernardino Cave (Giacobini and Malerba, 1998) are among the most representative contexts whose assemblages contain bone retouchers. During the Upper Palaeolithic, these tools continued to be utilized in Europe (Tartar, 2012; Jéquier et al., 2012, 2013) and in China (Zhang et al., 2018), only to disappear with the advent of the metal ages and the disuse of stone for tool production.

The first identifications of bone retouchers date back to the end of the nineteenth century and the early twentieth century (Leguay, 1877; Henri-Martin, 1906, 1907, 1910; Giraux, 1907; Mortillet and Mortillet, 1910), after which many functional studies followed, including even several experimental approaches (Mallye et al., 2012; Mozota Holgueras, 2012, 2013, 2014, 2018; Tartar, 2012; Hutson et al., 2018).

Mostly, retouchers result from the recycling of bones following the butchery of large herbivores and sometimes carnivores (Abrams et al., 2014). Evidence also exists for retouchers having been made with inorganic materials: mainly pebbles (Taute, 1965; Bertola et al., 1999; Bourguignon, 2001; De Lumley et al., 2004; Raynal et al., 2005; Nicoud, 2010, among others), occasionally cores and handaxes (Thiébaut et al., 2010) and rarely flint tools – the so-called "bulb retouchers" (Tixier, 2000; Mathias and Viallet, 2018; Centi et al., 2019, among others). Regarding bone retouchers, the majority of them are obtained from long bone shaft fragments belonging to both upper and lower limbs, though there are examples of the employment of different skeletal parts, such as epiphyses, ribs, mandibles, teeth, and phalanxes (Henri-Martin, 1906; Auguste, 2002; Jéquier et al., 2012, 2013, 2018; Daujeard et al., 2014; Costamagno et al., 2018). The faunal species used vary depending on the resources exploited in the site surroundings. Archaeological evidence

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also attests the use of human bones in some rare cases at La Quina Cave (Verna and d'Errico, 2011), Krapina (Patou-Mathis, 1997), Les Pradelles (Mussini et al., 2011) and Goyet Cave (Rougier et al., 2016). The term "bone retoucher" will be shortened to "retoucher" hereafter, unless a different raw material was used.

Retouchers appear very frequently in association with Mousterian Quina contexts in several parts of Europe (Henri-Martin, 1906; Chase, 1990; Chase et al., 1994; Valensi, 2002; Mozota Holgueras, 2012; Niven et al., 2012; Castel et al., 2017; Costamagno et al., 2018; Ready and Morin, 2019). Quina Mousterian ascribes to a specific lithic industry (Bordes, 1981) though it has not been clearly demonstrated to be a discrete, unified cultural entity characterized by well-defined technological and behavioural patterns. The most diagnostic evidence of this techno-complex is the high rates of retouched tools, mainly scrapers, and core-reduction aimed at the production of thick, wide and often asymmetric flakes. These show a further reduction, part of the so-called "ramification cycle", having the double objective of tool-retouching and obtaining small, usable flakes (Bourguignon, 1996, 1997; Turq, 2000). One of the consequences of this technical behaviour is the Quina retouch, that consists of the removal of scaled invasive flakes, from the dorsal face, using soft-hammer percussion with bone or antler (Bourguignon, 1997, 2001; Turq, 2000; Bourguignon et al., 2013). Aside from the Quina scrapers, a correlation between bone retouchers and denticulate tools has also been suggested (Rosell et al., 2011). In the definition of Quina complex, the exploitation of animal resources, for food and/or technological purposes, is strictly related to human mobility and subsistence strategies (Castel et al., 2017; Costamagno et al., 2018). Despite the broad dietary spectrum, the critical component of subsistence was the exploitation of ungulates. In Europe, Quina contexts are dominated by mono-specific assemblages, mainly consisting of remains attributable to large and medium-large sized cervids (above all red deer and reindeer, followed by giant deer), bovids (bison and auroch) and horse (Jéquier et al., 2012, 2013, 2018; Mozota Holgueras, 2012; Costamagno et al., 2018; Discamps and Royer, 2017). Therefore, focusing on the exploitation of osseous material could contribute to a more comprehensive definition of the Neanderthal toolkit and clarify the behavioural hallmarks that identify Quina human groups.

De Nadale Cave, the only Quina Mousterian context currently being investigated in Italy and in south-central Europe (Jéquier et al., 2015; Livraghi et al., 2019) could give an important contribution. In this small cavity, large numbers of retouchers have been found, some of which (NR = 204) have already been presented in preliminary publications (Jéquier et al., 2015, 2018). Recent excavations at De Nadale Cave extended to almost the entire deposits, adding more than one hundred retouchers made of giant deer, red deer, and bovid bones to the published sample. Here we present the complete assemblage of retouchers recovered until the last field campaign conducted in 2017. They are analysed from a morphological and a technological perspective. The aim is to provide a complete description of their techno-morphological features to contextualise them in a specific technocomplex of the Middle Palaeolithic, through comparison with other Quina Mousterian sites in Europe; this comparison takes into account the used areas, the represented faunal species, and the selected skeletal parts in relation to the morphometric data.

2. Materials and methods

2.1. De Nadale cave context

De Nadale Cave is a small cavity located 130 m above sea level on the Berici Hills, in the Province of Vicenza, in north-eastern Italy (Fig. 1). The exploration of this area in recent decades yielded evidence of Palaeolithic human occupation, with the most relevant recorded at Broion Cave and Broion Shelter, and San Bernardino Cave (Leonardi, 1979; Peresani, 2001). Research at De Nadale Cave started in 2013 when a first excavation campaign led to the discovery of a cave entrance (8 m wide) after the removal of reworked sediments (unit 1Rim). Later, six campaigns were carried out between 2014 and 2017 in order to investigate the deposits preserved in the cave entrance (Jéquier et al., 2015; Livraghi et al., 2019) and to recover additional cultural and faunal material from the sediments reworked in badger dens.

The excavations exposed a 2-meter-thick stratigraphic sequence at the entrance, thinning to one meter in the cave-mouth, which includes a single anthropogenic layer (unit 7) embedded between two almost sterile layers (units 6 and 8). Close to the lower boundary of unit 6 and the upper boundary of unit 8, some bone fragments and lithic implements were recovered and attributed to unit 7 (Jéquier et al., 2015). Unit 8 lays on the carbonate sandstone bedrock. Further ongoing

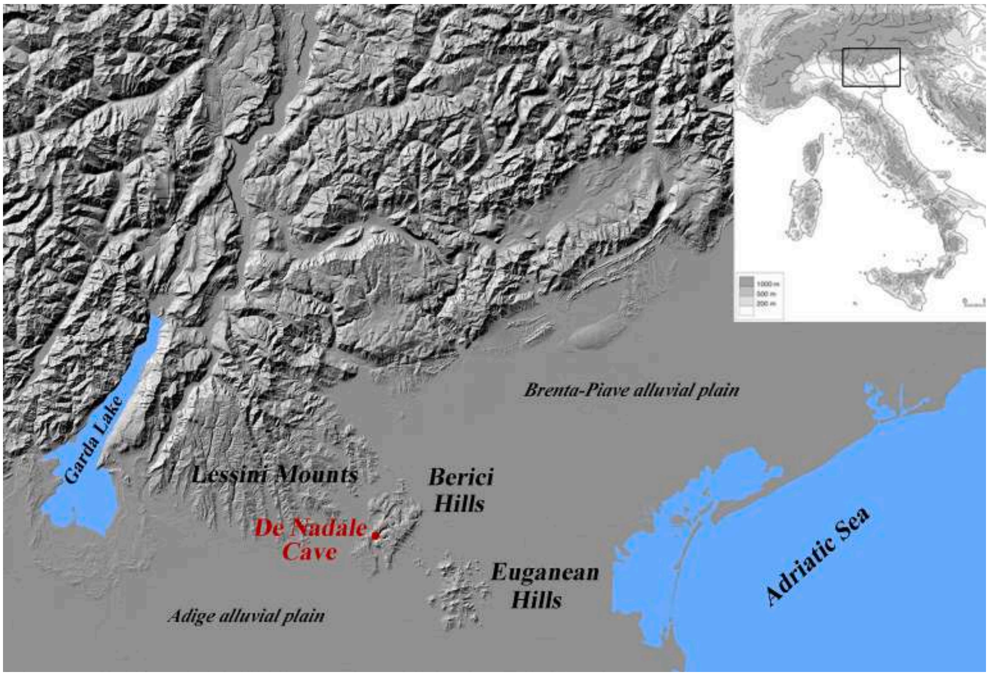


Fig. 1. Localization of De Nadale Cave in the North-east of Italy.

excavations will soon survey the complete planimetry of the site and the depth of the cavity. Unit 7 is disturbed by some badger's dens (defined as units 12, 13, 14, 15, 16), along the cave walls and back of the cave, partially emptied during the excavations. The resulting sediment provided a substantial amount of bone and lithic fragments, mixed with recent bones and organic matter. Besides these disturbances, unit 7 is well preserved and extended within the cavity, and it yielded thousands of osteological materials and lithic implements, some small charcoal fragments, and a deciduous tooth of a Neanderthal (Arnaud et al., 2017).

A molar of a large-sized ungulate was U/Th dated to 70.2 ± 1/0.9 ka BP as minimum age (Jéquier et al., 2015). These results are consistent with the paleoclimatic and paleoenvironmental reconstruction based on the small mammal association, where the prominence of *Microtus arvalis* identifies a cold climatic phase and correlates to a landscape dominated by open woodlands and meadows. Together, these results provide hints for placing the human occupation at De Nadale Cave to an initial phase of MIS 4 (López-García et al., 2018).

The lithic industry from of De Nadale differentiates technologically and typologically from the Mousterian elsewhere in the region, especially with regard to the core reduction methods and the types of flakes and retouched tools (Jéquier et al., 2015). The reduction sequences include polyhedral and multi-faceted cores with secant surfaces, alternated cores (Bourguignon *sensu*) and the minor presence of centripetal schemes such as recurrent centripetal Levallois. Moreover, the predominance in the assemblage of retouched implements or retouch by-products is evident, proven by more than 300 among tools and retouch flakes. The retouched assemblage includes several scrapers with stepped-scaled invasive retouches, and it is therefore comparable to Quina assemblages in Italy and in south-western France (Bourguignon, 1997; Palma di Cesnola, 2001).

2.2. Faunal assemblage

The zooarchaeological assemblage found in units 7 and correlates (6base, 8tetto, interfaces, hereafter unit 7) is largely of an anthropogenic nature (Livraghi et al., 2019) (Table 1). At De Nadale cave, Neanderthals hunted and exploited predominately three taxa: the red deer (*Cervus elaphus*), the giant deer (*Megaloceros giganteus*) and bovids (*Bison priscus* and *Bos primigenius*) (Terlato et al., 2019). In smaller quantities, other ungulates such as the roe deer (*Capreolus capreolus*), the chamois (*Rupicapra rupicapra*), and the wild boar (*Sus scrofa*) have also been identified. Carnivores are rare: bear (*Ursus spelaeus* and *Ursus* sp.), wolf (*Canis lupus*), fox (*Vulpes vulpes*), and badger (*Meles meles*) have been identified, though none show human modification. The majority of identifiable remains belong to adult individuals. In regard to the skeletal elemental representation, limb and cranial bones are more abundant than the elements from the axial skeleton. A large amount of anthropogenic traces is observed, largely attributed to different stages of the butchery process and to the fragmentation of the bones for marrow extraction. Finally, a large amount of bone fragments carries traces of fire exposure, assuming a colour gradient from brown, to black, to white. This evidence coincides with the presence of two charcoal accumulations named structures 7SI and 7SII found in the north-eastern area of the cave interpreted as dumping areas or residual fire-places.

Table 1
NISP and %NISP values calculated among the whole faunal assemblage at De Nadale Cave. The calculations have been made through all the stratigraphic units (7 and correlates).

Taxa	NISP	% NISP
Lepus europaeus	2	0.2
Lepus sp.	8	0.7
TOTAL Lagomorpha	**10**	**0.9**
Canis lupus	5	0.4
Vulpes vulpes	15	1.3
Ursus spelaeus	35	3.1
Ursus sp.	38	3.4
Meles meles	6	0.5
Mustelidae	1	0.1
Martes sp.	2	0.2
Felis sp.	2	0.2
Carnivora ND	35	3.1
TOTAL Carnivora	**139**	**12.3**
Sus scrofa	5	0.4
Alces alces	8	0.7
Megaloceros giganteus	292	25.9
Cervus elaphus	269	23.8
Capreolus capreolus	50	4.4
Cervidae	118	10.5
Bison priscus	26	2.3
Bos cf. *primigenius*	1	0.1
Bos/Bison	188	16.7
Capra ibex	2	0.2
Rupicapra rupicapra	9	0.8
Caprinae	12	1.1
Ungulata ND	2755	
TOTAL Ungulata	3735	
TOTAL NISP	**1129**	**100.0**

2.3. Retouchers

The retouchers analysed in this study were collected among all the stratigraphic units, including the reworked sediments and the infills of the badger dens. These specimens have been included in the present research considering that their conservation is comparable with the osseous remains of the Unit 7, and because this unit is the only anthropic layer identified in the site. By including bone fragments collected in other units besides Unit 7, the number of analysable retouchers increases considerably, and despite their stratigraphic unreliability, their attribution to a Mousterian assemblage is undeniable. The sample is temporarily stored at the Department of Humanities at the University of Ferrara. In this study, 335 retouchers from units 1Rim, 3, 5, 6, 6tana, 7, 8, 13, 14 were taken into consideration. Among them, 48 yielded stigmata in more than one portion of their surface, for a total of 385 use areas.

All retouchers were identified and registered during the excavation which was carried out with trowels and small wooden digging sticks, or after scrutinization of sediments wet sieved for recovering smaller fragments. Surfaces have been examined with naked eyes and by the aid of a stereomicroscope Leica S6D (magnification 6.3x-40x), when necessary; pictures of the use areas have been taken with camera Leica EC3 (scale in millimetres).

Every bone blank was anatomically and taxonomically determined using the complete Alpine fauna reference collection of the Section of Prehistory and Anthropological Sciences at Department of Humanities, the University of Ferrara. When the taxonomical identification was not possible, the cortical bone fragments were categorised based on the thickness: I - small (i.e. *Lepus* sp. and other lagomorphs, *Mustelidae, Vulpes vulpes*); II - small-medium (i.e. *Capreolus capreolus*, *Rupicapra rupicapra*, *Canis lupus*); III - medium (i.e. *Capra ibex, Sus scrofa*); IV-medium-large (i.e. *Cervus elaphus, Megaloceros giganteus*, *Ursidae*); V-large (i.e. *Bovinae*).

The degree of preservation of the bone and the bone surfaces is excellent (Livraghi, 2015; Livraghi et al., 2019), making it possible to define the surface alterations and to discern human traces from animal ones (pits, punctures, scores, furrowing, scooping-out, etc.), trampling abrasion, and mechanical modifications due to excavation tools. Reference was made to taphonomic literature for the purpose of identifying and distinguish those post-depositional modifications from anthropogenic ones (see Livraghi et al., 2019 for references). Butchering and percussion marks for dietary purposes have been recognized and distinguished from retouch-induced stigmata by observing their morphology, position and orientation. Cutmarks include incisions and scraping marks.

Anthropogenic traces linked to bone breakage for marrow extraction, such as cortical percussion notches, impact flakes, peeling, percussion pits, adhering flakes and micro-notches, were also taken into account following the well-established literature (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; White, 1992; Blasco et al., 2013; Vettese et al., 2017). Among them, only two traces were present in the De Nadale faunal record: cortical percussion notches and impact flakes. Percussion marks are described as notches, semi-circular in their morphology, observed in proximity to the fracture edges, and associated to negative flake scars. Impact flakes correspond to positive flakes of the notches resulting from the percussion action due to the breakage of diaphyses. The analysis of the morphology fragmented bone shafts revealed an intentional action of breaking the diaphyses to access marrow (Villa and Mahieu, 1991; Blumenschine, 1995; Fisher, 1995; Outram, 2001; Grunwald, 2016; Coil et al., 2017). Marks ascribable to natural post-depositional degradation and animal chewing, therefore not related to anthropic actions, were identified only on taxonomically determined remains, and on fragments longer than 5 cm.

The maximum length and the maximum width (mm) were registered for every bone fragment. The cortical bone thickness (mm) in the point where the use area is located, was also registered in order to determine if it could be correlated with the selection of anatomical portions and/or species. Finally, the weight (g) was registered only for the sake of completeness. The post-depositional processes lead to the loss of weight of the bones, and therefore the current weight does not correspond to the original weight of the tool.

The analysis of the technological stigmata on the surface of the retouchers was carried out following Mallye et al. (2012) and Mozota Holgueras (2012), although more nomenclatures are present in literature (e.g., Daujeard et al., 2014, 2018). The location of the use areas, the retouch intensity (i.e. the concentration of impact marks), and the number of the areas were recorded; the values of maximum length and width (mm) were registered only of the complete use areas. Regarding the orientation of retouchers and the positioning of the areas, the anatomical identification of the bone fragments was not considered. Each tool was oriented based on the long axis, defined at its largest length, and the use areas are generally located on the surface of one or both the extremities of the retoucher. Retouchers showing more than one use area are reoriented, and the areas are analysed individually.

The stigmata were counted and grouped in four morphological categories:

- pits: triangular or ovoidal depressions of the osseous surface, due to the impact of the bone surface with the dihedral morphologies corresponding to the irregularities of the lithic edge;
- linear impressions: long, narrow and deep depressions, with asymmetrical V-shaped section; they show a generally linear course, sometimes also sinuous, concave or convex; their inner surface could be smooth or rough, and they could be associated to the impact between the retoucher and a sharp lithic edge;
- retouch-induced striae: short, shallow striations, with a linear or slightly curved profile, parallel and close to each other; these could be produced when bone and lithic edge impact with an oblique direction; in this case, the blow is arrested less brutally and the lithic edge almost scratches on the bone surface;
- notches: massive, deeper and wider depressions these could be described as an erosion of the bone surface, caused by a continuous percussion; their morphology depends on their extension and the most common category of stigmata identifiable in the use area.

These categories of stigmata often occur together in the same use area. Moreover, four categories of retouch intensity were distinguished, according to Mallye et al. (2012) (Fig. 1c, p. 1133): (1) isolated, (2) dispersed, (3) concentrated and (4) concentrated and superimposed (hereafter, superimposed).

