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Neanderthal resilience and adaptability: insights from the Abric Pizarro faunal assemblage during the MIS 4

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The examination of faunal assemblages through zooarchaeological analyses constitutes a fundamental approach for gaining insight into the intricate behaviours of Neanderthals. Previous investigations have primarily focused on periods of relative environmental stability, and this has provided a wealth of relevant archaeological data. However, our understanding of Neanderthal resilience during the MIS 4, a period presumably characterised by harsh environmental conditions, remains limited. This study presents the first comprehensive analysis of the faunal assemblages from Levels M and P at Abric Pizarro. The geographic location of Abric Pizarro in the southeast Pre-Pyrenees, combined with chronometric dating, offers a unique opportunity to explore Neanderthal behaviours during a poorly known chronological period. The detailed zooarchaeological analysis comprised taxonomic identification, taphonomic analysis and age-at-death profiling to explore the adaptability and flexibility in the Neanderthal diet. The findings indicate that Neanderthal groups incorporated a diverse range of protein resources from small herbivores (e.g., caprids) to very large herbivores (e.g., Bos/Bison). These results not only demonstrate an adaptability to changing environments in an area traditionally deemed unsuitable for long-term occupation, but also contributes significantly to our understanding of the complex behaviours exhibited by Neanderthals.

KEYWORDS

Neanderthal behaviour, zooarchaeology, adaptability, resilience, Neanderthal diet, MIS 4, MIS 3

1 Introduction

Since their discovery in the 19th century, Neanderthals have been historically characterised as “primitive,” “brutish,” and “ape-like,” denoting an inherent inferiority compared to anatomically modern humans (AMH) (e.g., [Busk, 1865](#); [Trinkaus and Shipman, 1993](#)). This assumption was perpetuated by prevailing religious ideologies that influenced scientific research, resulting in a biased exclusion of complex behaviours traditionally attributed solely to AMH ([Trinkaus and Shipman, 1993](#)). However, in recent decades, multidisciplinary investigations, encompassing archaeology and genetics among others, have challenged these prevailing perceptions, prompting a profound reassessment of Neanderthals' cognitive capacities and their position within the broader framework of human evolutionary history (see an updated review in [Romagnoli et al., 2022](#)).

Archaeological and biomolecular research conducted since the mid-20th century has generated compelling evidence that has reshaped our understanding of Neanderthals. This accumulating corpus of data reveals that Neanderthals exhibited behaviours previously

regarded as exclusive to AMH (Sankararaman et al., 2014; Hajdinjak et al., 2021; Romagnoli et al., 2022). One such behaviour is the spatial organisation of Neanderthal living sites, implying cognitive complexity and social structure (Vaquero, 2022). Additionally, Neanderthals demonstrated a remarkable ability to adapt and thrive in diverse environments, displaying resilience amidst fluctuating conditions, thus attesting to their considerable adaptability (Hardy, 2022; Sánchez Goñi, 2022; Fernández-García et al., 2023; Nabais et al., 2023).

The field of zooarchaeology has emerged as a pivotal avenue for elucidating the complex behaviours of Neanderthals. Zooarchaeological inquiry provides critical insights into the dietary patterns, subsistence strategies, and hunting practises of ancient human populations. Recent advancements in zooarchaeology have significantly challenged conventional notions regarding Neanderthals' dietary preferences and hunting capabilities (Blasco et al., 2022; Rendu, 2022). Contrary to earlier assumptions that Neanderthals subsisted primarily on large game, emerging evidence suggests their consumption of small prey such as rabbits (Lloveras et al., 2009, 2011; Fa et al., 2013; Martínez-Polanco et al., 2017; Carvalho et al., 2018; Pelletier et al., 2019), tortoises/turtles (Blasco, 2008; Nabais and Zilhão, 2019), birds (Blasco and Fernández Peris, 2009; Blanco et al., 2021), and other marine resources (Zilhão et al., 2020; Nabais et al., 2023).

The present study seeks to contribute further to the burgeoning field of zooarchaeological research by investigating the adaptability and flexibility of the Neanderthal diet during the Marine Isotope Stage 4 (MIS 4; ca. 71–58 ka), a period traditionally characterised by climatic instability (d'Errico and Sánchez Goñi, 2003; Fernández-García et al., 2023). This temporal window offers a unique opportunity to explore how Neanderthals adjusted their subsistence strategies in response to fluctuating environmental conditions.

By employing a comprehensive analysis of animal remains derived from a well-preserved Neanderthal site within MIS 4, this study aims to address key research inquiries. Firstly, it seeks to delineate the spectrum of animal species exploited by Neanderthals during this interval, examining any discernible shifts in prey preferences. Moreover, through the examination of animal bone assemblages for evidence of processing and butchery techniques, this research endeavours to shed light on the level of the standardisation of butchery practises within Neanderthal subsistence practises.

2 Materials and methods

2.1 Study site and excavation history

The Abric Pizarro site is situated in the Barranc de les Coves valley, 697 m above sea level at the foothills of the southeastern Pre-Pyrenees (Figure 1; Pizarro et al., 2013; Vega Bolivar et al., 2015; Samper Carro et al., under review¹). The rock shelter is 35 m in

length, 4.3 m in height, and 6.4 m in depth, with a sedimentary sequence exceeding 1.5 m in depth (Vega Bolivar et al., 2015).

Discovered in 2007, the site underwent its first test excavation in 2009, followed by extended excavation seasons between 2010–2013, 2016, 2017, and 2022. The excavations revealed four distinct archaeological units, labelled as M, P, Q, and S, which were separated by culturally sterile layers. The identification of these discrete Neanderthal occupations was made possible through the application of three-dimensional recording techniques for artefacts, features (e.g., hearths), and sedimentary elements (e.g., large rocks; Figure 2).

To establish the chronological framework for the analysed levels, thermoluminescence (TL) dating was initially performed on thermally altered chert artefacts. The obtained dates position level M at $58,971 \pm 5,359$ BP and level P at $62,602 \pm 6,110$ BP, placing them within MIS 4 even when considering the statistical error margins associated with this dating method (Vega Bolivar et al., 2015). Optically stimulated luminescence (OSL) samples were subsequently collected from units P and Q to enhance the chronological resolution of the deposit. These samples returned an age of 67.7 ± 4.9 ka for level P and an age of 74.4 ± 5.1 ka for level Q, in broad agreement with the previously obtained TL dates, and supporting a MIS 4 chronology for the deposit (see text footnote 1).

2.2 Faunal assemblage

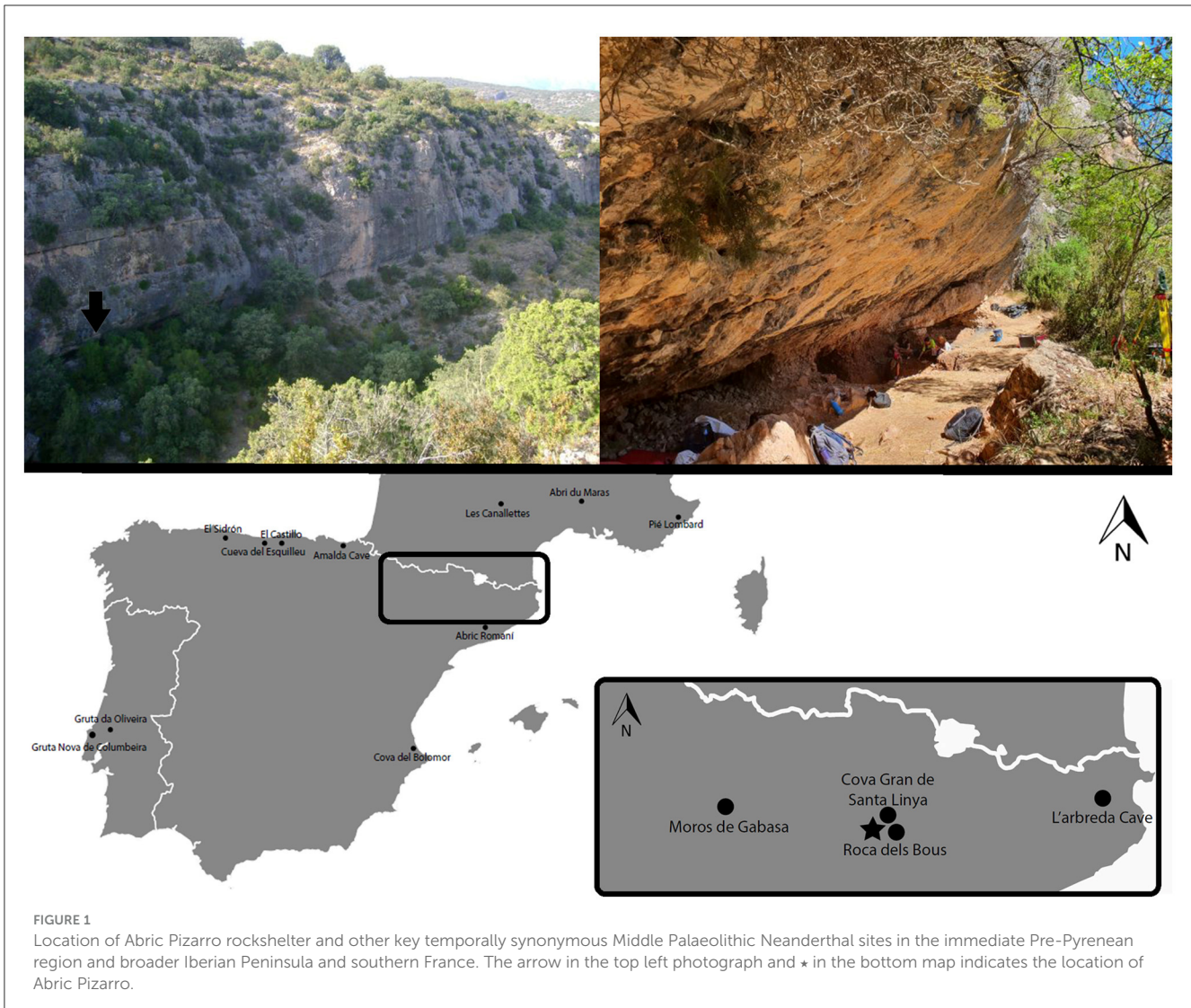
A general overview of the complete faunal assemblage recovered in Abric Pizarro has been previously published (Vega Bolivar et al., 2015) (see text footnote 1). This study focuses on the comprehensive analysis of the large vertebrates recovered from levels M and P within the Abric Pizarro site. The analysis included quantitative assessment, taxonomic identification, and taphonomic analysis to gain insights into subsistence practises, taphonomic processes, and potential cultural activities during the period of occupation at Abric Pizarro.

It is important to note that due to bone sampling and recovery strategies, many bones of small vertebrates were collected in “non-coordinate” bags and omitted from detailed recording. Resultingly, the small vertebrates analysed during the zooarchaeological investigation do not constitute the entire assemblage of small vertebrate remains and are therefore not discussed in this study. Current research is focusing on assessing the collection of small vertebrate remains from Abric Pizarro to provide a more comprehensive and holistic interpretation of Neanderthal behaviour at the site.

2.3 Bone preservation

Bone preservation was evaluated based on the degree of weathering, adapting the criteria established by Behrensmeier (1978) to match the fossilisation state of the assemblage (Samper Carro et al., 2020). The weathering stages included stage 1 (minimal calcareous coating and cracking), stage 2 (less than half of cortical surface affected by calcareous coatings and some cracking), and

1 Samper Carro, S. C., Vega Bolivar, S., Pizarro Barbera, J., Westbury, E., Connor, S., Martínez-Moreno, J., et al. (under review). Living on the edge: Abric Pizarro, a MIS 4 Neanderthal site in the lowermost foothills of the southeastern Prepyrenees (Lleida, Iberian Peninsula).



stage 3 (more than half of cortical surface covered with calcareous coatings or extreme cracking and flaking). Abrasion was classified into stage 0 (no abrasion), stage 1 (light abrasion), and stage 2 (polishing of the cortical surface).