Retouchers defined as complete were isolated. Such identification was carried out on the basis of the observation of the fresh bone fractures (Villa and Mahieu, 1991; Grunwald, 2016; Coil et al., 2017) and therefore observing the angle of the fracture, its general morphology, and the texture of the edge (smooth or rough). We are aware that the application of these parameters might lead to an underestimation of the sample of the complete retouchers, since it takes into consideration only tools obtained by bones fractured in a fresh state and excludes other ways of support procurement. We think that more focused studies on the microscopic features of fractures based on different states of freshness of the bone could be useful for a better definition of such a parameter. However, in this context it was needed to distinguish the complete retouchers in order to carry out a preliminary morphometric analysis, in which we observed the relationship among the length, width and thickness values of the tools looking for any morphometric pattern.

3. Results

3.1. Raw materials

A total of 335 retouchers from De Nadale Cave were analysed. Of these, 35 retouchers were considered complete on the basis of the observation of the fresh bone fractures (Table 2).

Of the taxonomically species-level determinable specimens, the most represented are *Megaloceros giganteus* (NR = 52, 15.5% of the total analysed retouchers), *Cervus elaphus* (NR = 39, 11.6%), and large bovids (*Bos/bison*, NR = 36, 10.7%, and *Bison priscus*, NR = 4, 1.2%), in line with the general faunal spectrum recognised at the site (Livraghi et al., 2019; Table 1). A significant proportion (50.3%) of bone fragments could only be identified as ungulates, but it was possible to group them into the large-sized animal category. (Fig. 2, Table 3).

49% of the analysed retouchers was identifiable at a skeletal element-level (Table 3; SM1). Long bones are the most selected element (91.5%; 13.3% of the total NISP), in particular tibiae (32.3%; 4.7% of the total NISP), followed by radii, femurs, metacarpals and metatarsals. Diaphyses were mainly selected (97% of the total analysed bone retouchers) (Fig. 3). Only one epiphysis is recognised, belonging to a radius of *Bos/Bison*. That is the only epiphysis identified in the entire faunal assemblage. Peculiar anatomical portions used as retouchers are ribs (7) (Fig. 4a), mandibles (3, among which one bears two teeth), scapulae (2) and one horn core of *Capra ibex* (Fig. 4b).

With regard to the taphonomy, manganese stains represent the most common alteration of the surface (66.4%). Degradation due to root-etching is observed to a lesser but still relevant extent (44.6%). A significant proportion of the analysed retouchers is affected by the presence of carbonate concretions (34.2%), which in some cases (10%) cover part of the use area, making the identification of stigmata difficult. Trampling traces are common (36%), attributable to the elevated content in stones of the deposit. Several shafts bear slight weathering traces (36.6%), mostly referable to the Behrensmeyer stages 1 or 2, while exfoliation (3.6%) and corrosion (3.3%) marks are observed on a smaller scale. Traces due to the action of animals are very few: 9.8% are carnivores' tooth-marks and only 0.6% rodents'.

Anthropic traces due to butchering activities are observed on 82% of retouchers (NR = 274). Among them, cut-marks are the mostly frequent registered (67.5%). Some shafts present impact notches (30.7%) and few of them have been recognized as impact flakes (1.1%). Finally, scraping marks are present on the 21.5%. These traces always locate underneath the retouch stigmata; they are oriented parallel to the long axis of the shaft, covering an area larger than the use area but never the entire shaft fragment.

3.2. Metric data

The average sizes of the complete retouchers are reported in Table 4 and more detailed information can be found in Supplementary Materials (SM1). The maximum lengths range from 54 to 150 mm, and the maximum widths range from 20 to 46 mm. The thickness of the cortical bone ranges from 5 to 19 mm. The average weight of these specimens is

Table 2
Inventory of complete and fragmented bone retouchers at De Nadale Cave.

	Units																		Tot
	1Rim		3		5		6		6tana		7		8		13		14		
	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	
Complete	9	11	1	33	1	17	3	31	–	–	13	12	1	20	3	8	4	15	35
Fragment	79	89	2	67	5	83	9	69	15	100	115	88	4	80	48	92	23	85	300
Total	88		3		6		12		15		128		5		51		27		335

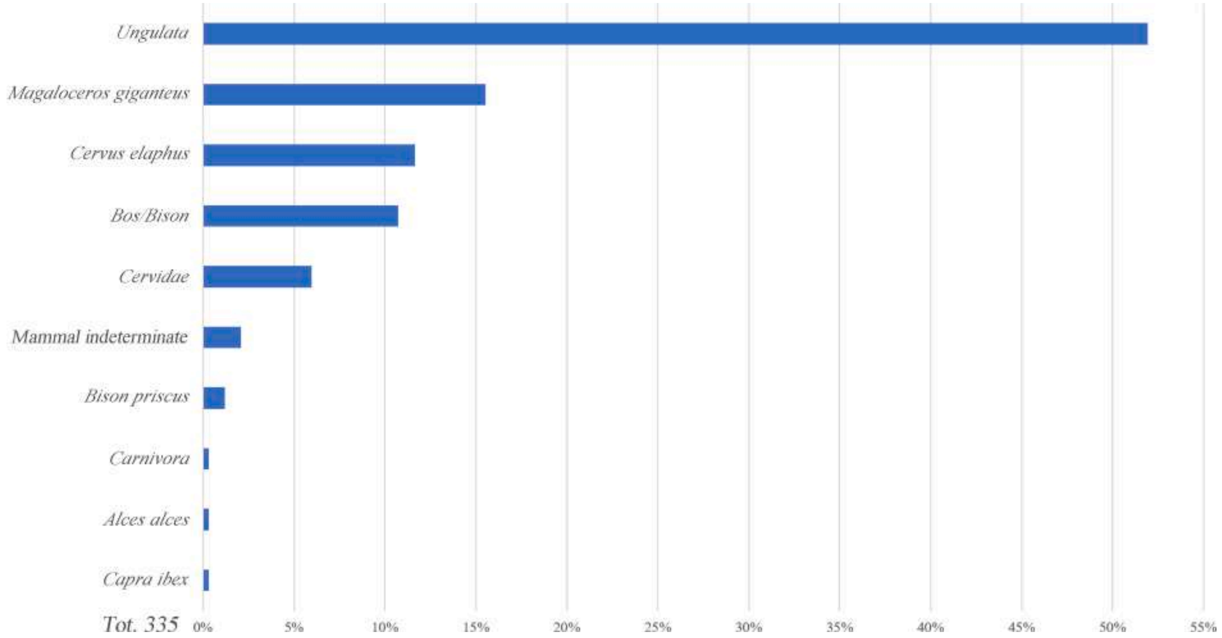


Fig. 2. Faunal spectrum of bone retouchers at De Nadale Cave. The calculations have been made taking into consideration the entire sample (NR = 335).

22.1 g. Retouchers are usually elongated, rectangular, and commonly flat. Although some shafts show accentuated convex surfaces in relation to the anatomical element, it seems that the flattest portion of the surface was preferred for use.

3.3. *Use areas and stigmata*

Of the 335 analysed tools, 46 (14%) were used as double retouchers, and two as triple retouchers. About 62% of the areas are complete, while the others are cut by fractures either from use or post-depositional processes (Fig. 5). It is worth noting that on double retouchers one area always looks more intensively used than the other, suggesting primary and secondary phases. The maximum length of the use areas goes from 3 to 37 mm, while the maximum width ranges from 3 to 25 mm (more detailed information could be found in Supplementary Material – SM1). On single retouchers, use areas are always located on the apical portion of the tool face. The presence of three use areas is registered on two retouchers: a tibia of *Cervus/Megaloceros* (Fig. 6a) and a femur of *Cervus elaphus* (Fig. 6b). In these cases, two areas are adjacent to each other - they are distinguishable due to the different orientation of the stigmata (Fig. 6.1 and 5.3) – while the third area is located either in an adjacent (Fig. 6.2) or opposite (Fig. 6.4) position on the diaphysis in relation to the others. On retouchers with two areas, each area is generally located on the two extremities of the same shaft, although in some cases the two areas could be adjacent (Fig. 7).

All four stigmata categories have been observed (Fig. 8). Linear impressions prevail (58.7%), followed by punctiform impressions (28.7%), retouch-induced striae (7.1%) and notches (5.4%). Linear (Fig. 9.1) and punctiform (Fig. 9.2) impressions are often deep and marked; the striations, when present, are superficial and parallel to each other. Notches are extensive and deep (Fig. 9.3), indicating an intense retouch activity. In terms of distribution (Fig. 10), most of the stigmata are concentrated (48.2%), then dispersed (27.3%), superimposed (13.3%) and isolated (9.6%) stigmata follow. In 2% of the sample it was not possible to evaluate the density of the stigmata because of the small size of the fragment and/or the alteration of the surface.

Although the most used elements are tibias (NR = 54; Fig. 3g-h), there are very few double (3.7%) or triple (1.8%) retouchers among them, made from bones of *Megaloceros giganteus* and *Cervus elaphus*. Radii/ulnas instead, despite being less represented (NR = 21 on diaphysis; Fig. 3c-d) record a very high number of double retouchers (42.8%). Among them, three are made from bones of *Megaloceros giganteus* and four from bones of *Bos/Bison*, while one is made from a bone of *Cervus elaphus* and another one has been only identified as *Cervidae*. A similar situation is recognisable among the metapodials, where three out of five retouchers are double: two of them have been identified as bones of *Bos/Bison*, while the other was not identifiable at a species-level, instead only being identified as large-size *Ungulata* (Fig. 11; see also SM1 for more details on double and triple retouchers).

4. Discussion

4.1. *Raw material*

4.1.1. *Faunal spectrum*

The analysis of the species selected to obtain blanks for retouchers is a very significant issue given the use of animal raw material is strictly related to the subsistence strategies and the mobility of Neanderthal

Table 3
Inventory of the analyzed bone retouchers, divided by species, size, skeletal element and bone portion. “NR” = “number of remains”. The percentages are calculated in relation to the total NISP (1129) contained in Table 1.

SPECIES	SIZE	SKELETAL ELEMENT	BONE PORTION	NR	% NR / NISP
Ungulata	large	indeterminate	diaphysis	142	12.6
Ungulata	large	rib	diaphysis	3	0.3
Ungulata	large	mandible	indeterminate	1	0.1
Ungulata	large	metapodial	diaphysis	1	0.1
Ungulata	large	humerus	diaphysis	1	0.1
Ungulata	large	tibia	diaphysis	4	0.4
Ungulata	large	femur	diaphysis	1	0.1
Ungulata	medium/large	indeterminate	diaphysis	9	0.8
Ungulata	medium	tibia	diaphysis	2	0.2
Ungulata	medium	rib	diaphysis	1	0.1
Ungulata	medium	indeterminate	diaphysis	1	0.1
Ungulata	indeterminate	indeterminate	diaphysis	8	0.7
Megaloceros giganteus	medium/large	mandible	body + M3	1	0.1
Megaloceros gignteus	medium/large	femur	diaphysis	7	0.6
Megaloceros gignteus	medium/large	metacarpal	diaphysis	10	0.9
Megaloceros gignteus	medium/large	metapodial	diaphysis	1	0.1
Megaloceros gignteus	medium/large	metatarsal	diaphysis	10	0.9
Megaloceros gignteus	medium/large	humeus	diaphysis	3	0.3
Megaloceros gignteus	medium/large	radius	diaphysis	6	0.5
Megaloceros gignteus	medium/large	radius/ulna	diaphysis	1	0.1
Megaloceros gignteus	medium/large	tibia	diaphysis	13	1.2
Cervus elaphus	medium/large	rib	diaphysis	2	0.2
Cervus elaphus	medium/large	femur	diaphysis	7	0.6
Cervus elaphus	medium/large	metacarpal	diaphysis	6	0.5
Cervus elaphus	medium/large	metapodial	diaphysis	1	0.1
Cervus elaphus	medium/large	metatarsal	diaphysis	3	0.3
Cervus elaphus	medium/large	humerus	diaphysis	4	0.4
Cervus elaphus	medium/large	radius	diaphysis	2	0.2
Cervus elaphus	medium/large	scapula	caudal	1	0.1
Cervus elaphus	medium/large	tibia	diaphysis	13	1.2
Bos/Bison	large	rib	diaphysis	1	0.1
Bos/Bison	large	mandible	body	1	0.1
Bos/Bison	large	femur	diaphysis	1	0.1
Bos/Bison	large	indeterminate	diaphysis	1	0.1
Bos/Bison	large	metacarpal	diaphysis	2	0.2
Bos/Bison	large	metapodial	diaphysis	4	0.4
Bos/Bison	large	metatarsal	diaphysis	4	0.4
Bos/Bison	large	humerus	diaphysis	2	0.2
Bos/Bison	large	radius	diaphysis	6	0.5
Bos/Bison	large	radius	epiphysis	1	0.1
Bos/Bison	large	radius/ulna	diaphysis	2	0.2
Bos/Bison	large	scapula	caudal	1	0.1
Bos/Bison	large	tibia	diaphysis	10	0.9
Cervidae	medium/large	pelvis	ileum	1	0.1
Cervidae	medium/large	femur	diaphysis	3	0.3
Cervidae	medium/large	indeterminate	diaphysis	2	0.2
Cervidae	medium/large	metapodial	diaphysis	1	0.1
Cervidae	medium/large	metatarsal	diaphysis	1	0.1
Cervidae	medium/large	humerus	diaphysis	1	0.1
Cervidae	medium/large	radius	diaphysis	4	0.4
Cervidae	medium/large	tibia	diaphysis	7	0.6
Mammal indeterminate	indeterminate	indeterminate	diaphysis	4	–
Mammal indeterminate	medium	indeterminate	diaphysis	1	–
Mammal indeterminate	medium/large	indeterminate	diaphysis	2	–
Bison priscus	large	humerus	diaphysis	1	0.1
Bison priscus	large	tibia	diaphysis	3	0.3
Carnivora	large	indeterminate	diaphysis	1	0.1
Alces alces	large	tibia	diaphysis	1	0.1
Capra ibex	medium	horn	indeterminate	1	0.1

groups.

The over 300 retouchers from De Nadale show a predominance of cervids (*Megaloceros giganteus* and *Cervus elaphus*) and large bovids (*Bos/Bison*, *Bison priscus*) bones.

A specific selection of species for making retouchers could be linked to the availability of resources or if it could be based on precise technological criteria. This issue seems to vary from site to site. In some cases, retouchers are obtained from bones belonging to dominant species in the faunal spectrum, suggesting that their manufacture is not subjected to a technological choice of the anatomical element, but rather to the availability of faunal elements produced from the butchering process (Armand and Delagnes, 1998; Auguste, 2002; Daujeard et al., 2014). In other cases, retouchers are not obtained from the dominant species of the faunal assemblage, meaning that Neanderthals did not use indistincriminantly all the bones produced from butchery, but that they carefully selected some fragments following criteria grounded on morphological, metrical, and technological features (Mallye et al., 2012; Daujeard et al., 2014; Costamagno et al., 2018; Alonso-García et al., 2020; Martellotta et al., 2020).

At De Nadale Cave, the predominant species selected for manufacturing retouchers are consistent with the composition of the faunal assemblage (Livraghi et al., 2019, Table 1) (Table 3; Fig. 12),

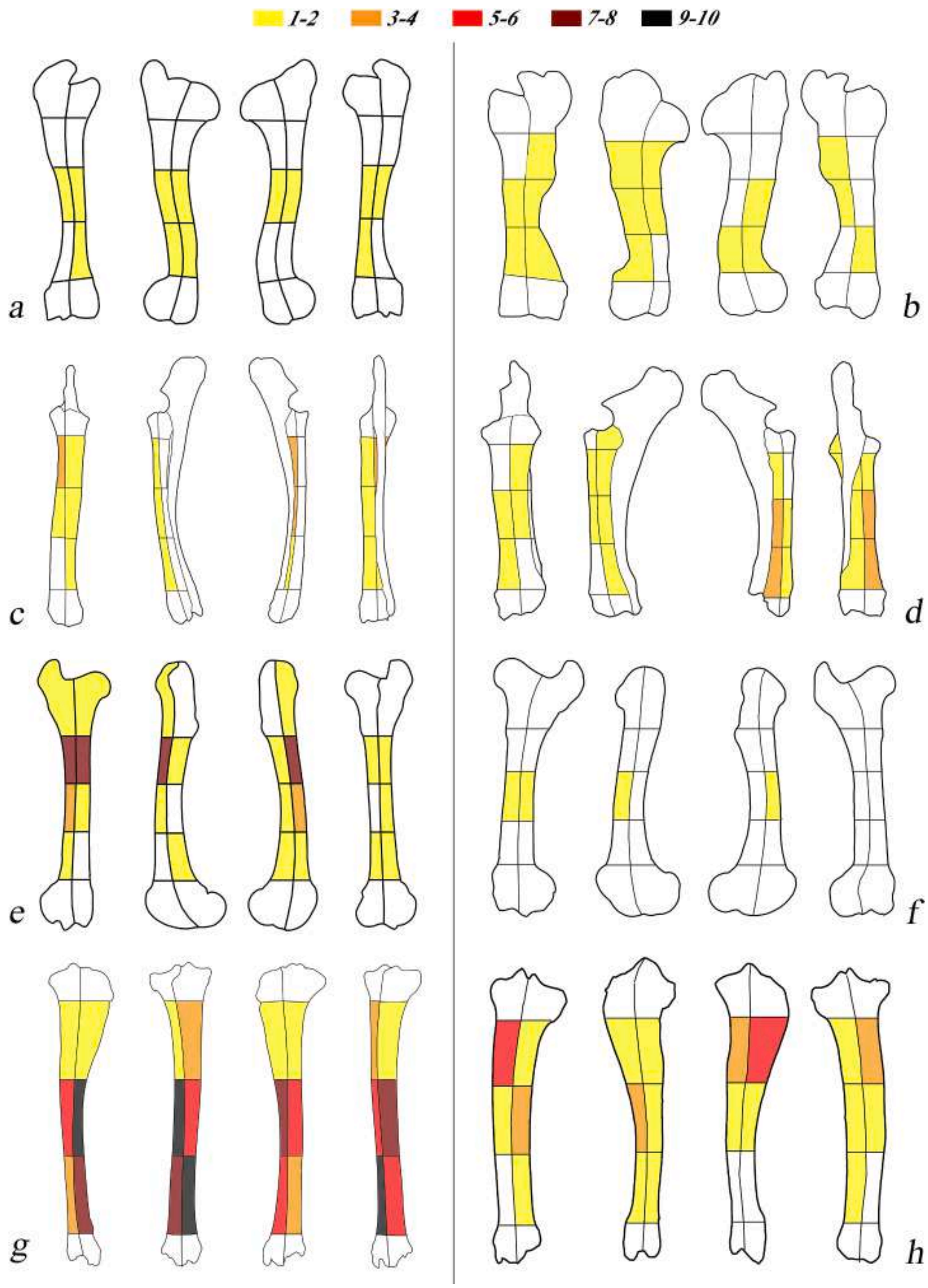


Fig. 3. Distribution of retouchers shaft portions: a) humerus of *Cervidae*, b) humerus of *Bos/Bison*, c) radius/ulna of *Cervidae*, d) radius/ulna of *Bos/Bison*, e) femur of *Cervidae*, f) femur of *Bos/Bison*, g) tibia of *Cervidae*, h) tibia of *Bos/Bison*. The illustration takes into consideration only the identifiable species and shaft portions (NR = 93).

where cervids (*Megaloceros giganteus*, NISP = 25.9%, and *Cervus elaphus*, NISP = 23.8%) and *Bos/Bison* (NISP = 16.7%) are the most represented species. Among the taxonomically species-level determinable retouchers (NR = 134), we can observe a similar predominance: the sample is dominated by *Megaloceros giganteus* (NR = 33.8%), followed by *Cervus elaphus* (NR = 25.3%) and *Bos/Bison* (NR = 23.4%) (Fig. 12a). Comparing these three species in relation to the NISP (NR retouchers/ NISP for each species) we can see that they are generally equally distributed within the faunal spectrum (*Megaloceros giganteus* = 40.9%, *Cervus elaphus* = 30.7%, *Bos/Bison* = 28.3%) (Fig. 12b). The selection of a particular species has often been associated to the thickness of the compact bone (Daujeard et al., 2014; Costamagno et al., 2018). Therefore, based on the consistency between the species used for making retouchers and the whole faunal assemblage, we could argue that at De Nadale Cave species were selected for making retouchers according to the availability of environmental resources, and that this selection seems to overlook the thickness parameter. This result integrates the framework of the exploitation strategies of animal raw materials during the Quina techno-complex. Such a predominance in cervids and large bovids as sources for retouchers is also observed in other Mousterian sites in Europe: in Spain, at Axlor Cave (Mozota Holgueras, 2012), and in the Swabian Jura (Toniato et al., 2018). On the other hand, in other regions - especially southwestern France – reindeer was the main source for these bone tools (Castel et al., 1998; Costamagno et al., 2018).