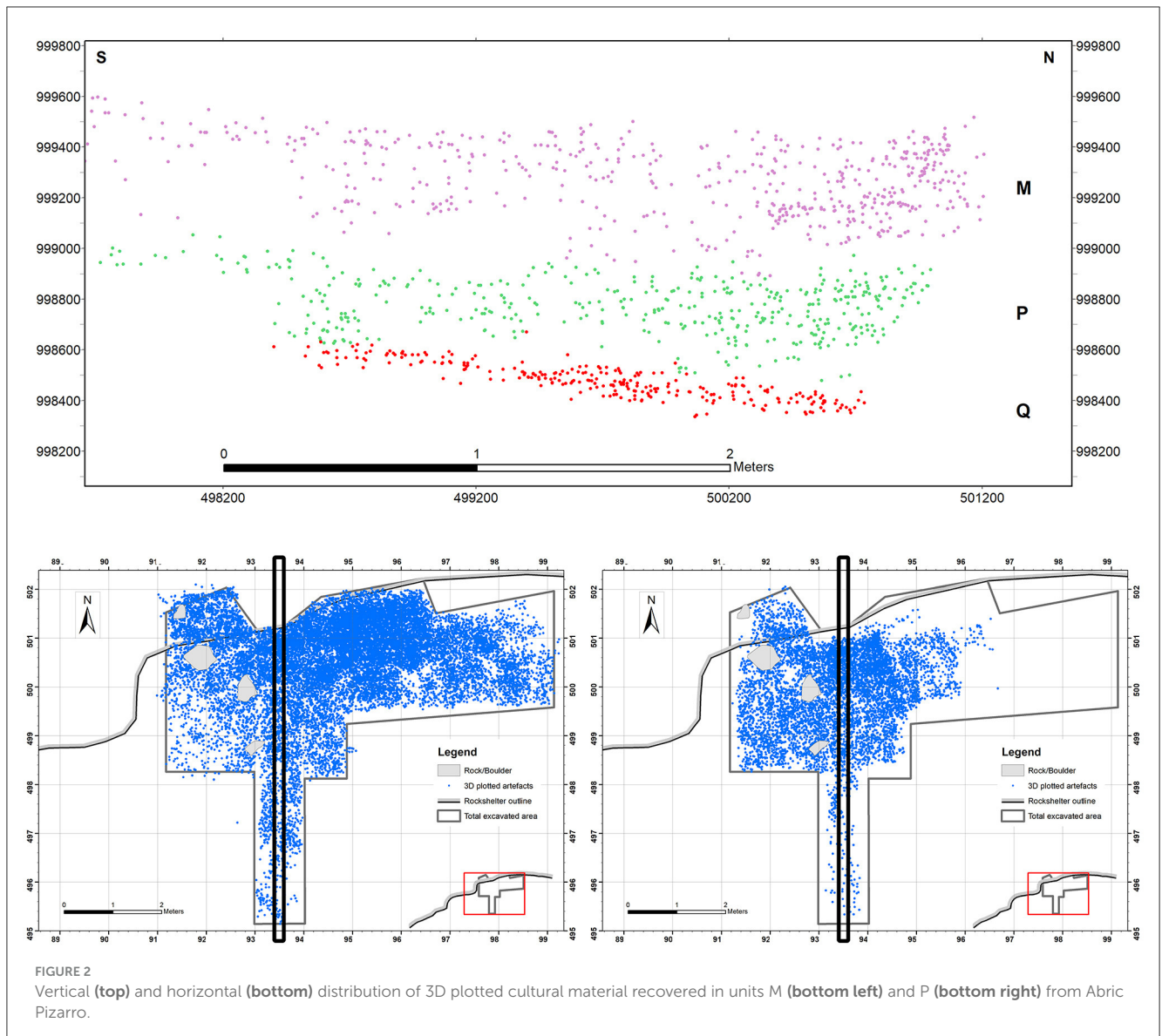
2.4 Quantitative analysis

Quantitative units were calculated to assess the faunal composition. This involved, where appropriate, distinguishing between diaphyses and other skeletal components following standardised guidelines (e.g., [Marean and Kim, 1998](#)). The total number of fragments (NRT) was determined, encompassing both identified and unidentified specimens. Additionally, the number of remains (NR) was recorded, including fragments identified to taxa or size/weight-class. The number of identifiable specimens (NISP) represented the identified fragments at the lowest taxonomic level. Furthermore, the minimum number of elements (MNE) was calculated, considering aspects such as age-at-death, side, and anatomical position, to assess the minimum representation of each

skeletal element within taxa (i.e., skeletal representation). MNE was calculated in tandem with the percentage of minimum animal units (%MAU) to assess the relative representation of the different species and size classes within the assemblage. The minimum number of individuals (MNI) was calculated to estimate the relative abundance of each taxonomic group present in the assemblage. Where appropriate, age-at-death determinations contributed to the calculation of MNI.

2.5 Taxonomic identification

Taxonomic identification was conducted with assistance from the osteological collection housed at the Centre d'Estudis del Patrimoni Arqueològic (UAB) and osteological reference manuals ([Pales and Garcia, 1981](#); [Brown and Chapman, 1991](#); [Hillson, 1991, 2005](#)). For non-diagnostic bone fragments that could not be identified to specific taxa, classification by size classes was employed, following criteria established in previous studies ([Bunn, 1986](#); [Saladié et al., 2011](#); [Samper Carro et al., 2020](#)). The size



classes included size 1 (up to 100 kg; *Sus scrofa*, *Capra pyrenaica*, infantile *Cervus elaphus*), size 2 (100–300 kg; sub-adult and adult *C. elaphus*, infantile *Equus ferus* and *Equus hydruntinus*), size 3 (300–500 kg; sub-adult and adult *E. ferus* and *E. hydruntinus*), size 4 (500–800 kg; sub-adult and adult *Bos/Bison*), and size 5 (over 800 kg; Rhinocerotidae). It is important to note that the size classes excluded remains attributable to small prey, such as turtles and rabbits.

2.6 Age-at-death profiling

Age-at-death profiling was conducted to gain insights into the age composition of the faunal assemblages. This process involved the examination of tooth eruption and wear patterns, and epiphyseal fusion. This age-at-death profiling analysis was carried out following established methodologies and reference standards for age determination in extant mammalian species (Grant, 1982;

Brown and Chapman, 1991; Hillson, 2005; Greenfield and Arnold, 2008; Lemoine et al., 2014). Age categories include infantile (no epiphyseal fusion, deciduous teeth with no wear, incomplete tooth eruption sequence), juvenile (some epiphyseal fusion, deciduous teeth with minimal wear, eruption of first permanent teeth), immature/sub-adult (nearly complete epiphyseal fusion, loss of deciduous teeth, eruption of most permanent teeth with minimal wear), adult (complete epiphyseal fusion, eruption of all permanent teeth with some wear), and senile (presence of all permanent teeth with extreme wear). Skeletal indicators were compared with age categories defined based on the developmental stages of modern comparative species and known growth patterns of related taxa.

2.7 Bone modifications

Additionally, bone colour was documented to assess potential diagenetic alterations, including natural burning and manganese

staining (López-González et al., 2006; Marín Arroyo et al., 2008). The colour stages included stage 0 (no change to bone colour), stage 1 (black spots; manganese staining), stage 2 (brown; manganese staining), stage 3 (black; burning), stage 4 (grey and/or white; burning), and stage 5 (bluish white; burning). The identification of bone surface modifications, both anthropogenic and non-anthropogenic, was conducted through preliminary observations at 30× magnification, followed by more detailed examination at up to 80× magnification using a DinoLite microscope (AM4815-FJT Dino-Lite Edge). Anthropogenic modifications included butchery-related marks, such as incisions, scrapes, and chop marks, as well as intentional breakage through impact points and indirect percussion, following identification criteria previously published (e.g., Fisher, 1995; Fernández-Jalvo and Andrews, 2016). Furthermore, bone fracture angles, morphology, diaphysis length, and circumference were recorded following the methodology established by Villa and Mahieu (1991). The identification of burning considered the presence of colour changes, cracking, and shrinking (Nicholson, 1993; Stiner et al., 1995).

3 Results

3.1 Faunal assemblage preservation

The complete faunal assemblage from levels M and P of the Abric Pizarro rockshelter comprises a total of 246,913 fragments (NRT; the “complete assemblage”). Notably, a large proportion of these fragments (95.90%), were smaller than 2 cm, indicating a high fragmentation rate and the preservation integrity of the site. For the purpose of this study, only fragments larger than 2 cm were considered for taphonomic and taxonomic analysis (the “identifiable assemblage”; $n = 10,116$).

Bone preservation within the identifiable assemblage was generally characterised by the good integrity of cortical surfaces. Approximately 99.95% of the identifiable assemblage was found with sediment concretion, indicating favourable preservation conditions through the protection and stabilisation of cortical bone surfaces. Only a small proportion of the identifiable assemblage (0.06%) exhibited signs of abrasion.

Most fragments (86.72%) from the level M identifiable assemblage (n of level M identifiable fragments = 8,373) displayed a brown colouration. A dominance (71.37%) of bones from the level M identifiable assemblage also featured black spots, including on burned fragments. Within the level M identifiable assemblage, burning was observed on 11.44% of fragments. Similar patterns were observed in the level P identifiable assemblage (n of level P identifiable fragments = 1,743), with a dominance of bones (84.22%) exhibiting brown colouration, a significant portion (76.94%) of bones displaying black spots and burned remains contributing 10.90% to the assemblage.

In Level M, the burned faunal assemblage ($n = 958$ fragments) consists of 37.58% indeterminate bones and 62.42% identifiable bones. Fragments predominantly exhibit black colouration (70.67%), with lesser occurrences of grey (22.65%) and white (6.68%) hues. Among the burned assemblage, caprines and size 1 herbivores account for 4.59%, primarily represented by unidentifiable long bones alongside few humeri, isolated instances

a radius, femur, metacarpal, and metatarsal, and small, irregular bones like patellae. Cervids and size 2 herbivores are the most commonly occurring identifiable species, constituting 20.04% of the burned assemblage. These fragments predominantly feature long bones (primarily unidentifiable, though also including humeri, ulnae, radii, femora, tibiae, metapodials, and phalanges), as well as a few teeth and small bones such as sesamoids. Equids and size 3 herbivores contribute 3.77% to the burned assemblage, primarily represented by unidentifiable long bones with minimal instances of humeri, radii, and tibiae, with few teeth and an unidentifiable vertebra. Size 4 herbivores are exclusively represented by unidentifiable long bones, accounting for 0.42% of the burned assemblage. Size classes that defy definitive classification, such as size 1/2, 2/3, and 3/4 herbivores, account for 14.41%, 2.51%, and 0.84% of the burned assemblage, respectively, predominantly comprising unidentifiable long bones. Undiagnostic ungulates or mammals constitute 14.61% of the burned assemblage, primarily characterised by unidentifiable epiphyses and flat bones, with occasional cranial and mandibular elements, ribs, scapulae, and vertebrae represented.