4.1.2. Anatomical elements

The selection of limb bones for manufacturing retouchers is an extremely widespread pattern. De Nadale Cave fits in this model in that almost all retouchers are obtained from long bones; among the most selected elements, tibias are the most represented, followed by radii,

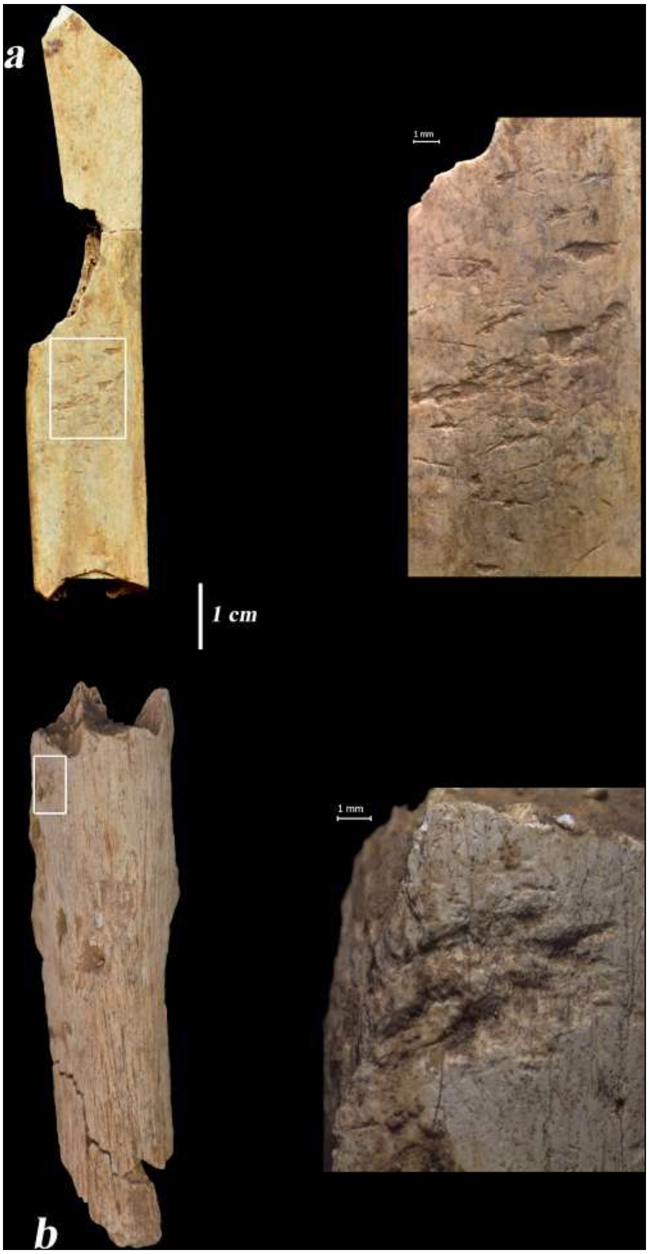


Fig. 4. (a) Retoucher. n. CN2494: *Cervus elaphus*, rib (fragment) : an extended use area is observed on the mesial portion, mostly composed of linear and punctiform impressions; in the central portion of the use area, the intensity of retouch resulted in some notches, created by the superimposition of several linear stigmata; (b) Retoucher n. 198: *Capra ibex*, horn core (fragment): a small use area is present on the proximal portion; the area is interrupted by the fracture, and it is mostly composed of notches created by the superimposition of linear and punctiform stigmata.

Table 4
Metric data (in mm) of the bone retouchers identified at De Nadale Cave. Only the complete retouchers were taken into account (NR = 35).

	Length	Width	Thickness cortical bone
Minimum	54	20	5
Maximum	150	46	19
Average	88.7	30.4	8.9
Standard deviation	20.3	6.5	2.9

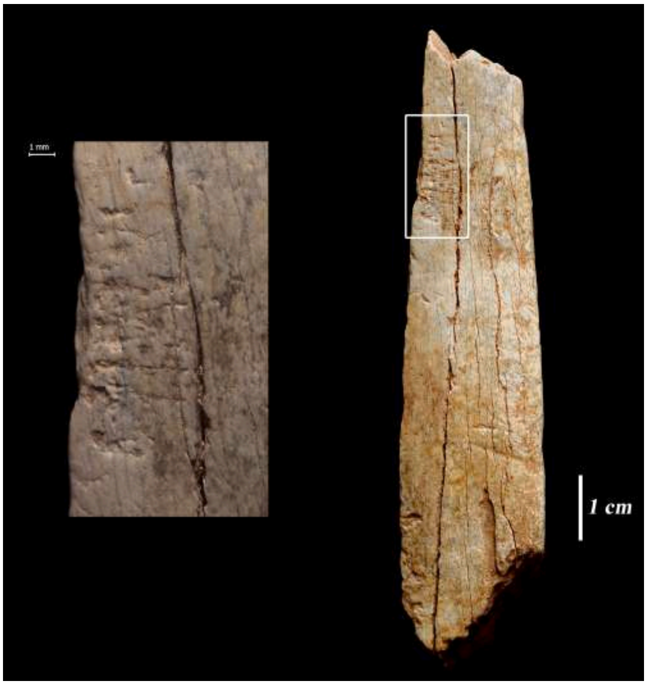


Fig. 5. Example of a use area interrupted by post-depositional fragmentation (retoucher n. 3312): the line of fracture superimposes to the stigmata, and it removes part of the use area; the fracture is defined as post-depositional based on the observation of its edges.

femurs, metacarpals and metatarsals. Humeri, on the contrary, are extremely rare (Table 3; Fig. 3; Fig. 11). These data are consistent with others in Quina sites in Europe, like Les Pradelles (Costamagno et al., 2018). Diaphyses are almost the only bone portions used as retouchers, a fact that is consistent with several Quina contexts; although in some sites (Auguste, 2002; Valensi, 2002) epiphyses also appear to be used. At De Nadale, only one retoucher made from an epiphysis was found, and it represented the only epiphysis in the entire assemblage (Table 3). The lack of this skeletal element could be ascribed to several factors: the high fragmentation rate in the deposit (Livraghi et al., 2019), the use of epiphyses as fuel (Costamagno et al., 2005) – since this assemblage contains a high number of burned and calcinated bones – or the fact that epiphyses may possess less of the technological features suitable for retouching as diaphysis do.

Focusing on the skeletal elements selected for retouching is important for several reasons. On one hand, it helps to understand the carcass exploitation strategies adopted by Neanderthals given retouchers normally result from the breakage of bones for subsistence purposes. On the other hand, since precise anatomical elements respond to morphological criteria – mandatory for such retouch activity - it is possible to infer that their selection was driven by a technological purpose (Alonso-García et al., 2020; Martellotta et al., 2020). Most of the analysed bone retouchers bear cut-marks and percussion marks on their surface, meaning that the selected blanks result from butchery. The number of expected elements (NEE) at De Nadale Cave suggests that the treatment of the carcasses was partitioned, with a first phase carried out at the killing site instead (Livraghi et al., 2019). Indeed, the bias between the frequency of appendicular and the axial elements is not due to post-depositional events, rather than to selection carried out by the human groups, who preferably introduced into the site the leg quarters.

The morphology of the anatomical elements seems to acquire greater importance in relation to double retouchers. If the use of more than one portion of the surface of the same retoucher occurred randomly, or was driven by non-technological factors, we would expect that most of the double retouchers were obtained from the most represented anatomical element – in De Nadale case, tibias. The study of the use areas, instead,

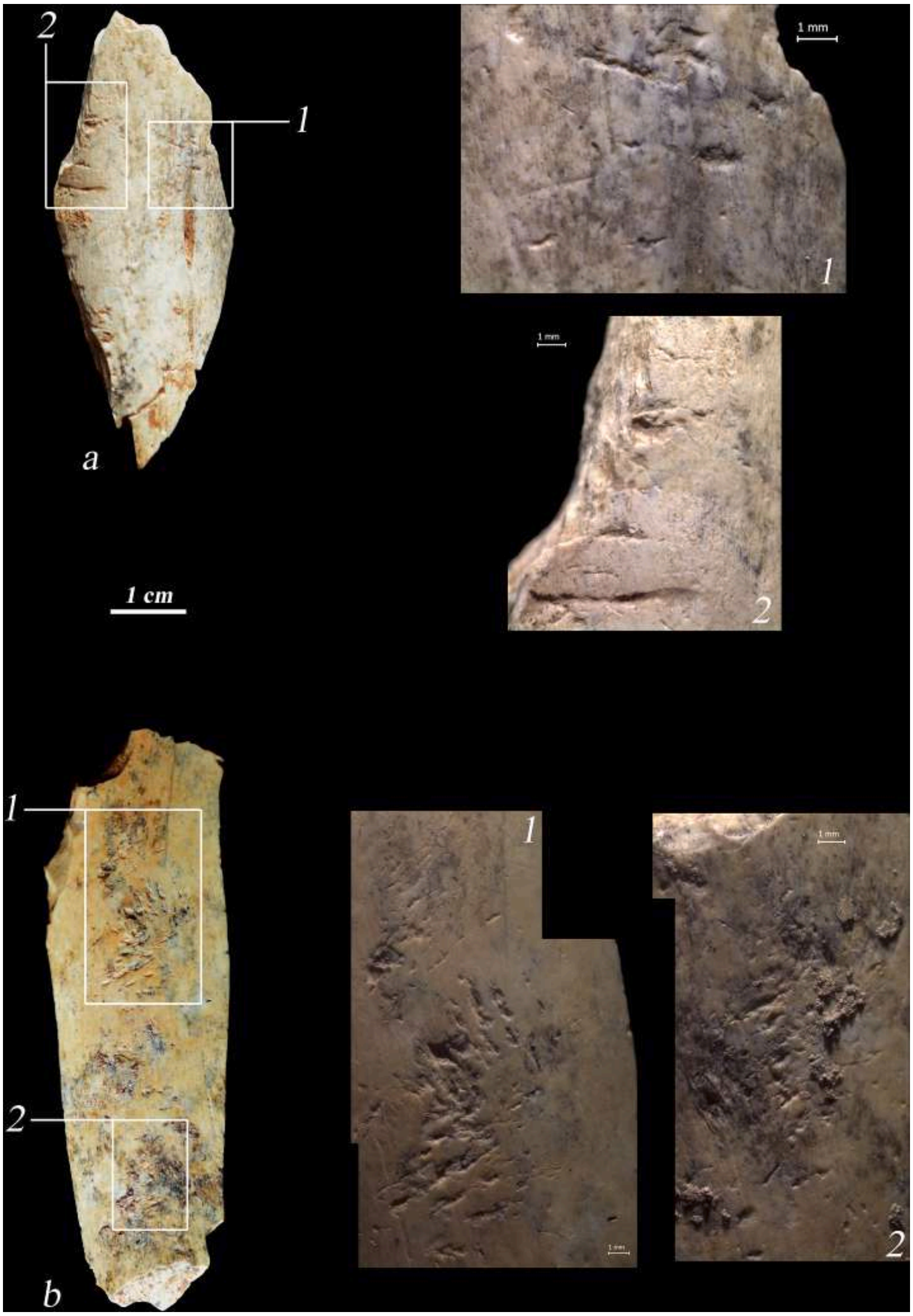


Fig. 6. (a) Retoucher n. 792: tibia of *Cervus/Megaloceros* bearing three distinct use areas: 1) two of them are adjacent and, even if there are few stigmata, we can observe how they group in two distinct areas of the bone surface and that they are oriented differently in relation to the longitudinal axis of the retoucher; 2) the third area is located on the opposite edge of the retoucher: some linear impressions which have been interrupted by a post-depositional fracture can be observed. (b) Retoucher n. 251: femur of *Cervus elaphus* bearing three distinct use areas: 1) two of them are adjacent, they superimpose but they are distinguishable based on the different orientation of the linear impressions regarding to the longitudinal axis of the retoucher; 2) the third area is located on the opposite apical extremity, and it is composed of both linear and punctiform impressions.

shows that radius is the element in which double retouchers are observed most frequently, compared to the total amount of radius in the sample (Fig. 11). To a lesser extent, we could infer the same pattern among the metapodials: of a total of five metapodials computed in the assemblage, three were used as double retouchers. Therefore, we can suppose that the choice of using a retoucher in different parts of its surface suggests that only specific anatomical elements are suitable for being used as double retouchers. Moreover, although most of the blanks consist of limb bones, at De Nadale other anatomical elements – such as mandibles, ribs, scapulae, horns – have been used as retouchers. This further supports the fact that the blank was chosen depending on specific technological criteria, probably linked to the surface morphology and its grasping properties. The selection of particular anatomical elements besides long bones is not unusual in Quina sites: ribs at Les Pradelles (Costamagno et al., 2018); mandibles at La Quina (Verna and d'Errico, 2011) and Les Pradelles (Costamagno et al., 2018); phalanxes at La Quina (Valensi, 2002), Abri Lartet (Ready and Morin, 2019) and Les Pradelles (Costamagno et al., 2018); pelvises and scapulae at Les Pradelles (Costamagno et al., 2018). The selection of specific morphologies for making retouchers assumes importance when considering the relevance of the retouch activity from a techno-economic perspective in Quina contexts.

4.2. Metric data

Length and width measurements of complete retouchers from De Nadale are slightly larger than ones in other Quina sites. With regard to the length, De Nadale retouchers are comparable to those at La Quina (Verna and d'Errico, 2011) and Axlor (Mozota Holgueras, 2012), while – at Les Pradelles (Costamagno et al., 2018) – these tools show smaller length ranges (50–120 mm). The same situation is registered regarding the width of De Nadale Cave specimens: while there is similarity with

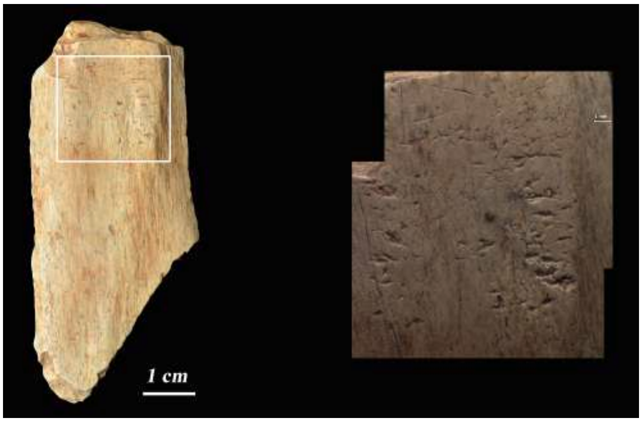


Fig. 7. Retoucher n. CN3125 : Stigmata of retouching group into two distinct areas of the bone surface due to the spatial distribution and their different orientation relative to the longitudinal axis of the retoucher.

the retouchers from La Quina (Verna and d'Errico, 2011) and Axlor (Mozota Holgueras, 2012), in Les Pradelles (Costamagno et al., 2018) the width ranges 10 to 40 mm. The thickness of the cortical bone could be one of the selection criteria linked to the carcass processing (Costamagno et al., 2018). At De Nadale, the thickness (Table 4; SM1) is similar to retouchers at Les Pradelles (Costamagno et al., 2018) and Axlor (Mozota Holgueras, 2012), but they are definitely thicker than those in La Quina (Verna and d'Errico, 2011), where they do not typically exceed 11 mm.

Regarding the specific sizes, the general morphology of De Nadale retouchers is elongated and flat. These morphological features could be associated to a better grasping of the tool (Bourguignon, 2001; Daujeard et al., 2014). That is consistent with Axlor (Mozota Holgueras, 2012). Among a wide selection of useful bone flakes, Neanderthals tended to choose the longest and thickest ones. Although the choice of the blanks has often been linked to the selection among the food wastes (Armand and Delagnes, 1998; Daujeard et al., 2014), some experimental studies suggest that bone breakage was driven to obtain fragments with specific and predetermined features suitable for retouching (Mozota Holgueras, 2012, 2013).

4.3. *Use areas*

The use areas identified and analysed on the retouchers from De Nadale fit with the ones observed in several Quina sites, and, in general, in Middle Palaeolithic sites. Most of the De Nadale tools have one area located in apical position. Although double retouchers are common in several assemblages, triple retouchers occur rarely, mostly because the findings are often fragmentary. When two areas are registered, they are both located in apical position, but on opposite sides. In triple retouchers, two areas are adjacent to each other, and are distinguishable due to the different orientation of the stigmata. Stigmata orientation is often taken into consideration during the analyses of the use area, and it could be ascribed to several factors: the bone morphology (Costamagno et al., 2018), the habitual body position of the knapper during the retouching activity (Vincent, 1993), the shape of the lithic edge, the orientation of the retoucher towards the lithic edge (Tartar, 2012), and the knapper's handedness.

The most frequently observed stigmata at De Nadale Cave are linear impressions, followed by punctiform marks. Both are often deep, and it is not unusual that an intense retouch activity leads to the detachment of entire bone portions (resulting in notches). Such a pattern is observed at Les Pradelles (Costamagno et al., 2018), La Quina (Valensi, 2002), and Axlor (Mozota Holgueras, 2012). The morphology of the stigmata varies in relation to the retouch intensity and the retouching angle, but experimental studies revealed an association between the physical properties of the lithic tool and the stigmata morphology (Mallye et al., 2012; Tartar, 2012).

With regard to the intensity of retouching activity at De Nadale, stigmata are mostly densely patterned. The intensity of stigmata impressed on the bone surface could depend on several factors. Since this parameter seems to not be dependent on the morphological features

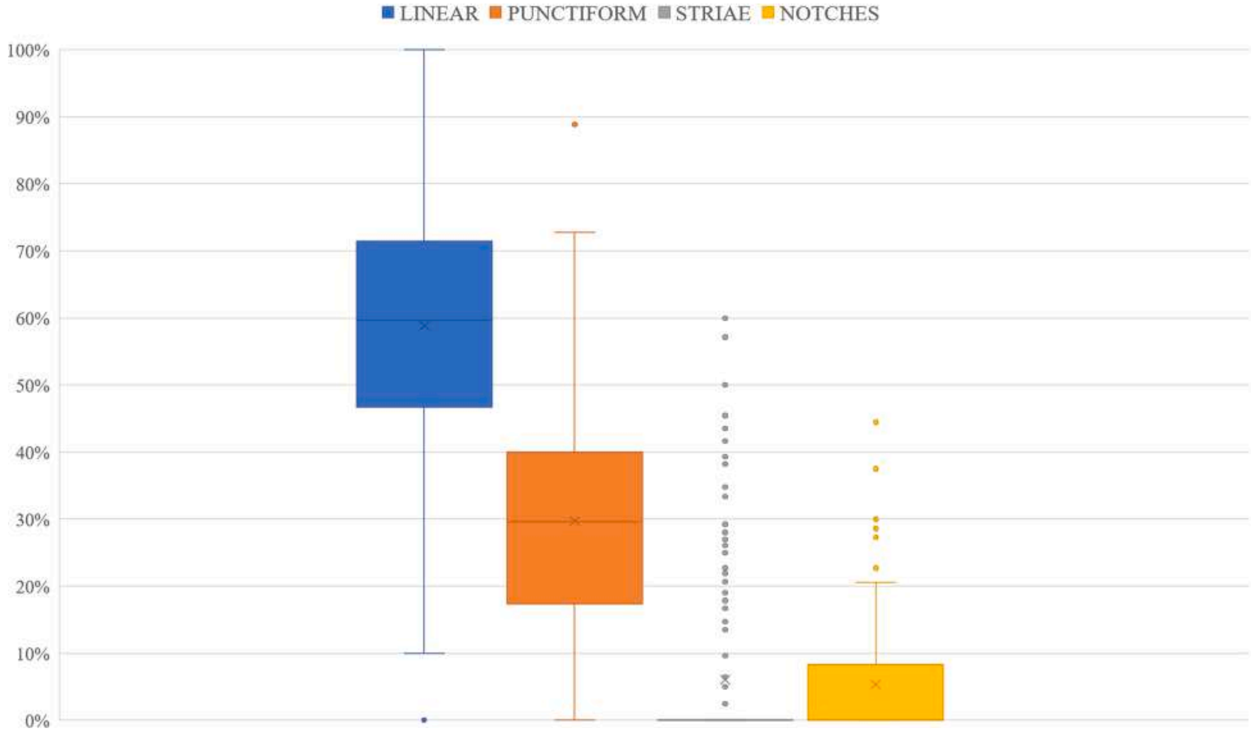


Fig. 8. Morphological categories of the observed retouch-induced stigmata. Only the complete use areas (211) were used for the calculations. N.B. Two or three complete use areas might be present on the same retoucher (NR = 179).

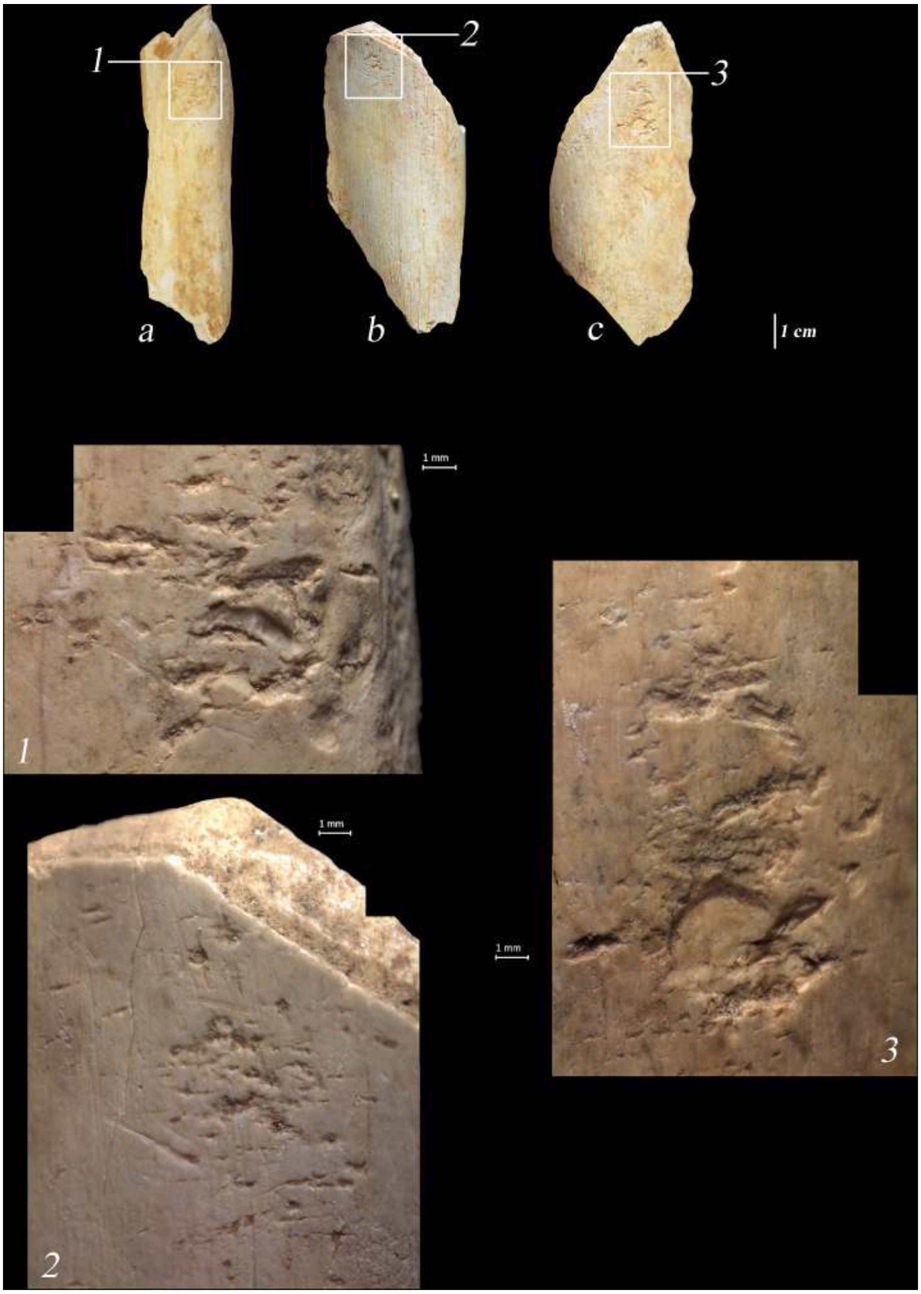


Fig. 9. Examples of stigmata: (a) Retoucher n. CN344: use area mostly composed of linear impressions; they are long and deep, with a convex or sinusoidal course, and they have similar orientation to each other in relation to the longitudinal axis of the retoucher; some punctiform impressions are also present (1); (b) Retoucher n. CN2051: use area mostly composed of punctiform impressions, both of triangular and ovoidal shape; in the center of the area the stigmata slightly superimpose; some linear impressions and few striations are also present (2); (c) Retoucher n. CN3304: use area mostly composed of notches; they are the results of the superimposition of linear impressions, though some triangular punctiform impressions are recognizable; few isolated linear and punctiform impressions are also present (3).

of the retoucher, we suppose that it was related to the type of retouch and the lithic raw material. This hypothesis has been proposed by different authors within experimental studies where concentrated and superimposed areas result from a greater number of retouch blows (Mallye et al., 2012; Mozota Holgueras, 2012). In De Nadale cave, more than 250 retouched tools (Fig. 13) have been recovered so far, equal to 21.6% of the whole lithic assemblage. Among these, more than half are represented by scrapers and limaces characterized by supra-elevated, scaled removals on one or several edges. If we suppose that one single retoucher was used every time a tool was manufactured or resharpened, the extremely high number of bone retouchers (and their use intensity) can be explained with the curation of such lithic tools, bearing several retouch phases. Moreover, we can assert that the human group that occupied De Nadale cave was characterized by high mobility strategies, confirmed by the use of exogenous raw materials and, again, by extremely reduced lithic blanks. More tools could have been produced, then exported and used in kill-butchering sites or other temporary campsites. Anyway, at De Nadale Cave variations of the intensity are only observed between areas located on the same blank (double retouchers); shifts from a primary, more intensively used area, and a secondary, less used area are observed systematically.

At De Nadale, scraping marks are frequently observed on the retouchers' surface, always covered by the retouch-induced stigmata. As 17% of retouchers bear scraping marks, similar proportions are observed in Les Pradelles (18%, Costamagno et al., 2018); in general, scraping marks are observed on the majority of retouchers. A scraping action is carried out either to prepare the bone surface by removing the periosteum (Armand and Delagnes, 1998; Auguste, 2002; Mallye et al., 2012; Daujeard et al., 2014) - even if it is not strictly necessary (Mozota Holgueras, 2012) - or to prepare the edges of the lithic blank (Jéquier, 2014; Costamagno et al., 2018). Therefore, we could argue that at De Nadale Cave scraping action was not carried out to remove the flesh or the periosteum from a specific anatomical element, but it could be linked to the preparation of the edge of the lithic tool. Regardless of the

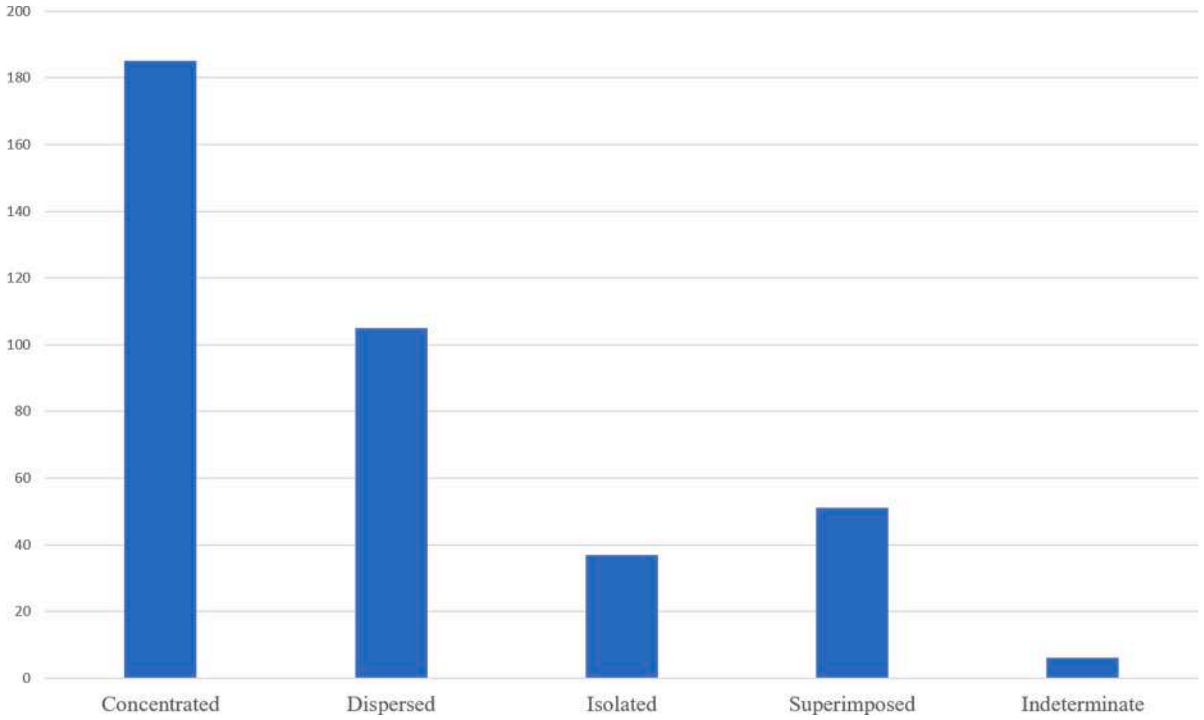


Fig. 10. Intensity of the retouch-induced stigmata. The calculations are made considering the total number of use areas (385) identified on the retouchers (NR = 335).

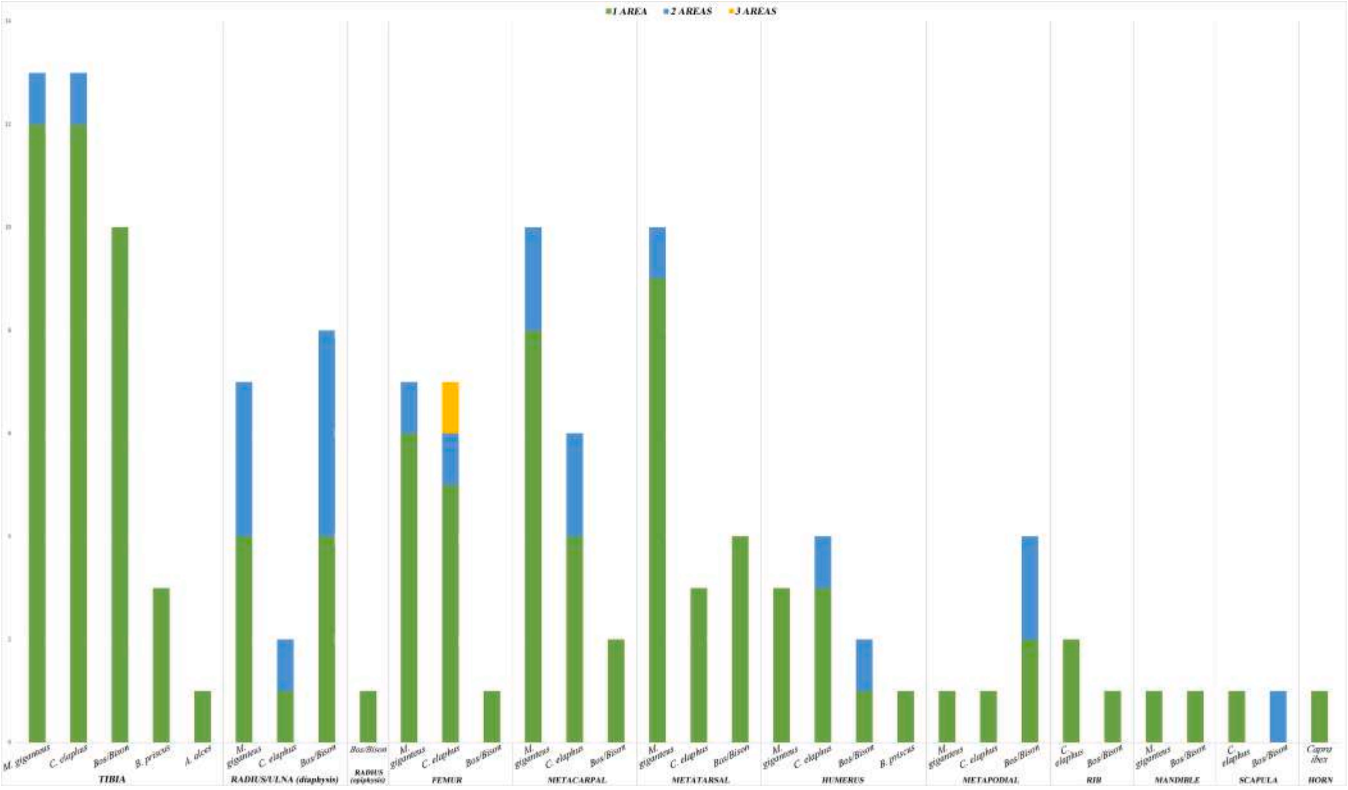
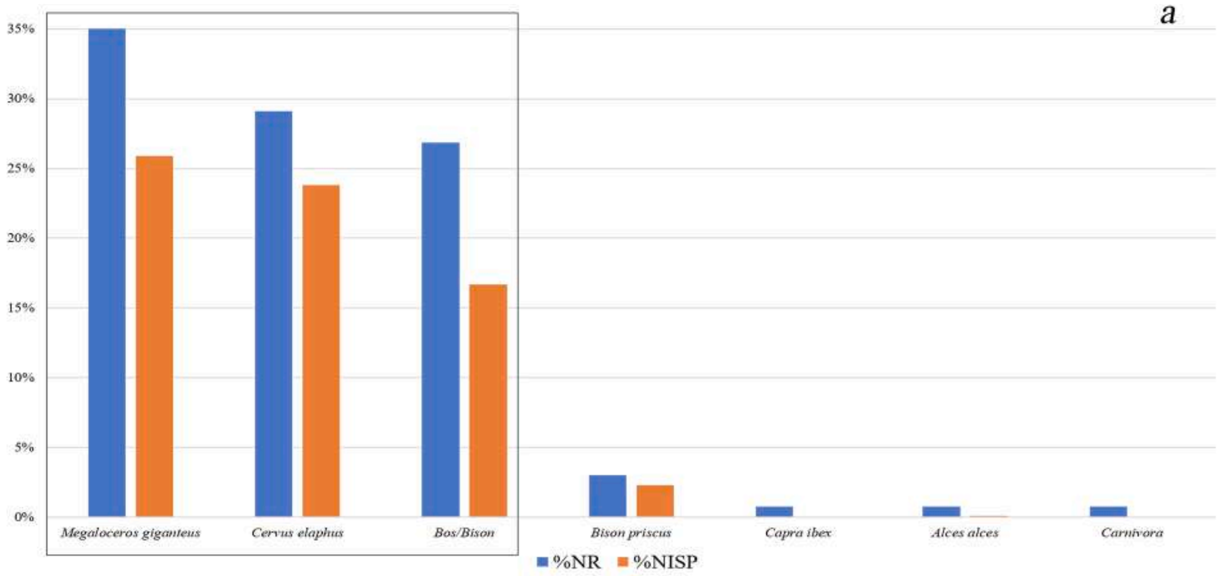


Fig. 11. Relation between the anatomical element and the number of use areas, calculated for each species identified in the sample. The calculations have been made based only on the anatomically and taxonomically species-level identifiable skeletal elements (NR = 132).

motivation, the presence of scraping marks should be indicative of the bone tool being used at a fresh state, since, according to Tartar (2009), the absence of scraping marks means that the periosteum was already dry when the retoucher was used – meaning that a considerable amount of time had passed after the death, especially in glacial contexts.