In Level P, the burned faunal assemblage ($n = 190$ fragments) consists of 44.21% indeterminate bones and 55.79% identifiable bones. Over half of the fragments display a black coloration (55.27%), with lesser occurrences of grey (35.26%) and white hues (9.47%). Among the identifiable remains, caprines and size 1 herbivores account for 14.74% of the burned assemblage, primarily represented by unidentifiable long bones, along with isolated instances of a humerus, femur, and metapodial, and a few radii and teeth. Cervids and size 2 herbivores are again the most commonly occurring identifiable species, constituting 24.74% of the burned assemblage, predominantly represented by unidentifiable long bones, with some humeri, single instances of an ulna and tibia, and a few metapodials and isolated teeth. Equids and size 3 herbivores contribute 6.84% to the burned assemblage, primarily through isolated teeth, as well as a few femora, and single instances of a humerus, radius, tibia, and unidentified long bone. No size 4 herbivores are identified. Size 1/2 herbivores (4.74%), size 2/3 herbivores (0.53%), and size 3/4 herbivores (0.53%) are exclusively represented by unidentifiable long bones. Undiagnostic mammals account for 14.21% of the burned assemblage, primarily characterised by unidentifiable epiphyses, alongside a few ribs, unidentifiable flat bones, and teeth, and single instances of a mandible and dorsal vertebra.

3.2 Faunal assemblage composition

A relatively small number of specimens from both levels M and P ($n = 6,090$; 2.47% of the complete faunal assemblage), were confidently identified to taxa or size class (NR; i.e., excluding undefined and unidentified specimens). Despite the limited identification, the taxonomic composition of the faunal assemblage revealed a diverse array of fauna, with variations between the two archaeological units (Table 1).

In the level M identifiable assemblage, the faunal composition comprises 5.21% caprines and small-sized (size 1) herbivores (including *Capra pyrenaica*), 29.20% cervids and medium-sized

TABLE 1 NISP, MNE, and MNI of Abric Pizarro levels M and P faunal assemblage.

	M			P		
	NISP	MNE	MNI	NISP	MNE	MNI
<i>Rana rana</i>	0	0	0	1	1	1
Testudinae	201	8	2	35	2	1
<i>Talpa europaea</i>	1	1	1	0	0	0
Rodentia	1	1	1	0	0	0
<i>Oryctolagus cuniculus</i>	31	23	3	56	39	10
<i>Lepus europaeus</i>	11	10	3	3	3	1
Lagomorpha	24	17	4	0	0	0
<i>Lynx lynx</i>	1	1	1	0	0	0
Felidae	1	1	1	0	0	0
Hyaenidae	2	2	1	0	0	0
<i>Vulpes vulpes</i>	1	1	1	0	0	0
<i>Canis sp.</i>	1	1	1	0	0	0
Ursidae	6	5	2	0	0	0
Carnivora	6	5	1	0	0	0
<i>Sus scrofa</i>	6	6	1	3	3	1
<i>Cervus elaphus</i>	421	183	13	72	36	5
Cervidae	839	207	16	165	31	2
<i>Capra pyrenaica</i>	14	12	1	5	3	1
Caprinae	204	77	7	52	11	1
Large Bovinae (<i>Bos sp./Bison</i>)	16	6	1	7	6	2
Rhinocerotidae	3	2	1	1	1	1
<i>Equus ferus</i>	186	105	9	32	15	2
<i>Equus hydruntinus</i>	161	101	6	16	15	3
<i>Equus sp.</i>	213	33	3	57	9	1
Herbivore 1	218	–	–	157	–	–
Herbivore 2	1,185	–	–	253	–	–
Herbivore 3	189	–	–	21	–	–
Herbivore 4	46	–	–	12	–	–
Herbivore 5	1	–	–	0	–	–
Herbivore 1/2	717	–	–	71	–	–
Herbivore 2/3	260	–	–	25	–	–
Herbivore 3/4	70	–	–	9	–	–
Undefined ungulate	144	–	–	4	–	–
Undefined mammal	1,404	–	–	240	–	–
Aves sp.	1	1	1	0	0	0
Unidentified	1,788	–	–	446	–	–
Unidentified <2 cm	153,109	–	–	83,694	–	–
Total	161,475	968	98	85,438	195	42

(size 2) herbivores, 8.94% equids and large-sized (size 3) herbivores, and 0.74% large bovids and very large-sized (size 4) herbivores. However, certain fragments could not be confidently assigned to

a single size class, resulting in 8.56% being categorised as size 1/2 herbivores, 3.10% as size 2/3 herbivores, and 0.84% as size 3/4 herbivores. Other species including moles, rodents, lynx, wild

TABLE 2 Age-at-death determinations for caprines/size 1 herbivores, cervids/size 2 herbivores, and equids/size 3 herbivores from Abric Pizarro levels M and P.

	Level M			Level P		
	Caprines and size 1 herbivores	Cervids and size 2 herbivores	Equids and size 3 herbivores	Caprines and size 1 herbivores	Cervids and size 2 herbivores	Equids and size 3 herbivores
Infant	4	8	2	0	0	0
Juvenile	17	125	142	3	13	16
Immature	1	2	8	0	0	0
Adult	2	4	5	0	0	4
Senile	2	5	8	1	3	2
Total	26	144	165	4	16	22

cats, hyenas, foxes, canids, bears, undefined carnivores, wild boars, rhinoceros, very large (size 5) herbivores and birds constituted only 0.37% of the level M identifiable assemblage.

Similarly, in the level P identifiable assemblage, the faunal composition includes 12.28% caprines and small-sized (size 1) herbivores, 28.11% cervids and medium-sized (size 2) herbivores, 7.23% equids and large-sized (size 3) herbivores, and 1.09% large bovines and very large-sized (size 4) herbivores. As in level M, some fragments in level P could not be confidently assigned to a single size class, with 4.07% being designated as size 1/2 herbivores, 1.43% as size 2/3 herbivores, and 0.52% as size 3/4 herbivores. Other species, including frogs, wild boar, and rhinoceros, constituted only 0.29% of the level P identifiable assemblage. No carnivores were identified in this unit.

3.3 Age-at-death determination

The prevailing composition of the assemblage is characterised by highly fragmented long and flat bone fragments, which impeded precise determinations of age-at-death for most specimens. To mitigate this challenge and gain insights into the age structure of the assemblage, comparisons were undertaken with a subset of material from several taxa (caprines and size 1 herbivores, cervids and size 2 herbivores, and equids and size 3 herbivores) that permitted reliable age-at-death identifications ($n = 377$; Table 2). This subset comprised isolated teeth exhibiting preserved dentine, complete and nearly complete mandibles demonstrating tooth eruption sequences, as well as long bones and epiphyses displaying discernible fusion rates. Within this subset, a notable proportion (83.82%) comprised juveniles, constituting 84.78% of the Level M subset and 76.19% of the Level P subset.

When considering the subset of material permitting age-at-death determinations to the larger identifiable assemblage of Level M, the mortality profiles indicate minimal representation of infants (0.17%), a modest presence of juveniles (3.39%), a marginal presence of immature individuals (0.13%) and adults (0.13%), and a nominal presence of senile individuals (0.18%). In contrast, consideration with the identifiable assemblage of Level P exhibited

a distinct composition with 1.84% juveniles, 0.23% adults, and 0.34% senile individuals.

The cumulative age-at-death determinations derived from the subset of material allowing for demographic analysis reveal a notable predominance of juveniles compared to other age categories, particularly evident within Level M. However, the extensive fragmentation observed in the complete faunal assemblage results in the majority of specimens being classified as 'unknown' in terms of age-at-death. Consequently, this poses a significant challenge in comprehensively assessing mortality profiles, necessitating a cautious interpretation of these findings.