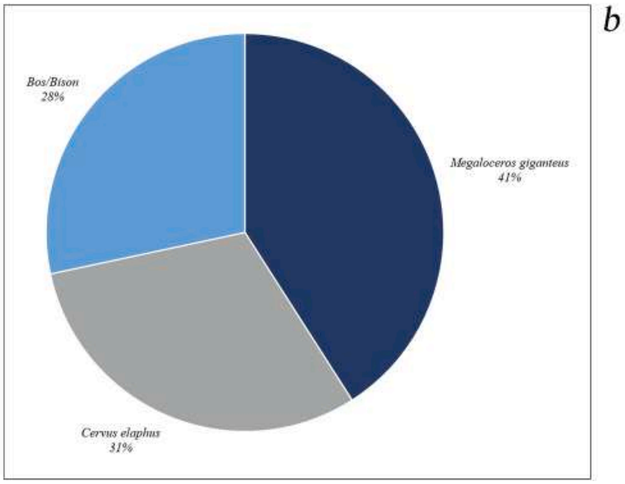


Fig. 12. (a) Relationship between the percentages of bone retouchers (%NR) and the identified species within the whole faunal assemblage (%NISP). The calculations have been made based on the taxonomically species-level determinable sample of retouchers (NR = 133). Details about the NISP are available in Table 1. (b) Detail of the distribution of the most represented species (*Megaloceros giganteus*, *Cervus elaphus*, *Bos/Bison*) in relation to the whole faunal assemblage. The calculation of the percentage corresponds to NR retouchers / NISP for each taxon.

5. Conclusions

De Nadale Cave revealed a remarkable assemblage of bone retouchers that will surely increase the collection of retouch-induced stigmata and the morpho-technological features of these particular tools in the Middle Palaeolithic. This analysis revealed several analogies with the ones recovered in various Middle Palaeolithic cultural complexes. Bone is almost always the preferred choice for the raw material, and its exploitation often focuses on the diaphysis of the limbs of large herbivores, frequently in consistence with the faunal spectrum of each site. Similarities are also highlighted regarding the retouch activity; the general morphology of the tool and the localisation of the retouch-induced stigmata observed on bone retouchers from De Nadale Cave fit well with the assemblages from other Middle Palaeolithic contexts.

Moreover, De Nadale Cave is an excellent example of how Neanderthals exploited animal resources, both for subsistence and technological purposes, in the cultural frame of the Mousterian Quina complex. The morpho-technological and metric features of the retouchers analysed here provide evidence to compare the De Nadale assemblage with others recovered in other Quina contexts in Europe. This study confirms that Neanderthals had knowledge of the technological properties of these bone tools applied to retouching. In fact, although the selection of the animal species for manufacturing the retouchers seems to be driven by the availability of resources, a pattern is equally observed with regard to the selection of specific morphologies suitable for double retouchers, supporting the notion of technological control and predetermination.

Another aspect to consider is the relation between bone retouchers and lithic techno-complexes for the Quina industries, on one hand, and for the other Palaeolithic industries, on the other. The Quina techno-complex is different among others during the Middle Palaeolithic, based on Levallois, Discoid and blade technologies. Quina *débitage* results in wide and thick flakes, and most of them are retouched into scrapers. These features are shared by the De Nadale lithic assemblage, even if the over-exploitation of cores and tools results in small and reduced blanks. Quina retouch is distinguishable due to the presence of invasive and superimposed removals, “fan-shaped” and with transverse hinged edges. The features of the Quina flakes facilitate their resharpening, by means of several sequences of retouch with steps in the modification of the morphology and the delineation of the edges. At the same time, the flakes could be subjected to recycling, obtaining smaller

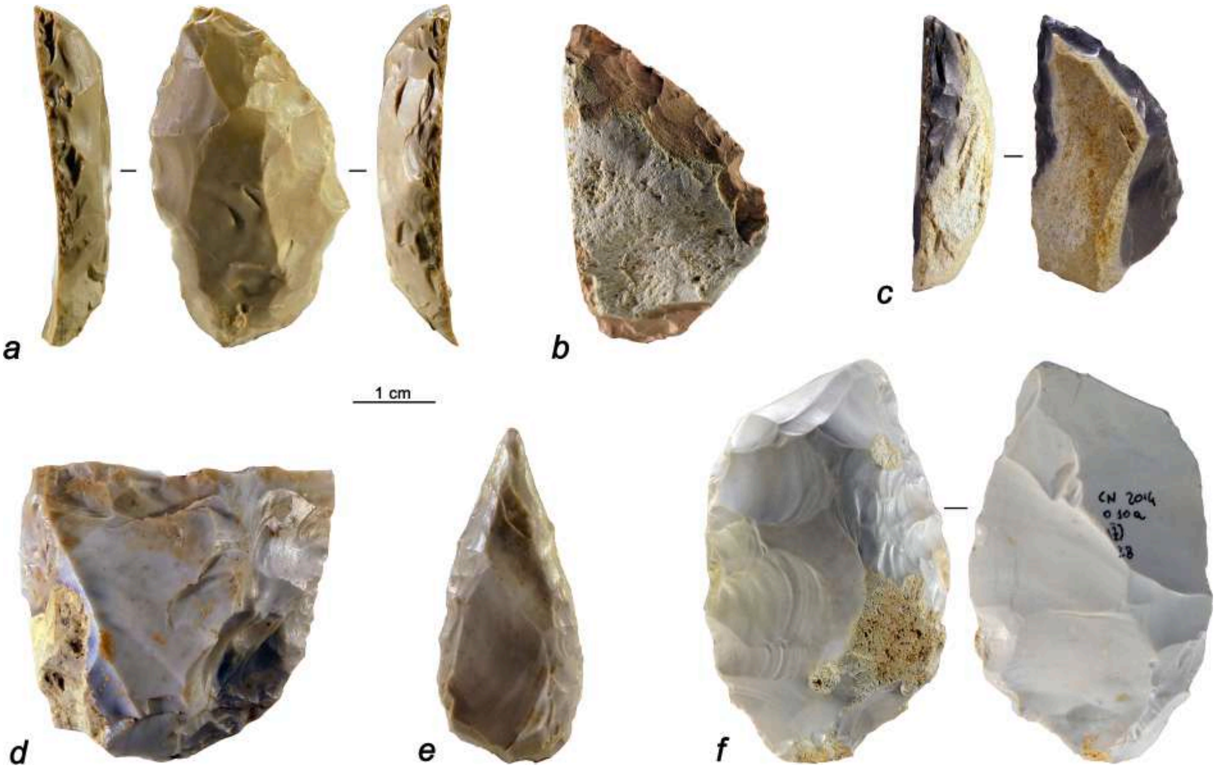


Fig. 13. Retouched lithic tools from De Nadale Cave: convergent double-convex scraper (a), transverse rectilinear scraper (b), convergent rectilinear-convex scraper (c), simple convex scraper (d), retouched point (e), bifacial scraper (f). These tools reveal several stages of resharpening, documented by the invasive, stepped or scaled retouching on one or more edges.

products, behaviour known as "Quina ramification cycle" (Bourguignon et al., 2006). Even though not all the flakes produced by the Quina method are retouched, the retouch activity surely plays a key-role in the reduction sequence of this lithic techno-complex. Moreover, a high presence of lips (Fig. 14) has been observed on the lithic edges of primary products derived from core-knapping, which could suggest the use of bone retouchers as soft hammer, rather than retouchers *per se*. That is confirmed by the numerous and intensively used bone retouchers found in association with Quina industries. These modalities of exploitation of both lithic and animal raw material could be linked to a high mobility and specific subsistence strategies. From this perspective, bone retouchers could be an element of interest in the definition of the Neanderthal tool-kit which could help clarify the economic and behavioural characteristics of the human groups living during the Quina techno-

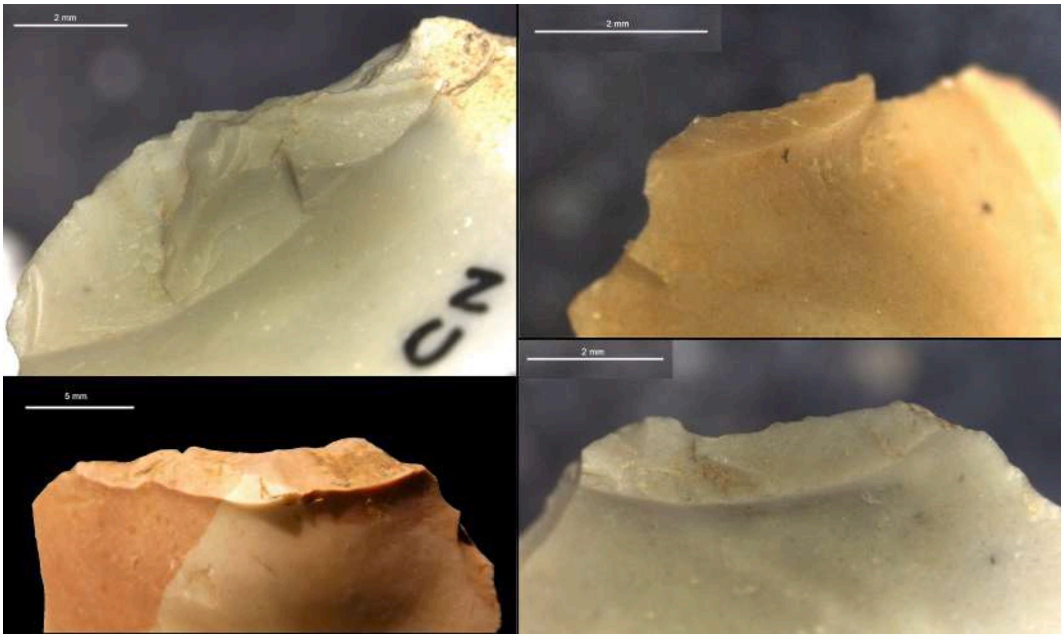


Fig. 14. Prominent knapping lips in correspondence of the proximal end of core-reduction flakes. These widespread technical stigmata may suggest the use of soft hammers (bone, antler or limestone) during knapping activities.

complex.

The analysis of De Nadale bone retouchers could expand our knowledge of the equipment of the Quina Neanderthals, seen as a bridge between lithic and bone industries. Finally, a similar study - carried out among many Palaeolithic contexts - could shed light on the technological evolution of bone retouchers and, since they are present in association to the lithic industries from the Lower to the Upper Palaeolithic, add details on the technological human history from our origins to the dawn of the Metal Ages.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2021.102864.

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4.4 Paper 4

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ORIGINAL PAPER

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

Alessandra Livraghi[1,2] · Florent Rivals[1,3,4] · William Rendu[5] · Marco Peresani[2,6,7]

The paper focuses on the combined application of two high resolution techniques to large sized ungulates' teeth, to infer the seasonality and the extent of site occupation at De Nadale and San Bernardino Cave. The application of both methodologies allowed us to overcome the possible lack of information, due to the use of a single method.

Combining the results coming from the two methodologies, 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. 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; López-García et al., 2017; Terlato et al., 2021; Peresani, 2001b; 2001a). The low intra-specific variability, inferred from the microwear analysis, suggests a short-term occupation while cementochronology point out one or more hunting event(s) during winter and minor events during the good season.

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. According to the cementochronological analysis, the tendency to settle in the two sites during winter emerged, with some brief occupations during the good season

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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 though 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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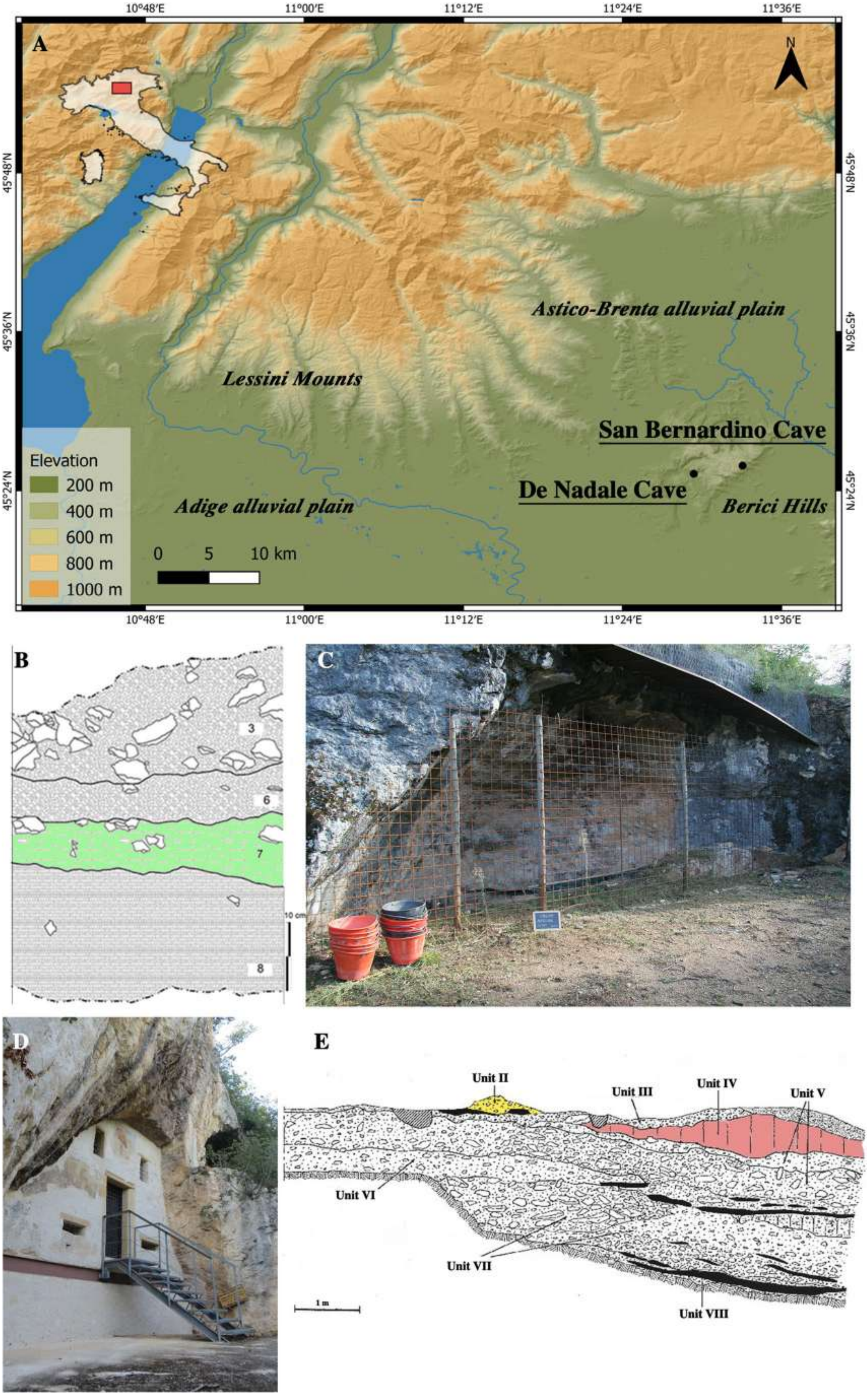
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Astico-Brenta alluvial plain
Lessini Mounts
San Bernardino Cave
De Nadale Cave
Berici Hills
Adige alluvial plain
Elevation
200 m
400 m
600 m
800 m
1000 m
0 5 10 km
B
3
6
7
8
10 cm
C
D
E
Unit II
Unit III
Unit IV
Unit V
Unit VI
Unit VII
Unit VIII
1 m

◂**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 + 1/ − 0.9 ka BP by U/Th (Jéquier et al. 2105). 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 bovids (*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
Alces alces				3			3
Megaloceros giganteus	6	5	11	2			2
Cervus elaphus	8	3	11	15	5		20
Capreolus capreolus	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 × 10, × 20, × 40, and × 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 cuspids 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 Mihlbachler 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 × 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 significative 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 translucid band (TB) in one case and a complete TB on the other case.

Giant deer shows some significative 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 translucid 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
Megaloceros giganteus	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
Cervus elaphus	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
Capreolus capreolus	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
Megaloceros giganteus	II	SB914	LM	5	Thin OB/complete TB	OB	End of good season/beginning of bad season
Cervus elaphus	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
		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
Capreolus capreolus	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).

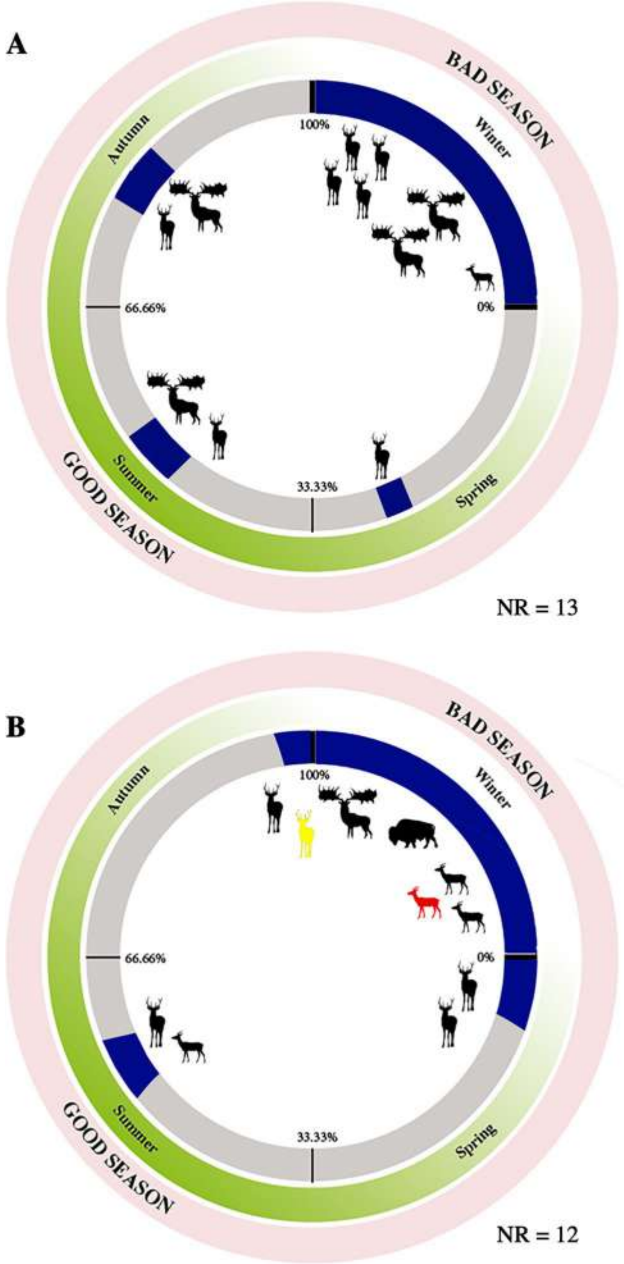

Fig. 2 **A** Schematic representation of hunting events for *Megaloceros giganteus*, *Cervus elaphus*, and *Capreolus capreolus* at De Nadale Cave. **B** Schematic representation of hunting events for *Megaloceros giganteus*, *Cervus elaphus*, *Capreolus capreolus*, and bovids at San Bernardino Cave. (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 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 significative 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 significative 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, *Npit* 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	Npit	SD	CV	Nscr	SD	CV	%LP	%G	%XS	SWS
De Nadale Cave	*Megaloceros giganteus*	Mg	7	2	2.0	6	6.75	2.16	0.31	10.25	0.36	0.13	66.67	50	0	1.5
	Cervus elaphus	Ce	7	3	1.0	5	4.9	1.60	0.33	10.4	2.01	0.20	100	60	40	1.2
	Capreolus capreolus	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
	Cervus elaphus	Ce_IV	IV			2	9.75	3.18	0.33	6.5	0.71	0.11	50	50	0	0.5
	Capreolus capreolus	Cc_IV	IV			1	5.0			9.0			0	0	0	2
	Alces alces	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
	Cervus elaphus	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
	Capreolus capreolus	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.

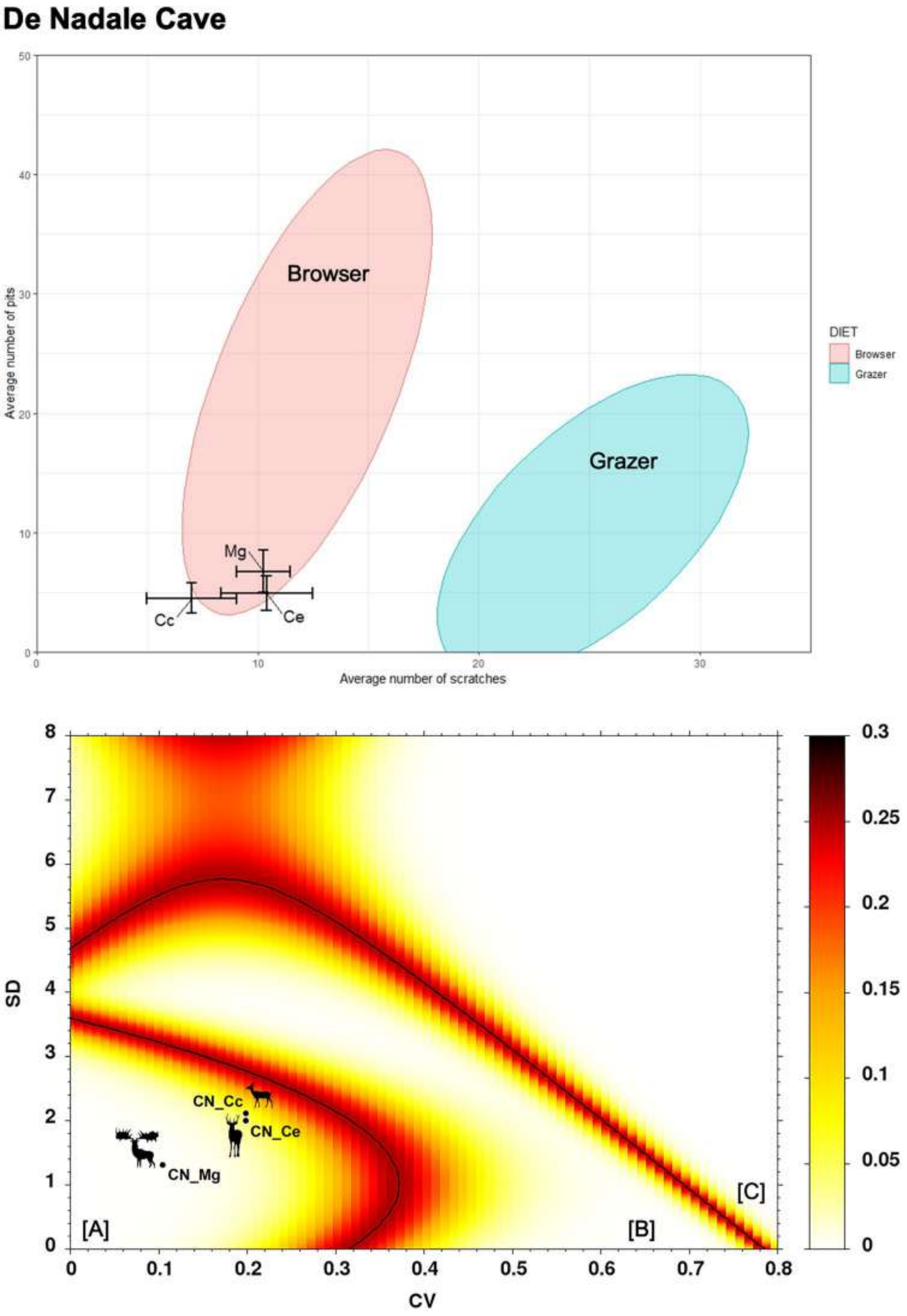

Fig. 3 Above: bivariate plot of the average number of pits and scratches in the selected taxa from De Nadale Cave: *Megaloceros giganteus* (Mg); *Cervus elaphus* (Ce), *Capreolus capreolus* (Cc). Error bars correspond to standard deviation (±1 SD) for the fossil samples. Plain ellipses correspond to 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.

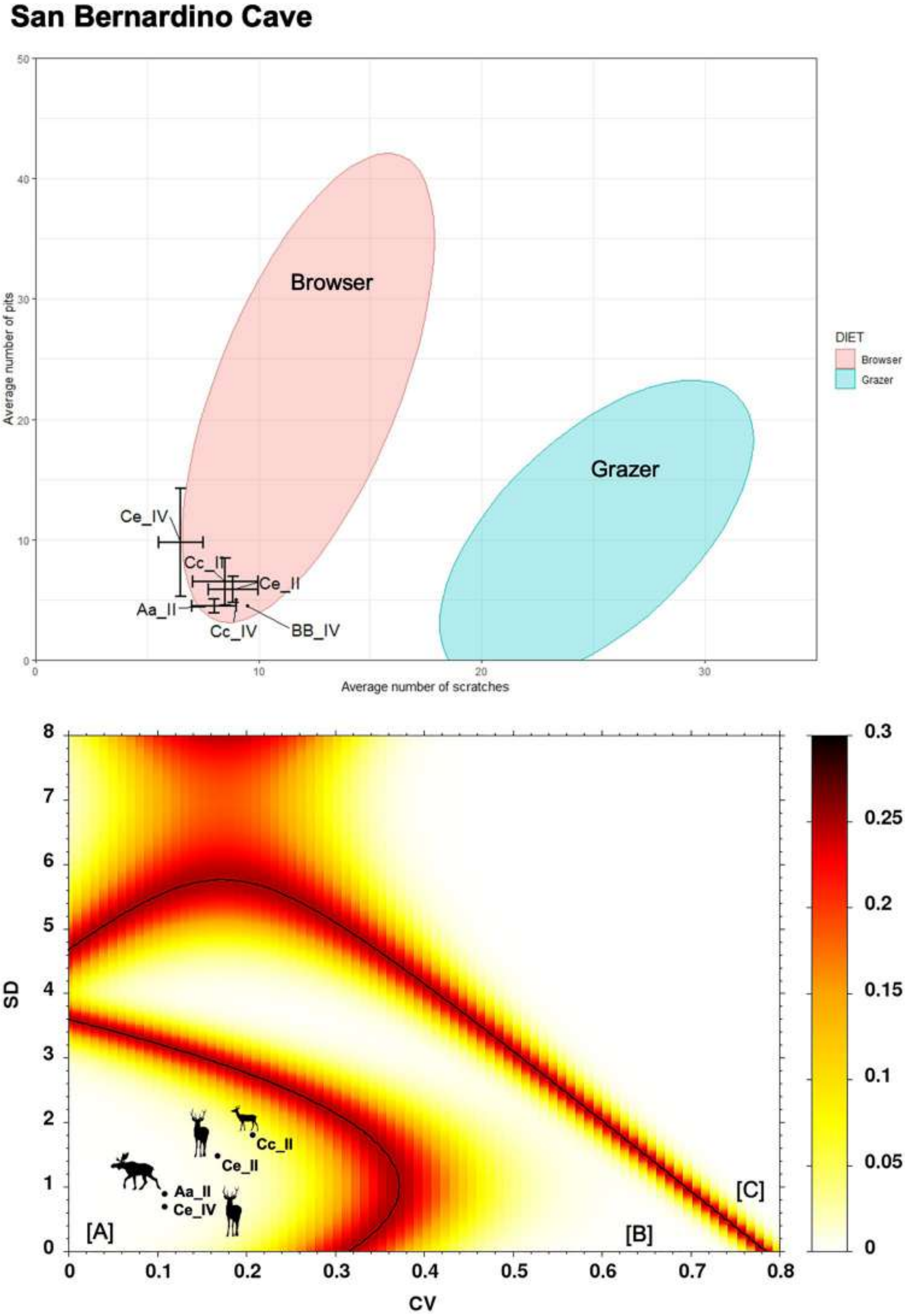

Fig. 4 Above: bivariate plot of the average number of pits and scratches in the selected taxa from San Bernardino Cave: *Alces alces* (Aa); *Cervus elaphus* (Ce), *Capreolus capreolus* (Cc), and bovids (BB). Roman numbers next to the abbreviations of the taxa indicate the unit of provenance (II, Unit 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 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)

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.

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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).

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Declarations

Conflict of interest The authors declare no competing interests.

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4.5 Extent of site occupation at Fumane Cave: preliminary results

On the material yielded by Fumane Cave, only dental wear analyses were performed on 43 teeth yielded by the stratigraphic complex A5-A6 (NR: 22) and by Unit A9 (NR: 21) (Table 3). We decided to avoid cementum analysis to preserve the specimens for future studies.

4.5.1 Mesowear

At Fumane Cave, we were able to apply the mesowear technique only on 11 specimens. since the cusps were not always well preserved, fractured, or biased by post-depositional events. Among them, 7 molars were found in Unit A5-A6 and belong to red deer (NR: 3) and roe deer (NR: 4), while 4 were yielded by Unit A9 and were determined as roe deer.

The two taxa analysed for Unit A5-A6 show a quite homogeneous trend, with mesowear scores (MWS) ranging from 1 for *C. capreolus* to 1.33 for *C. elaphus.* Accordingly, data suggest that the roe deer and the red deer have a browser diet. MWS for roe deer from Unit A9 show a very similar result: with a value of 0.75, indicates once again that the animal was a browser.

Nevertheless, the number of specimens that allowed us to apply the methodology is too modest to give a meaningful interpretation of the data.

4.5.2 Microwear

Microwear analysis was applied to a broader sample: 22 teeth from Unit A5-A6 and 21 from Unit A9 gave positive results when observed under the microscope (Table 3).

The average numbers of pits (Npit) and scratches (Nscr) are very close for all the species considered, and, when plotted, they fall within the limits of the confidence ellipse for modern browsers (Fig. 3). Only the data for giant deer slightly deviate from this trend but it can be due to the exiguity of the sample (NR: 2). 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, all taxa have high rates of individuals showing large pits (LP), with a maximum of 81.82% for red deer from Unit A9, and a minimum of 50% for giant deer from the same unit. We also observed significative percentages of gouges, which are features of a browse dietary preference with the possibility of fruit and seed consumption.

Only the bovid specimen (Unit A9) shows a high percentage of cross scratches (XS), which can be detected only on a low percentage of red deer molars from Unit A5-A6. 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.

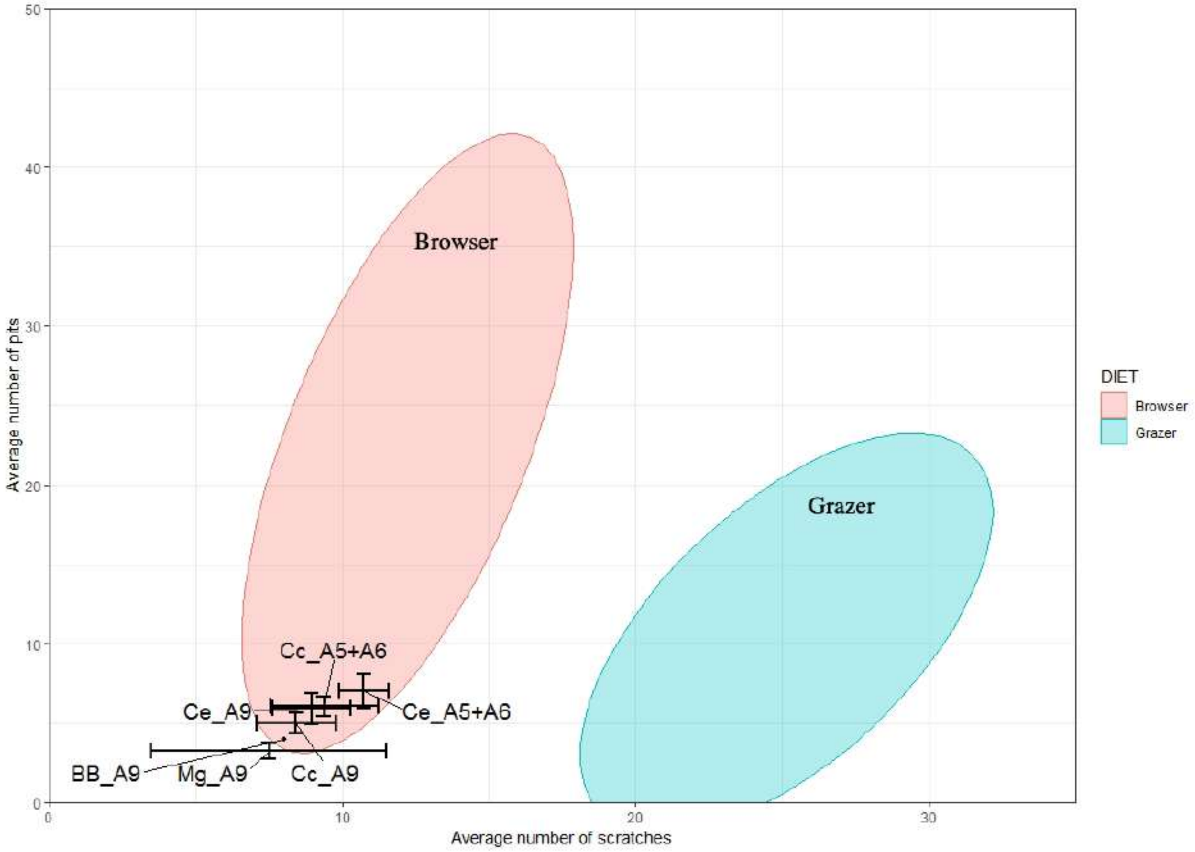


Fig. 3. Bivariate plot of the average number of pits and scratches in the selected taxa from Fumane Cave: *Cervus elaphus* (Ce_A5+A6) and *Capreolus capreolus* (Cc_A5+A6) from Unit A5-A6; *Megaloceros giganteus* (Mg_A9); *Cervus elaphus* (Ce_A9), *Capreolus capreolus* (Cc_A9) and bovids (BB_A9) from Unit A9. 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 (Solounias and Semprebon, 2002).

When plotted into the heat map (Fig. 4), data available give significative results for all the taxa sampled – we only excluded the bovid tooth.

In Unit A5-A6, affordable data was available only for *C. elaphus* which plot in zone [A]. Results for *C. capreolus* present a high degree of unreliability since they plot too close to the boundary line between zone [A] and zone [B] and thus we cannot identify the extent of the mortality event. In Unit A9, the three selected taxa show some discrepancies, presenting a high interspecific variability: roe deer values plot in zone [A] while giant deer data plot in zone [B]. No affordable data are available for red deer since the values fall too close to the error line.