3.4 Skeletal profiles

Skeletal profiles of the most abundant prey species (i.e., caprines; *C. elaphus*, Cervidae; *E. ferus*, *E. hydruntinus*, *Equus* sp.), were documented for each archaeological level using MNE and %MAU calculations for each skeletal element within taxa (Table 3; Figure 3). In level M, size 1 herbivores exhibit representation by teeth, mandibles, vertebrae, scapulae, humeri, radii, ulnae, pelvises, femora, patellae, tibiae, metapodials, and phalanges, with humeri and femora being the most well-represented elements. Similarly, size 2 herbivores are represented by teeth, mandibles, scapulae, humeri, radii, ulnae, femora, tibiae, metapodials, and sesamoids, with metatarsals and tibiae among the most well-represented elements. Size 3 herbivores in Level M are represented by teeth, mandibles, vertebrae, ribs, scapulae, humeri, radii, ulnae, pelvises, femora, tibiae, metapodials, and phalanges, with humeri and femora being most abundant.

In Level P, size 1 herbivores are represented by a narrower range of bones, including mandibles, vertebrae, humeri, radii, femora, tibiae, and metapodials, with a relatively even representation across all bones. Size 2 herbivores are represented by the same skeletal elements as in Level M, with femora and metatarsals being most well-represented. Size 3 herbivores in Level P exhibit a reduced representation compared to Level M, including humeri, radii, ulnae, pelvises, femora, tibiae, metapodials, and phalanges, with humeri being the most abundant element as observed in Level M.

TABLE 3 MNE and %MAU for key Neanderthal prey species from Abric Pizarro levels M and P.

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
<i>Capra pyrenaica</i>	Maxilla	1	0.13	–	–
	Upper second molar	1	0.26	–	–
	Mandible	2	0.52	–	–
	Lower fourth premolar	–	–	1	0.13
	Lower third molar	1	0.13	–	–
	Incisor/canine (indeterminate)	1	0.02	–	–
	Humerus	1	0.13	–	–
	Radius	1	0.13	1	0.13
	Capitate	1	0.13	–	–
	Semilunar	1	0.13	–	–
	Femur	1	0.13	1	0.13
	Tibia	1	0.13	–	–
Caprinae	Upper first premolar	1	0.13	–	–
	Upper third premolar	3	0.26	1	0.13
	Upper fourth premolar	2	0.13	–	–
	Upper premolar (indeterminate)	2	0.04	–	–
	Upper second molar	2	0.13	–	–
	Mandible	1	0.26	1	0.26
	Lower second premolar	1	0.13	–	–
	Lower third premolar	2	0.13	–	–
	Lower fourth premolar	4	0.26	–	–
	Lower premolar (indeterminate)	–	–	1	0.04
	Lower first molar	2	0.13	–	–
	Lower second molar	8	0.52	–	–
	Lower third molar	3	0.26	–	–
	Lower molar (indeterminate)	–	–	1	0.04
	Incisor (indeterminate)	–	–	–	–
	Cervical vertebra	1	0.04	–	–
	Scapula	1	0.13	–	–
	Humerus	15	1.03	1	0.13
	Ulna	1	0.13	–	–
	Radius	2	0.13	1	0.13
	Metacarpal	2	0.13	1	0.13
	Scaphoid	1	0.13	–	–
	Pelvis	1	0.13	–	–
	Dorsal vertebra	–	–	1	0.04
	Femur	10	0.65	1	0.13
	Patella	3	0.26	–	–
	Tibia	3	0.13	1	0.13
	Metatarsal	1	0.13	1	0.13
First phalanx	2	0.03	–	–	

(Continued)

TABLE 3 (Continued)

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
	Second phalanx	2	0.03	–	–
	Third phalanx	1	0.03	–	–
<i>Cervus elaphus</i>	Antler	1	0.13	–	–
	Petrous	–	–	1	0.13
	Maxilla	10	0.65	–	–
	Upper canine	3	0.26	–	–
	Upper second premolar	7	0.52	–	–
	Upper third premolar	7	0.52	–	–
	Upper fourth premolar	1	0.13	–	–
	Upper premolar (indeterminate)	2	0.04	1	0.04
	Upper first molar	4	0.26	–	–
	Upper second molar	3	0.26	–	–
	Upper molar (indeterminate)	6	0.04	–	–
	Mandible	12	3.10	1	0.26
	Lower first incisor	6	0.39	1	0.13
	Lower second incisor	6	0.39	–	–
	Lower third incisor	3	0.26	1	0.13
	Lower canine	2	0.13	1	0.13
	Lower second premolar	4	0.26	–	–
	Lower third premolar	1	0.13	1	0.13
	Lower fourth premolar	9	0.65	–	–
	Lower premolar (indeterminate)	3	0.04	–	–
	Lower first molar	9	0.65	–	–
	Lower second molar	5	0.39	–	–
	Lower third molar	7	0.52	–	–
	Lower molar (indeterminate)	–	–	1	0.04
	Scapula	1	0.13	1	0.13
	Humerus	2	0.13	3	0.26
	Ulna	2	0.13	1	0.13
	Radius	2	0.13	1	0.13
	Metacarpal	7	0.52	1	0.13
	Capitate	1	0.13	–	–
	Scaphoid	1	0.13	–	–
	Dorsal vertebra	4	0.04	–	–
	Sacrum	1	0.26	–	–
Femur	4	0.26	1	0.13	
Tibia	3	0.26	6	0.39	
Metatarsal	13	0.90	5	0.39	
Large sesamoid	1	0.13	8	0.52	
Small sesamoid	1	0.06	1	0.06	
Astragalus	5	0.39	–	–	

(Continued)

TABLE 3 (Continued)

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
	Calcaneus	1	0.13	–	–
	First phalanx	12	0.06	–	–
	Second phalanx	10	0.06	–	–
	Third phalanx	1	0.03	–	–
Cervidae	Antler	1	0.13	–	–
	Cranium (indeterminate)	1	0.03	–	–
	Petrous	2	0.13	1	0.13
	Upper third premolar	1	0.13	–	–
	Upper molar (indeterminate)	4	0.04	–	–
	Mandible	3	0.78	1	0.26
	Lower first incisor	3	0.26	1	0.13
	Lower third incisor	1	0.13	1	0.13
	Lower incisor (indeterminate)	2	0.04	–	–
	Lower canine	2	0.13	1	0.13
	Lower second premolar	1	0.13	–	–
	Lower third premolar	2	0.13	1	0.13
	Lower fourth premolar	3	0.26	–	–
	Lower first molar	2	0.13	–	–
	Incisor (indeterminate)	1	0.06	–	–
	Molar (indeterminate)	–	–	1	0.02
	Scapula	1	0.13	1	0.13
	Humerus	33	2.20	3	0.26
	Radius	11	0.78	1	0.13
	Ulna	4	0.26	1	0.13
	Metacarpal	8	0.52	1	0.13
	Capitate	1	0.13	–	–
	Hamate	3	0.26	–	–
	Dorsal vertebra	1	0.13	–	–
	Pelvis	3	0.78	–	–
	Sacrum	1	0.26	–	–
	Femur	12	0.78	1	0.13
	Tibia	27	1.81	2	0.13
	Metatarsal	9	0.65	5	0.39
	Metapodial	19	0.65	–	–
	Large sesamoid	2	0.13	8	0.52
	Small sesamoid	11	0.19	1	0.06
	Cuboidnavicular	1	0.13	–	–
	Calcaneus	1	0.13	–	–
First phalanx	17	0.10	–	–	
Second phalanx	7	0.03	–	–	
Third phalanx	6	0.03	–	–	