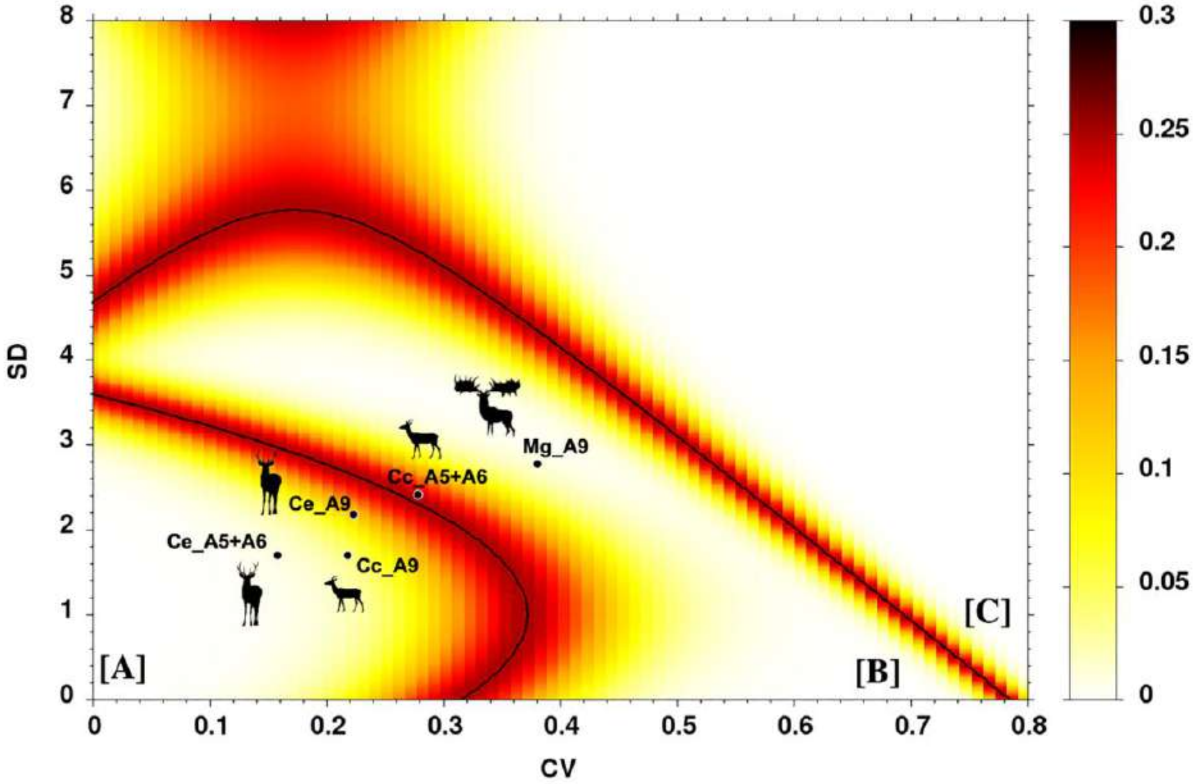


Fig. 4. Boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C)

Site	**Taxa**	**SPID**	**Level**	**Mesowear**		**Microwear**										
				N	**MWS**	**N**	**Npit**	**SD**	**CV**	**Nscr**	**SD**	**CV**	**%LP**	**%G**	**%XS**	**SWS**
Fumane Cave	*Cervus elaphus*	Ce_A5+A6	A5-A6	3	1.33	14	6.85	2.07	0.3	10.75	1.72	0.16	66.67	26.67	6.67	1.47
	Capreolus capreolus	Cc_A5+A6	A5-A6	4	1	8	6.06	0.86	0.14	9.38	2.6	0.28	62.5	12.5	-	1.63
	Megaloceros giganteus	Mg_A9	A9			2	3.25	0.35	0.11	7.5	2.83	0.38	50	-		1
	Cervus elaphus	Ce_A9	A9			11	5.91	1.61	0.27	8.95	2.23	0.25	81.82	36.36	-	0.91
	Capreolus capreolus	Cc_A9	A9	4	0.75	7	5	0.87	0.17	8.43	1.79	0.21	71.43	42.86	-	1.43
	Bovidae	BB_9	A9			1	4			8			-	-	100	2

Table 3. Summary of meso- and microwear data for the Fumane 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; Npit = average number of pits; %LP = percentage of individuals with large pits; %G = percentage with gouges; %XS = percentage with cross scratches; SWS = scratch width score.

5.

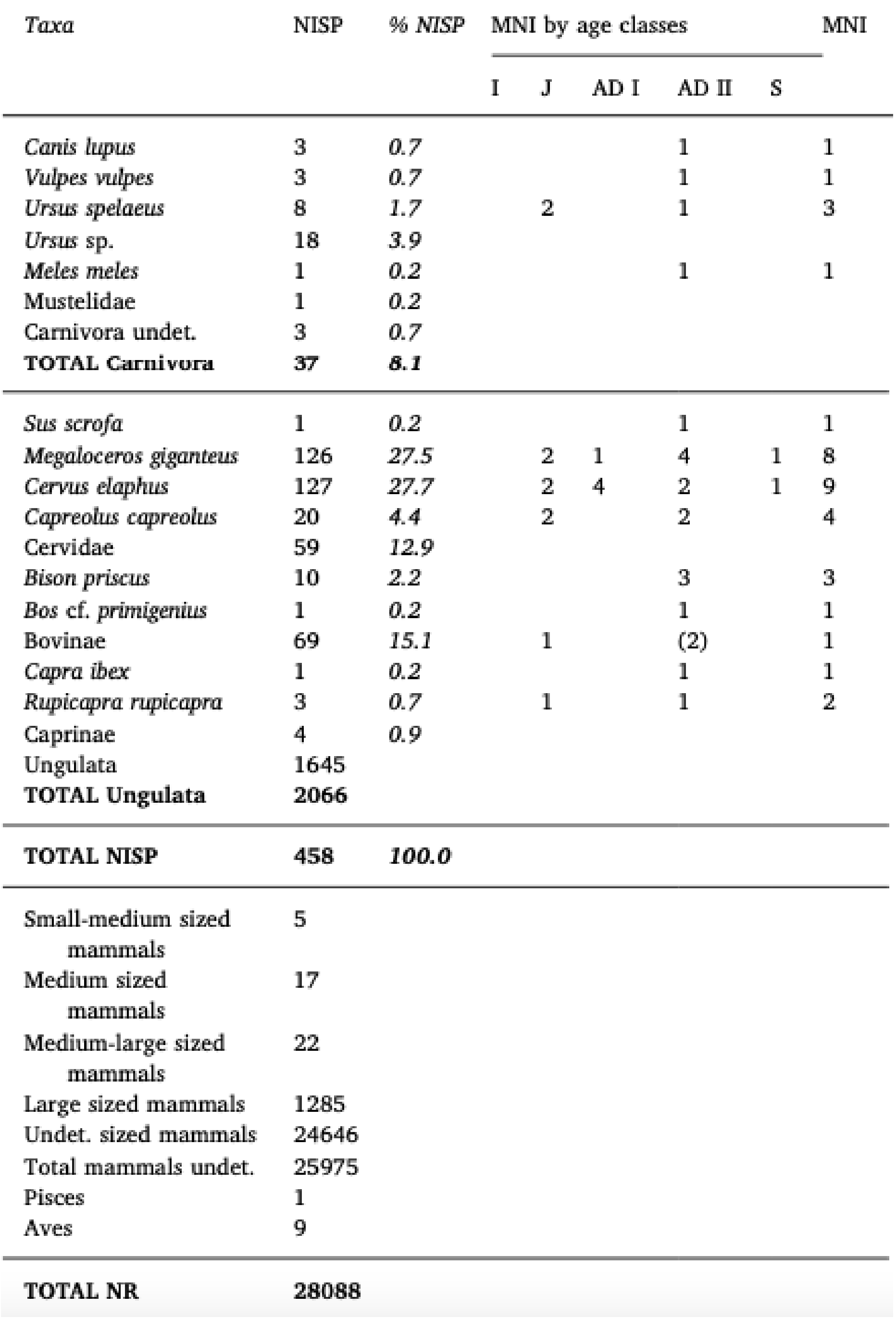
DISCUSSION

5.1 The anthropogenic nature of the De Nadale Cave deposit

Regarding the traditional zooarchaeological analyses, the anthropogenic nature of the faunal assemblage yielded by De Nadale Cave is outright. The deposit shows some peculiar features that leave no doubt:

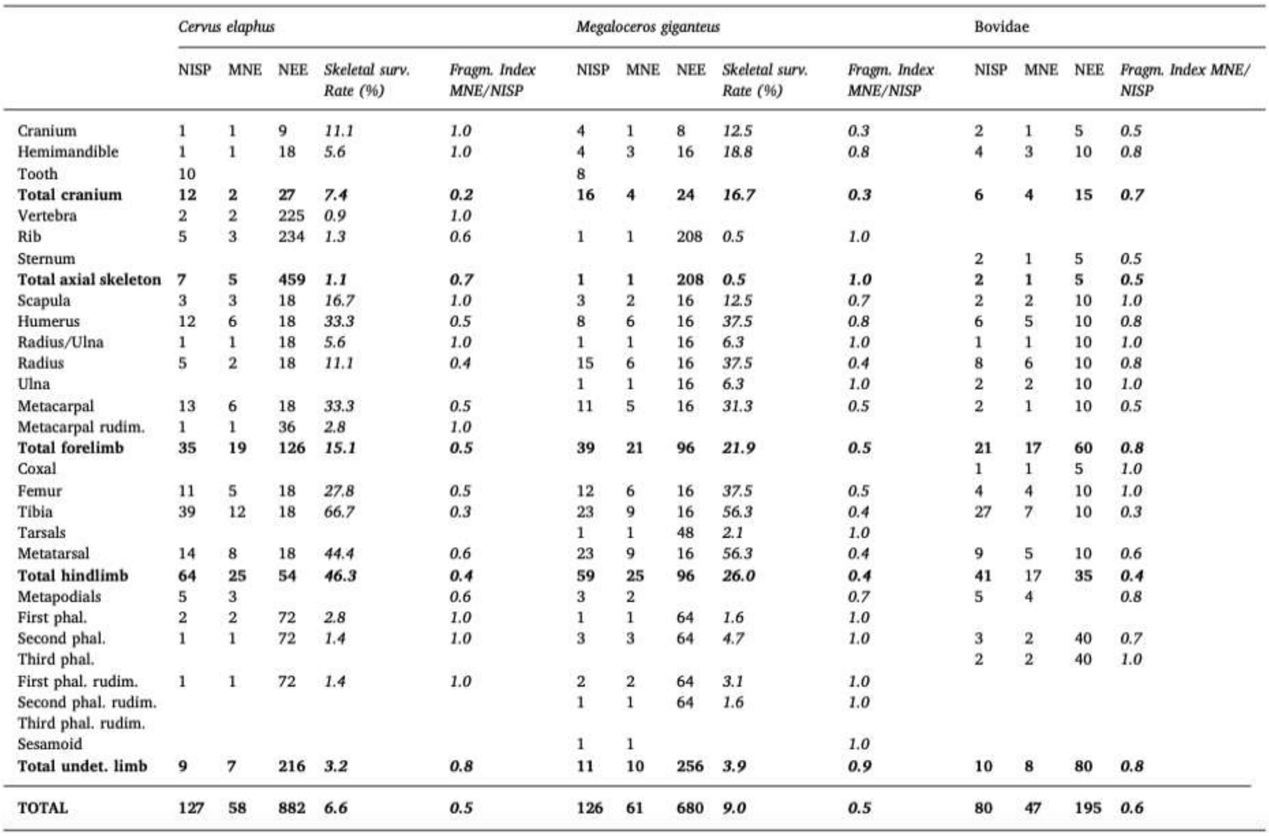
- the faunal spectrum does not reflect the natural composition of the ecotone, especially in quantitative terms. This means that there is a predominance of few specific taxa, that correspond to the base of Neanderthals subsistence (Binford, 1981; Gaudzinski, 2006) (Table 4).
- The mortality profile is not regular in term of age representation: most of the fragments can be referred to prime-adult individuals, predominant over senile and immature animals (Gaudzinski and Roebroeks, 2000; Bunn and Pickering, 2010) (Table 4).
- The body part representation is not homogeneous: limb and cranial bones are more abundant compared to the axial elements (Bunn, 1986; Bunn et al., 1988) (Table 5).
- The high number of cutmarks and intentional bone breakages for marrow recovering and the use of shafts as retouchers are related to a primary and immediate access to the ungulates and an intensive exploitation of the carcasses (Blumenschine, 1988; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo, 1999).

On the other hand, features produced by carnivores (pits, scores, digested bones, etc. but also the presence of deciduous teeth or other juvenile specimens) have been detected among the fragments, although the percentage of these traces is not enough substantial to indicate the action of natural agents in the process of deposition of the osteological material. In addition to this, the relevant quantity of burnt and calcined fragments is consistent with the human origin of this deposit.



Taxa	NISP	*% NISP*	MNI by age classes					MNI
			I	J	AD I	AD II	S	
Canis lupus	3	*0.7*				1		1
Vulpes vulpes	3	*0.7*				1		1
Ursus spelaeus	8	*1.7*		2		1		3
Ursus sp.	18	*3.9*						
Meles meles	1	*0.2*				1		1
Mustelidae	1	*0.2*						
Carnivora undet.	3	*0.7*						
TOTAL Carnivora	**37**	***8.1***						
Sus scrofa	1	*0.2*				1		1
Megaloceros giganteus	126	*27.5*		2	1	4	1	8
Cervus elaphus	127	*27.7*		2	4	2	1	9
Capreolus capreolus	20	*4.4*		2		2		4
Cervidae	59	*12.9*						
Bison priscus	10	*2.2*				3		3
Bos cf. *primigenius*	1	*0.2*				1		1
Bovinae	69	*15.1*		1		(2)		1
Capra ibex	1	*0.2*				1		1
Rupicapra rupicapra	3	*0.7*		1		1		2
Caprinae	4	*0.9*						
Ungulata	1645							
TOTAL Ungulata	**2066**							
TOTAL NISP	**458**	***100.0***						
Small-medium sized mammals	5							
Medium sized mammals	17							
Medium-large sized mammals	22							
Large sized mammals	1285							
Undet. sized mammals	24646							
Total mammals undet.	25975							
Pisces	1							
Aves	9							
TOTAL NR	**28088**							

Table 4. The faunal assemblage at De Nadale Cave: NISP, %NISP and MNI by age classes. The value written in brackets refers to two adult individuals recognized as generic bovids not distinguishable from the other B. priscus or B. primigenius adult individuals on the basis of age. Those, therefore, have not been added to the bovids MNI (from (Livraghi et al., 2021).



	Cervus elaphus					*Megaloceros giganteus*					Bovidae			
	NISP	MNE	NEE	*Skeletal surv. Rate (%)*	*Fragm. Index MNE/NISP*	NISP	MNE	NEE	*Skeletal surv. Rate (%)*	*Fragm. Index MNE/NISP*	NISP	MNE	NEE	*Fragm. Index MNE/NISP*
Cranium	1	1	9	*11.1*	*1.0*	4	1	8	*12.5*	*0.3*	2	1	5	*0.5*
Hemimandible	1	1	18	*5.6*	*1.0*	4	3	16	*18.8*	*0.8*	4	3	10	*0.8*
Tooth	10					8								
Total cranium	**12**	**2**	**27**	***7.4***	***0.2***	**16**	**4**	**24**	***16.7***	***0.3***	**6**	**4**	**15**	***0.7***
Vertebra	2	2	225	*0.9*	*1.0*									
Rib	5	3	234	*1.3*	*0.6*	1	1	208	*0.5*	*1.0*				
Sternum											2	1	5	*0.5*
Total axial skeleton	**7**	**5**	**459**	***1.1***	***0.7***	**1**	**1**	**208**	***0.5***	***1.0***	**2**	**1**	**5**	***0.5***
Scapula	3	3	18	*16.7*	*1.0*	3	2	16	*12.5*	*0.7*	2	2	10	*1.0*
Humerus	12	6	18	*33.3*	*0.5*	8	6	16	*37.5*	*0.8*	6	5	10	*0.8*
Radius/Ulna	1	1	18	*5.6*	*1.0*	1	1	16	*6.3*	*1.0*	1	1	10	*1.0*
Radius	5	2	18	*11.1*	*0.4*	15	6	16	*37.5*	*0.4*	8	6	10	*0.8*
Ulna						1	1	16	*6.3*	*1.0*	2	2	10	*1.0*
Metacarpal	13	6	18	*33.3*	*0.5*	11	5	16	*31.3*	*0.5*	2	1	10	*0.5*
Metacarpal rudim.	1	1	36	*2.8*	*1.0*									
Total forelimb	**35**	**19**	**126**	***15.1***	***0.5***	**39**	**21**	**96**	***21.9***	***0.5***	**21**	**17**	**60**	***0.8***
Coxal											1	1	5	*1.0*
Femur	11	5	18	*27.8*	*0.5*	12	6	16	*37.5*	*0.5*	4	4	10	*1.0*
Tibia	39	12	18	*66.7*	*0.3*	23	9	16	*56.3*	*0.4*	27	7	10	*0.3*
Tarsals						1	1	48	*2.1*	*1.0*				
Metatarsal	14	8	18	*44.4*	*0.6*	23	9	16	*56.3*	*0.4*	9	5	10	*0.6*
Total hindlimb	**64**	**25**	**54**	***46.3***	***0.4***	**59**	**25**	**96**	***26.0***	***0.4***	**41**	**17**	**35**	***0.4***
Metapodials	5	3			*0.6*	3	2			*0.7*	5	4		*0.8*
First phal.	2	2	72	*2.8*	*1.0*	1	1	64	*1.6*	*1.0*				
Second phal.	1	1	72	*1.4*	*1.0*	3	3	64	*4.7*	*1.0*	3	2	40	*0.7*
Third phal.											2	2	40	*1.0*
First phal. rudim.	1	1	72	*1.4*	*1.0*	2	2	64	*3.1*	*1.0*				
Second phal. rudim.						1	1	64	*1.6*	*1.0*				
Third phal. rudim.														
Sesamoid						1	1			*1.0*				
Total undet. limb	**9**	**7**	**216**	***3.2***	***0.8***	**11**	**10**	**256**	***3.9***	***0.9***	**10**	**8**	**80**	***0.8***
TOTAL	**127**	**58**	**882**	***6.6***	***0.5***	**126**	**61**	**680**	***9.0***	***0.5***	**80**	**47**	**195**	***0.6***

Table 5. MNE (Minimum Number Elements), NEE (Number Expected Elements), skeletal survival rate and fragmentation index of Cervus elaphus, Megaloceros giganteus and large bovids (Bos primigenius, Bison priscus and Bovines) (from (Livraghi et al., 2021).