(Continued)

TABLE 3 (Continued)

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
<i>Equus ferus</i>	Maxilla	1	0.13	–	–
	Upper third incisor	2	0.13	–	–
	Upper second premolar	2	0.13	–	–
	Upper premolar (indeterminate)	20	0.17	3	0.04
	Upper first molar	1	0.13	–	–
	Mandible	1	0.26	–	–
	Lower first incisor	2	0.13	–	–
	Lower second incisor	6	0.39	–	–
	Lower third incisor	2	0.13	–	–
	Lower incisor (indeterminate)	5	0.04	1	0.04
	Lower second premolar	10	0.65	–	–
	Lower third premolar	5	0.39	1	0.13
	Lower fourth premolar	1	0.13	–	–
	Lower premolar (indeterminate)	14	0.13	1	0.04
	Lower first molar	2	0.13	–	–
	Lower second molar	1	0.13	–	–
	Lower third molar	11	0.78	–	–
	Lower molar (indeterminate)	1	0.04	–	–
	Incisor (indeterminate)	1	0.04	–	–
	Humerus	2	0.13	3	0.26
	Ulna	3	0.26	1	0.13
	Radius	5	0.39	1	0.13
	Metacarpal	1	0.13	–	–
	Femur	2	0.13	1	0.13
Tibia	2	0.13	1	0.13	
Metapodial	–	–	1	0.06	
First phalanx	2	0.03	–	–	
Second phalanx	–	–	1	0.03	
<i>Equus hydruntinus</i>	Cranium	1	0.03	–	–
	Maxilla	2	0.26	–	–
	Upper second incisor	1	0.13	–	–
	Upper third incisor	3	0.26	–	–
	Upper first premolar	1	0.13	–	–
	Upper premolar (indeterminate)	9	0.09	1	0.04
	Upper first molar	3	0.26	–	–
	Upper third molar	6	0.39	–	–
	Upper molar (indeterminate)	9	0.09	–	–
	Mandible	4	1.03	–	–
	Lower first incisor	3	0.26	–	–
	Lower second incisor	1	0.13	–	–
	Lower second premolar	8	0.52	–	–

(Continued)

TABLE 3 (Continued)

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
	Lower third premolar	2	0.13	–	–
	Lower fourth premolar	1	0.13	–	–
	Lower premolar (indeterminate)	4	0.04	2	0.04
	Lower third molar	3	0.26	–	–
	Lower molar (indeterminate)	5	0.04	–	–
	Premolar/molar (indeterminate)	1	0.01	–	–
	Atlas	1	0.26	–	–
	Cervical vertebra	1	0.04	–	–
	Scapula	2	0.13	–	–
	Humerus	9	0.65	3	0.26
	Ulna	3	0.26	1	0.13
	Radius	2	0.13	2	0.13
	Metacarpal	1	0.13	–	–
	Dorsal vertebra	1	0.04	–	–
	Femur	3	0.26	2	0.13
	Tibia	3	0.26	1	0.13
	Metatarsal	1	0.13	–	–
	Metapodial	1	0.06	1	0.06
	Calcaneus	1	0.13	–	–
	First phalanx	2	0.06	–	–
	Second Phalanx	2	0.06	2	0.06
	Third phalanx	1	0.06	–	–
<i>Equus</i> sp.	Petrous	2	0.13	1	0.13
	Upper third incisor	1	0.13	–	–
	Mandible	2	0.52	–	–
	Lower incisor (indeterminate)	2	0.04	–	–
	Lower third incisor	1	0.13	–	–
	Lower premolar (indeterminate)	2	0.04	–	–
	Canine (indeterminate)	1	0.06	–	–
	Incisor (indeterminate)	–	–	1	0.02
	Premolar (indeterminate)	–	–	1	0.02
	Scapula	2	0.13	–	–
	Humerus	4	0.26	1	0.13
	Ulna	1	0.13	–	–
	Radius	1	0.13	1	0.13
	Metacarpal	1	0.13	–	–
	Metatarsal	1	0.13	–	–
	Rib	1	0.01	–	–
	Pelvis	1	0.02	1	0.02
	Dorsal vertebra	1	0.04	–	–
	Femur	2	0.13	1	0.13

(Continued)

TABLE 3 (Continued)

Taxon	Element	Level M		Level P	
		MNE	%MAU	MNE	%MAU
	Tibia	4	0.26	1	0.13
	First phalanx	1	0.06	–	–
	Second phalanx	1	0.06	–	–
	Third phalanx	1	0.06	–	–
	Phalanx (indeterminate)	–	–	1	0.02

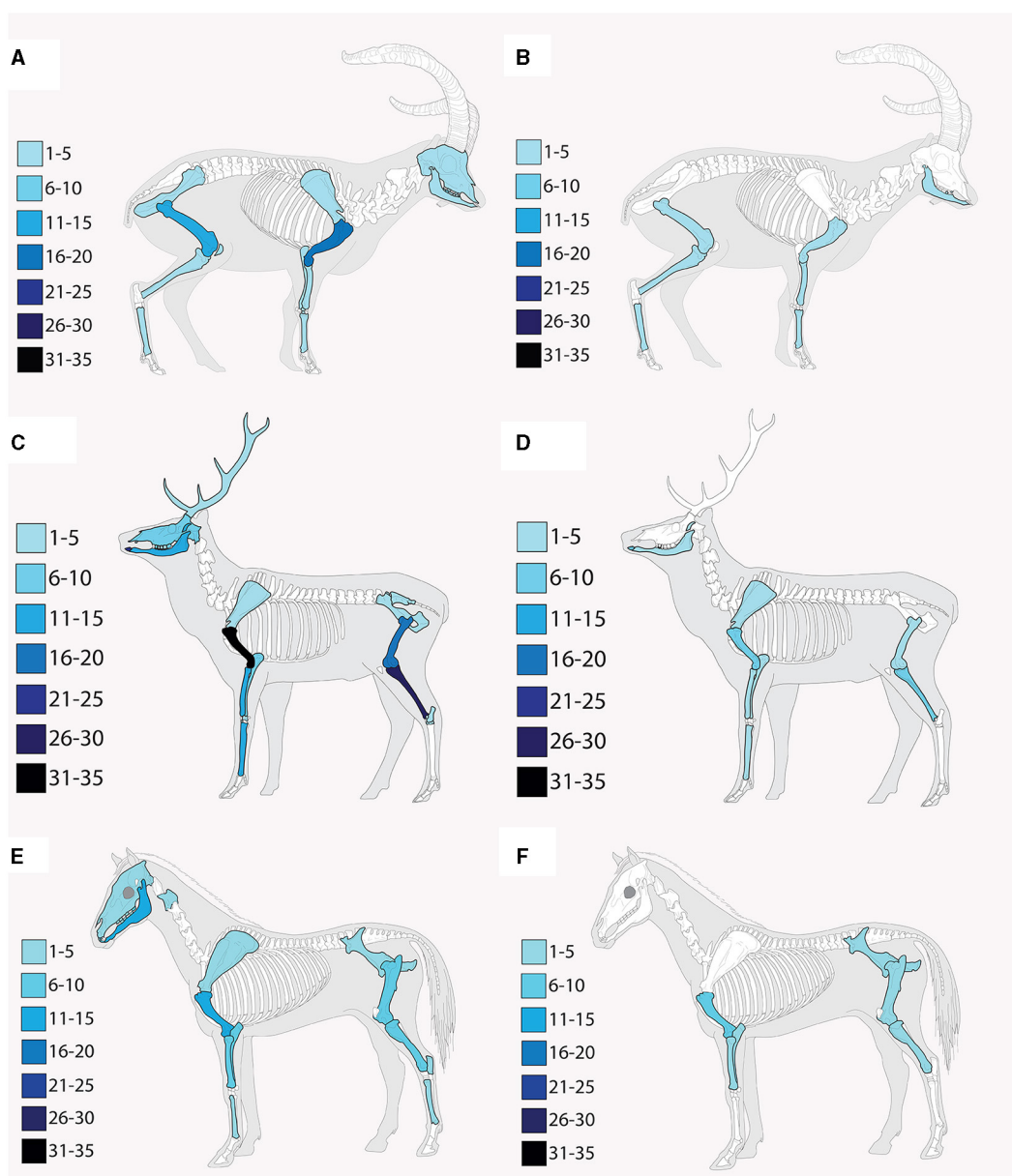


FIGURE 3

Skeletal profiles based on the MNE of the dominant hunted prey species at Abric Pizarro. (A) Level M caprines, (B) Level P caprines, (C) Level M cervids, (D) Level P cervids, (E) Level M equids, (F) Level P equids. Skeletal representations are based exclusively on identifiable remains, excluding indeterminate elements that cannot be confidently attributed to specific anatomical features (such as indeterminate teeth, cranial fragments, and metapodials, unnumbered vertebrae and ribs, and phalanges and sesamoids that cannot be assigned to the front or rear of the skeleton).

3.5 Breakage patterns

Long bones from each archaeological unit demonstrated varying shaft lengths and circumferences. In level M (n of level M long bones = 3,748), only 3.33% of shafts were complete in length. Rather, there was a dominance (53.69%) of shafts less than half of their original length, while 42.98% of shafts were more than half of their original length. Similarly, there was a marginal portion of shafts with complete circumference (1.28%) and of shafts with more than half of their original circumference (1.14%). Instead, most (97.58%) long bone shaft circumferences were less than half of their original circumference.

A similar pattern of long bone completeness was observed in the level P long bone assemblage (n of level P long bones = 799). A marginal percentage (4.95%) of shafts were complete in length, with most (62.83%) shaft lengths less than half of their original length, and some (32.22%) shafts more than half of their original length. Echoing this, complete shaft circumferences accounted for 3.07% of the long bone assemblage and shafts with more than half of their original circumference accounted for 1.07% of the long bone assemblage. The majority (95.86%) of level P long bones had shafts with less than half of their original circumference.

Distinct trends of bone fracture morphology were observed on long bones and epiphyses from both archaeological units. In level M (n of level M long bones and epiphyses = 4,261), spiral fracturing affected 97.75% of long bones and epiphyses. Irregular breakage was observed on 8.11% of bones. Transversal (3.44%) and V-shaped (1.30%) bone morphology contributed marginally to breakage patterns. A similar trend was observed in level P (n of level P long bones and epiphyses = 893), with a dominance (99.73%) of spiral fractures, marginal transversal (0.27%) and irregular (0.27%) breakage, and no V-shaped morphology.

Orthogonal bone morphology, as defined by the presence of right angles or sharp breaks on the cortical surface, was observed in 21.91% of the long bones and epiphyses contributing to the identifiable assemblage (n of level M and level P long bones and epiphyses = 5,154). Orthogonal bone morphology was slightly more pronounced in level P, accounting for 35.72% of the level P long bones and epiphyses, while affecting 26.50% of the level M long bones and epiphyses.

3.6 Non-anthropogenic bone surface modifications

Very few remains demonstrated non-anthropogenic bone surface modifications. Amongst the level M faunal assemblage, tooth pits from medium-sized carnivores were observed on 0.05% ($n = 4$) of the identifiable assemblage, affecting one *C. elaphus* second phalanx, a single Cervidae metacarpal and tibia, and two mammal epiphyses. Evidence of digestion, including crenulated edges, was observed on two size 2 herbivore long bone fragments, impacting 0.02% of the identifiable assemblage. Marks from rodent scavenging were additionally identified an Equidae humerus and a mammal epiphysis (0.02% of the level M identifiable assemblage).

Tooth pitting from medium-sized carnivores was the only non-anthropogenic modification observed within the level P faunal

assemblage, affecting a *C. elaphus* tibia, two size 2 herbivore long bone fragments, and a mammal epiphysis (0.23% of the level P identifiable assemblage).

3.7 Anthropogenic bone surface modifications

Anthropic bone surface modifications were documented in both levels M and P of the identifiable assemblage, encompassing a variety of features such as incisions, scrapes, chop marks, and direct (impact points and notches) and indirect percussion (Table 4; Figure 4). These modifications are primarily concentrated to undiagnostic fragments and unidentifiable herbivore long bones. However, other prime meat- and marrow-bearing portions (i.e., long bones, epiphyses, phalanges, and mandibles) from key prey species (i.e., caprids, cervids, and equids) are also well represented.

In the level M identifiable assemblage, 2.70% of bones displayed incisions, while 1.35% exhibited scrapes. Incisions were predominantly observed on unidentifiable long bone fragments (1.04%) from all sized herbivores and undiagnostic bone fragments (0.51%). Identifiable long bones with slicing marks include humeri (0.19%), radii (0.04%), a single tibia (0.01%), and metapodials (0.14%). Epiphyses (0.19%) were also affected by slicing marks. Several flat bones exhibited incisions, including crania (0.05%), mandibles (0.04%), scapulae (0.04%), ribs (0.06%), a single pelvis (0.01%), and unidentifiable flat bones (0.18%). Several vertebrae additionally demonstrated incisions (0.10%). Scrapes were similarly observed primarily on unidentifiable long bone fragments (0.47%) and non-diagnostic bone fragments (0.27%). Within the identifiable assemblage, scrapes impacted humeri (0.12%), a single radius (0.01%), a single femur (0.01%), tibiae (0.02%), metapodials (0.11%), a single mandible (0.01%), scapulae (0.02%), a single rib (0.01%), a single phalange (0.01%), epiphyses (0.14%), and unidentifiable flat bones (0.08%).

Chop marks were rare, affecting only 0.16% of bones in level M. Chop marks were identified on humeri (0.02%), a single metatarsal (0.01%), a single rib (0.01%), a single vertebra (0.01%), a single epiphysis (0.01%), unidentifiable long bones (0.06%), and unidentifiable flat bones (0.02%).

Direct percussion, represented by impact points and notches affected 2.53% of bones, and indirect percussion was observed on 3.12% of bones. Again, direct percussion is predominantly focused on unidentifiable long bones (0.90%) and undiagnostic bone fragments (0.55%). Identifiable long bones exhibiting direct percussion include humeri (0.11%), ulnae (0.02%), radii (0.04%), a single femur (0.01%), and metapodials (0.20%). Directly percussed epiphyses were also noted (0.18%). Flat bones exhibiting direct percussion are mostly unidentifiable (0.23%), though also include a single cranial fragment (0.01%), mandibles (0.02%), and ribs (0.08%). Other bones contributing to directly percussed elements include vertebrae (0.04%), phalanges (0.05%), and a single carpal (0.01%). Following the observed trend, indirect percussion is concentrated to unidentifiable long bones (1.03%) and non-diagnostic fragments (0.70%). Identifiable long bones with evidence of indirect percussion include humeri (0.14%), ulnae (0.02%), radii (0.04%), femora (0.04%), tibiae (0.02%), and

TABLE 4 Anthropogenic modifications identified on the Abric Pizarro levels M and P faunal material.