5.2 Skeletal representation: human choice or matter of differential preservation?

As the results of zooarchaeological analyses show, at De Nadale cave the frequency of axial elements is low (Table. 5). The almost total lack of these elements cannot be ascribed to a differential preservation process caused by post-depositional events, even considering that differences in bone diagenesis have been observed as a function of local physical and chemical sedimentary conditions and that parts of the vertebrae and ribs could not have been identified at a taxonomic level and they were consequently sorted into body-size categories.

Observing the skeletal part representation of the taxa yielded by the site, it is reasonable to assume that the treatment of the carcasses did not take place in the cave but presumably at a kill site. The human groups seem to have implemented a selective transport of the parts of the carcasses, bringing the most desirable elements into their consumption site and increasing the difference between the amount of useful anatomical elements recovered in the cave and those of "low caloric utility" (Binford, 1978; 1982; Metcalfe and Jones, 1988). From the data recovered, it is inferable that at least one complete carcass has been brought into the site, but the general trend was to introduce preferably the quarters.

According to several studies (Blumenschine, 1988) and experimental works (Marean and Spencer, 1991; Marean et al., 1992) hominids and carnivores are the primary agents that lead to this situation, in which vertebrae, ribs and the articular parts of long bones are scarcely present. Considering the scarcity of the features attributable to carnivores (pits, scores and so on), the bias in the skeletal profiles observed in Unit 7 could be interpreted as a consequence of the anthropic differential transport of skeletal parts, comparably to other Middle Palaeolithic assemblages (Marean and Kim, 1998; Gaudzinski and Roebroeks, 2000; Marean and Cleghorn, 2003; Costamagno et al., 2006; Daujeard and Moncel, 2010; Daujeard et al., 2012). If the entire animals were carried to the site, numerous ribs, vertebrae and spongy tissue remains should be found. This transport choice could have had several advantages from the cost-effectiveness point of view: only skeletal parts with high nutritive values (meat and marrow), easy to transport and advantageous in terms of nutritional gain, were introduced in the site, with a consequential optimisation of energy costs (Speth, 1983; Speth and Spielmann, 1983; Morin, 2007; Morin and Ready, 2013; Morin et al., 2020). Once the animal has been dismembered, in fact, limbs are easy to transport while the axial trunk is heavier and prevents the hunter from moving freely. Moreover, once the back muscles and the viscera have been removed, the thoracic skeleton results completely useless (at least for alimentary purpose) and could be left on place (Oliver, 1993).

However, this hypothesis alone cannot explain the absence of epiphyses of long bones and spongy element, such as vertebrae, ribs and articular short bones. The well-established presence of longitudinal and oblique scraping marks and cut marks on diaphysis suggests that limb bones were entire when they were introduced into the cave, and they lose their epiphyses after defleshing (Domínguez-Rodrigo, 1999). In addition to that, another possibility could be found in the anthropic processing and consumption patterns: epiphyses contain fat and grease that have a great nutritional utility and that can be extracted by heating the bones. For this purpose, the epiphysis must be separated from the diaphysis and crushed. The result of this activity is a systematic breakage that fits well with the high percentage of fragments less than 2 cm long and that has been recognized in other Middle Palaeolithic sites such as Abric Romaní (Rosell et al., 2012), Les Pradelles (Costamagno et al., 2006) and Grotte du Noisetier (Costamagno, 2013). A similar hypothesis can be made about spongy elements, although difficult to prove archaeologically (Daujeard, 2008; Costamagno, 2013; Speth, 2015; Morin and Soulier, 2017), as it has been observed in other Palaeolithic sites such as Roc de Marsal (Castel et al., 2017) and Abri du Maras (Daujeard et al., 2019) among the others. These data fit well also with the high rate of burnt and calcined bone fragments recovered at the site which can be linked to an intense use of bone material as a fuel, such as attested by Costamagno et al. (2005). Although it seems extremely unlikely that Neanderthal would have selected animals specifically for this purpose, the hypothesis of an opportunistic exploitation of fat-rich elements (i.e., the axial skeletal bones and the epiphysis) for burning as fuel cannot be excluded.

5.3 Palaeoecological implications

The De Nadale Cave is located at the centre of the Berici Hills, a physical landscape positioned between the wide Po plain to the south and the Alpine Mountain range to the north. Therefore, it opens on a tributary of a long valley cut (Val Liona) at a position dominating the valley bottoms and in proximity of the wide plateau above. This favourable location could have been suitable to control the movements of large herbivores, such as aurochs and bison, giant deer and red deer, also attracted from water springs located at the valley bottoms.

The faunal spectrum resulting from the zooarchaeological analysis is consistent with an environment characterized by open woodland formation and open dry meadows. The presence of *Megaloceros giganteus*, *Cervus elaphus* and large bovids enhances this hypothesis. Following Vislobokova (2012) and Van der Made (2006) the ecogenesis of the genus *Megaloceros* shows that the giant deer may have been a mixed feeder living in an open woodland or shrub environment since morphometric features typical of grazers are poorly pronounced (Chritz et al., 2009; Immel et al., 2015). *M. giganteus* seems to have preferred grass-shrub vegetation and open woodland with larch, spruce, pine and birch trees (Stuart et al., 2004). Moreover, red deer is a ubiquitous species, and its ecological niche can be considered over-lapping with the giant deer's one. These animals are highly adaptable and thrive in a variety of habitats. They prefer, nowadays, an interspersed environment including meadows, grasslands with fragmented forested areas and brushy zones (Clutton-Brock et al., 1982; Geist, 1998). The presence of large bovids completes the scenario: paleoenvironmental evidence suggests that, like the extant American bison, *Bison priscus* favoured extensive dry meadows and steppe grasslands (Brugal et al., 1999; Julien et al., 2012; Massilani et al., 2016). On the contrary, *Bos primigenius* inhabited a forested, fluvio-lacustrine, and marshy areas, even if the fossil record suggests that the aurochs could probably adapt to colder and drier climate conditions, at least to a certain extreme (Brugal, 1984; Van Vuure, 2002; 2005; Vercoutère and Guérin, 2010).

These data fit well with a recent study on small mammals (López-García et al., 2018) which highlights the presence of *Microtus arvalis* that is currently reported to be common in open areas and relatively drier regions of northern Italy (Amori et al., 2008). In addition to that, *Chionomys nivalis* and *Microtus agrestis*, which can be found nowadays at over 1000 m of elevation in the Veneto region (Bon et al., 1996), are indicators of harsh climatic conditions prevailing at the time when the formation of Unit 7 took place. This analysis agrees with the Italian terrestrial pollen sequences from Fimon Lake (Pini et al., 2010) and Azzano Decimo core in Friuli (Pini et al., 2009), revealing for MIS 4 a mosaic of open forest and steppe with a predominance of *Pinus-Picea* and an abundance of *Betula* and herbaceous plants.

5.4 Seasonality and extent of human occupation

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

Consequently, knowing that the three deposits have an anthropogenic origin, as stated before in this manuscript and as referred by the literature (Cassoli and Tagliacozzo, 1994; Jéquier et al., 2015; Terlato et al., 2021; Peresani, 2001b; 2001a among others), 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 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 mesowear and microwear, places them within the limits of the confidence ellipse of the extant browsers 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.

The low standard deviation and coefficient of variation of the number of scratches indicate that the accumulation event(s) lasted for a limited period in a timespan of a year, less than or equal to a season.

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. 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. 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; López-García et al., 2017; Terlato et al., 2021; Peresani, 2001b). Also in this case, the low SD and CV point out one or more short mortality events.

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. 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 would indicate short seasonal occupation(s).

Moreover, adding Fumane cave results is fundamental, even if they are partial at the current state of research. The teeth sampled from Unit A5-A6 (NR = 22) show that the two main taxa – *C. elaphus* and *C. capreolus* – have dietary traits typical of the extant browsers. Despite the zooarchaeological analysis not being complete for this macro-unit, this data fits well in the paleoenvironmental reconstruction made by (López-García et al., 2015) who indicated a high extension of woodland formations in association with temperate and moist climatic conditions, as inferred by the micro-mammals assemblage. When analysing microwear variability, affordable data from Unit A5-A6 are available only for *C. elaphus* which correspond to seasonal occupations. Results for *C. capreolus* present a high degree of unreliability since they plot too close to the boundary line between two zones (seasonal and long-term occupations) and thus we cannot identify the extent of the mortality event.

For Unit A9 (NR =21), all the three species or cervid that we selected – *C. elaphus*, *M. giganteus* and *C. capreolus* – and the Bovidae specimen were browsers. More paleoenvironments data are available for this unit: the large-mammal assemblage indicates temperate humid conditions and an expansion of woodland and forested habitats from A11 to A9 (Fiore et al., 2004; Romandini et al., 2014). The ecological framework shown from the avifaunal assemblage reflects diverse environments, rock cliffs and alpine meadows, mountainous zones and ponds, woodlands of high mountains and the subalpine forests. Compared to unit A6 and A5-A6, the avifauna from A9 confirms to reflect less rigid climatic conditions (Fiore et al., 2016). When analysing microwear variability to assess the duration of occupation, data available give significative results for all the taxa sampled – we only excluded the bovid tooth. In Unit A9, the three selected taxa show some discrepancies, presenting a high interspecific variability: the roe deer was hunted during an occupation of a season or shorter while the giant deer correspond to occupations longer than a season. No affordable data are available for red deer since the values are not significant.

The characterization of De Nadale Cave as a residential, short term seasonal occupation is supported by some recent studies on the lithic industry and the raw material procurement (Delpiano et al., n.d.). The site shares some features typical of the Quina assemblages: food resources management shows that the Quina system was adapted to high seasonal mobility based on the planned acquisition of migrating large ungulates (Delagnes and Rendu, 2011). On the other hand, lithic raw materials indicate that local resources were preferably exploited, while nonlocal materials increased with the deterioration of climate conditions, as it is recorded in Combe Grenal, Roc de Marsal and Espagnac assemblages (Jaubert et al., 2001; Turq et al., 2017). Seasonal scheduling of mobility patterns does not necessarily correspond on the high distance but rather on the frequency of the regional displacements (Delagnes and Rendu, 2011).

Even though Neanderthal mobility patterns and adaptations to environmental and ecological factors are still poorly known in Italy, we can consider some features that point out a great flexibility and techno-cultural variability within the human groups that inhabited the region. Chert is the main raw material exploited during the Middle Palaeolithic, and it was generally collected locally and regionally (within 30 km of the site). However, the presence of resources from distant areas located more than 100 km away has occasionally been identified, usually in low but constant percentages (Porraz and Peresani, 2006; Romagnoli et al., 2016). Resources collected from distant sources would usually arrive at the site as finished tools as part of a personal toolkit, as attested by the re-use of exogenous raw materials in many sites, such as Fumane, San Bernardino and Broion Cave in the North of Italy (Peresani et al., 2015) and Grotta del Cavallo in the South (Romagnoli, 2015).

This scenario is embedded in the complex mosaic that characterizes the Mediterranean Europe, where the complementarity between long-term and short-term, repeated occupations underlines the Neanderthal high behavioural flexibility and techno-cultural variability (Rivals et al., 2009b; Moncel and Rivals, 2011). Unfortunately, the specifics are still poorly known across this area.

Interpreted as a whole, all the data suggest 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., 2015a). Despite the few affordable data obtained from Fumane Cave, the results show some analogies with Portel-

Ouest: the mortality event(s) for roe is linked to a short-term occupation, while the values for giant deer indicate a long-term event. This result may be related to different hunting strategies, linked to the season or to other ecological bias. Further studies in this field would be fundamental to achieve a more complete view of this scenario.

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., 2015a), 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).

5.5 A deliberate economic strategy or a purely “ecological” specialization?

As the taxonomic data show, the majority of animal remains brought onto the three sites objects of this work was from species inhabiting lowlands, valley bottoms and plateaux.

The faunal spectrum at De Nadale differs from the assemblages at San Bernardino and Fumane Caves, in terms of size categories: the meat income was based mainly on large and medium-large sized herbivores (giant deer, deer and bovids), while in these last, smaller preys were more abundant (roe deer, ibex and chamois). In this scenario, questioning about the meaning of this prey composition seems natural since it does not reflect the probable natural association of species around the caves.

Given the concept of selection as a deliberate choice made by the hunter of exploiting exclusively some taxa – or a single species or only a specific part(s) of an individual – and the concept of opportunistic behaviour as the lack of this choice (Parker, 1978), the evidence at De Nadale Cave raises questions whether this faunal assemblage could be the result of a targeted exploitation or if it could have been driven by environmental/climatic/seasonal constrains. Moreover, understanding subsistence strategies cannot be limited to the dualism between prey selection and opportunism: the two behaviours can be strongly linked and the human groups can practise both adaptive solutions alternatively, depending on different parameters (environmental context, techno-cultural complexity, climatic or seasonal conditions etc.) (Rendu, 2022 and reference therein).

The hypothesis of a selection of large and medium-large sized preys, which may have had lower encounter rates or might have been disregarded on occasion if the hunters’ success rates were too low (Bird, 2009), is to take into account, although difficult to demonstrate. For example, selection could be hard or impossible to recognize because of the stratification of the archaeological deposits and this apparent opportunism could be a succession of different selective behavior, not distinguishable from each other.

Combining dental wear analyses and cementochronology contributed to widen the view on the hunting strategies and suggested the hypothesis that the narrow faunal spectra (especially at De Nadale Cave) can be linked to the season of occupation. However, the hypothesis that the large mammal assemblage may be the result of a deliberate subsistence choice, possibly related to techno-cultural features of the human groups, is not to completely to discharge. This scenario is made even more complex by the lack of data for the Italian peninsula. Nowadays, there are no sites in the North of Italy that yielded deposits dated or clearly referable to the MIS 4 and therefore comparable to De Nadale. A dominance of middle sized ungulates (red deer and ibex) has been preliminarily recorded at Fumane Cave Unit BR11 (Fiore et al., 2004), chronologically positioned at the end of MIS 4. Additional MIS 4 archaeofaunal assemblages from Tagliente Rockhelter, Ghiacciaia Cave and San Bernardino Cave require further chronological refinements and in-depth analyses to assess consistency in the range of medium-large or medium sized ungulates represented (Cassoli and Tagliacozzo, 1994; Bertola et al., 1999; Fiore et al., 2004; Thun Hohenstein, 2004). Moreover, extensive studies have been carried out on the faunal assemblage of Unit A9 of Fumane Cave (Romandini et al., 2014), which, however, dates to MIS 3 and cannot be directly compared with the case of De Nadale Cave. Anyway, the Unit A9 points out a different situation: medium-sized cervids, *Cervus elaphus* and *Capreolus capreolus*, were the primary meat income resources, in association with *Capra ibex* and *Rupicapra rupicapra*, exploited to a lesser extent. Bovids, *Megaloceros giganteus*, *Alces alces* and *Sus scrofa* are also present but in a less significant quantity.

Without specific comparisons for the North of Italy, the discrimination between “faunal specialization as a deliberate economic strategy” and “purely ‘ecological’ specialization” (Mellars, 2004) is uncertain. This scenario is complicated by the complete lack of information about seasonality and duration of the human occupation in the Italian peninsula.

Even if the De Nadale Cave has been occupied probably at the onset of a cold period, it is likely that the prey catchment zone around the site, which probably included the nearby Val Liona and Pozzolo plateau, would have provided species other than giant deer, red deer and bovids. Thus, the narrow species focus that characterizes the assemblage may reflect a particular hunting pattern, which is still not well known in Italy. However, a sort of specialized diet has been found, in the south-east of Italy, at the Oscurusciuto Rockshelter with its dominance of *Bos Primigenius* in Unit 4 (Boscato et al., 2011), at the Santa Croce Cave with the exclusive representation of *Bos primigenius* and *Equus ferus* (Boscato et al., 2010) and at the Cavallo Cave Unit F with the association of *Bos primigenius*, *Cervus elaphus* and *Equus ferus* (Boscato and Crezzini, 2006). Regarding the North-eastern part of Italy, a particular pattern is the one recognized at Rio Secco Cave where anthropically modified cave bear bones abound in the levels 5top+7 and 5 + 8 (Romandini et al., 2018a). Although the directionality in hunting behavior in Neanderthal context has always stimulated controversy, a large number of deposits, however, have been interpreted as probable accumulation resulting from specialized hunting. Narrow animal spectrum or even monospecific-based diet have been revealed at numerous Middle Paleolithic sites in different regions, for example, in the Zagros Mountains at Kobeh (Marean and Kim, 1998), in the Caucasus at Il'skaya I (Hoffecker et al., 1991), in Western Europe at Mauran (Girard and David, 1982; Farizy et al., 1994), La Borde (Jaubert et al., 1990), Coudoulous I (Mellars, 1996; Jaubert et al., 2005), Le Roc (Mellars, 1996), Jonzac (Niven et al., 2012) and Les Pradelles (Costamagno et al., 2006; Rendu et al., 2012) and in Central Europe at Wallertheim (Gaudzinski, 1995), Salzgitter Lebenstedt (Gaudzinski and Roebroeks, 2000; Gaudzinski, 2006) and Neumark-Nord (Gaudzinski-Windheuser et al., 2018).

6.

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. This result is not unexpected: it is easy to imagine the Berici Hills area as favourable for human groups, given the mild climatic conditions, the availability of trophic resources and the orientation of the caves (S-SE) that provided a protected refugia to overcome the harsh winter. On the other hand, preliminary studies at Fumane Cave present the hypothesis of a different settlement strategy, that is still not easy to interpret but it is worth investigating in future studies.

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.

The present manuscript is the first attempt to investigate seasonality and settlement dynamics in the Italian area, applying dental wear and cementum analyses. The road to a more complete knowledge of Neanderthal mobility patterns and land use is still long and many other perspectives for future research must be settled. A more comprehensive view of the scenario could be gained through the application of such methods to a higher number of sites in the area that can produce more detailed data, especially regarding deposits that cover a long time span and could give information about different techno-cultural groups. A more detailed point of view could come from the application of other high-resolution techniques, such as the analyses of carbon and nitrogen stable isotopes or of the dental microwear texture that can give information about the trophic relation between species, humankind included.

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