Species	Skeletal element	Modifications	Level M modification count	Level P modification count
<i>Oryctolagus cuniculus</i>	Cranium	Slicing	–	1
	Mandible	Slicing	1	1
		Scraping	–	1
	Tibia	Slicing	–	1
	Long bone	Slicing	–	1
<i>Lepus europaeus</i>	Dorsal vertebra	Slicing	1	–
Lagomorpha	Long bone	Slicing	1	–
Testudinae	Carapace	Slicing	9	3
		Scraping	3	–
		Impact point	5	–
		Notch	2	–
<i>Sus scrofa</i>	Second phalanx	Indirect percussion	1	–
<i>Capra pyrenaica</i>	Radius	Slicing	1	1
	Carpal	Notch	1	–
Caprinae	Humerus	Slicing	2	1
		Scraping	1	–
		Impact point	2	3
		Indirect percussion	2	–
	Radius	Slicing	–	1
		Indirect percussion	1	–
	Pelvis	Slicing	1	–
	Femur	Slicing	–	1
		Notch	1	–
		Indirect percussion	1	–
	Cervical vertebra	Impact point	1	–
	First phalanx	Notch	1	–
<i>Cervus elaphus</i>	Cranium	Indirect percussion	1	–
	Mandible	Slicing	1	–
		Indirect percussion	2	–
	Humerus	Slicing	1	1
		Notch	1	–
	Metacarpal	Slicing	1	–
		Impact point	1	–
	Pelvis	Notch	–	1
	Tibia	Slicing	–	1
		Scraping	1	–
	Metatarsal	Scraping	1	–
		Notch	1	–
		Indirect percussion	1	–
	Calcaneus	Indirect percussion	1	–
	First phalanx	Impact point	2	–
	Second phalanx	Indirect percussion	1	–

(Continued)

TABLE 4 (Continued)

Species	Skeletal element	Modifications	Level M modification count	Level P modification count
Cervidae	Mandible	Scraping	1	-
		Impact point	1	-
	Humerus	Slicing	6	-
		Scraping	4	1
		Chop mark	1	-
		Impact point	2	-
		Notch	2	1
		Indirect percussion	4	-
		Radius	Slicing	2
	Notch		1	-
	Indirect percussion		2	-
	Metacarpal	Slicing	2	2
		Scraping	1	-
		Impact point	4	-
		Notch	1	-
		Indirect percussion	4	-
	Femur	Slicing	-	1
		Indirect percussion	1	-
	Tibia	Slicing	1	1
		Scraping	1	-
		Impact point	-	1
	Metatarsal	Slicing	8	3
		Scraping	-	2
		Chop Mark	1	-
		Scraping	5	-
		Impact point	4	1
		Notch	2	-
		Indirect percussion	11	-
	Metapodial	Slicing	-	1
		Scraping	1	-
		Impact point	3	-
		Notch	1	-
		Indirect percussion	2	-
Dorsal vertebra	Slicing	1	-	
First phalanx	Scraping	1	-	
	Indirect percussion	3	-	
Second phalanx	Impact point	1	-	
	Indirect percussion	1	-	
Third phalanx	Indirect percussion	3	-	
<i>Equus asinus</i>	Mandible	Slicing	1	-
	Humerus	Indirect percussion	1	-
	Radius	Notch	1	-

(Continued)

TABLE 4 (Continued)

Species	Skeletal element	Modifications	Level M modification count	Level P modification count
<i>Equus caballus</i>	Scapula	Slicing	1	-
		Scraping	1	-
	Humerus	Slicing	1	-
		Scraping	1	-
		Notch	1	-
		Indirect percussion	2	-
	Ulna	Impact point	1	-
	Radius	Scraping	1	1
		Notch	1	-
	Femur	Slicing	-	1
		Notch	-	1
		Indirect percussion	1	-
	Cervical vertebra	Notch	1	-
	Dorsal vertebra	Slicing	1	-
Vertebra	Slicing	1	-	
Equidae	Humerus	Slicing	1	-
		Scraping	1	-
		Indirect percussion	2	1
	Ulna	Impact point	1	-
		Indirect percussion	1	-
	Femur	Scraping	1	-
	Tibia	Indirect percussion	1	-
Rhinocerotidae	Cranium	Slicing	-	1
Size 1 herbivore	Long bone	Slicing	10	13
		Scraping	5	4
		Impact point	3	1
		Notch	4	5
		Indirect percussion	1	-
Size 2 herbivore	Long bone	Slicing	35	21
		Scraping	17	8
		Chop mark	1	-
		Impact point	28	2
		Notch	12	5
		Indirect percussion	42	-
Size 3 herbivore	Long bone	Slicing	5	1
		Scraping	2	-
		Impact point	3	2
		Notch	3	-
		Indirect percussion	4	-
Size 4 herbivore	Long bone	Slicing	3	1
		Scraping	1	-
		Impact point	-	1

(Continued)

TABLE 4 (Continued)

Species	Skeletal element	Modifications	Level M modification count	Level P modification count
Herb 1/2 herbivore	Long bone	Notch	2	-
		Slicing	24	4
		Scraping	14	-
		Chop mark	3	-
		Impact point	4	2
		Notch	6	2
Size 2/3 herbivore	Long bone	Indirect percussion	27	-
		Slicing	6	1
		Scraping	3	-
		Chop mark	1	-
		Impact point	5	1
		Notch	3	-
Size 3/4 herbivore	Long bone	Indirect percussion	9	-
		Slicing	7	-
		Scraping	1	1
		Impact point	2	-
		Notch	1	-
Mammal	Cranium	Indirect percussion	2	-
		Slicing	4	1
	Mandible	Notch	1	-
		Indirect percussion	3	-
		Impact point	1	-
	Scapula	Indirect percussion	3	1
		Slicing	2	-
		Scraping	1	-
	Long bone	Indirect percussion	5	-
		Slicing	1	-
	Rib	Indirect percussion	1	-
		Slicing	5	5
		Scraping	1	1
		Chop mark	1	-
		Impact point	6	1
		Notch	1	-
	Cervical vertebra	Indirect percussion	12	-
		Indirect percussion	1	-
	Dorsal vertebra	Impact point	1	-
		Indirect percussion	1	-
	Vertebra	Slicing	4	-
		Chop mark	1	-
	Epiphysis	Slicing	16	8
		Scraping	12	-
Chop mark		1	-	

(Continued)

TABLE 4 (Continued)

Species	Skeletal element	Modifications	Level M modification count	Level P modification count
	Flat bone	Impact point	10	1
		Notch	5	5
		Indirect percussion	52	1
		Slicing	15	2
		Scraping	7	1
		Chop mark	2	–
		Impact point	10	2
		Notch	9	–
Unidentifiable	Unidentifiable	Indirect Percussion	10	–
		Slicing	43	33
		Scraping	24	3
		Chop mark	1	–
		Impact point	30	8
		Notch	16	14
		Indirect percussion	59	–

metapodials (0.24%). A similar proportion (0.19%) of indirectly percussed epiphyses was noted to that of directly percussed epiphyses. Indirectly percussed flat bones include cranial fragments (0.05%), mandibles (0.06%), scapulae (0.08%), ribs (0.14%), and unidentifiable long bones (0.12%). Other indirectly percussed skeletal elements include vertebrae (0.02%), phalanges (0.10%), and a single calcaneus (0.01%).

In the level P identifiable assemblage, the incidence of anthropic bone surface modifications was notably varied from that of level M. Incisions were found on 6.43% of bones, and scrapes affected 1.32% of bones. Similar to level M, incisions primarily impacted unidentifiable long bones from all herbivore sizes (2.41%) and non-diagnostic fragments (1.89%). Identifiable long bones demonstrating slicing marks include a single humerus (0.01%), radii (0.11%), femora (0.17%), tibiae (0.17%), and metapodials (0.34%). Incised epiphyses account for 0.46% of the identifiable assemblage. Flat bones affected by incisions include cranial fragments (0.17%), a single mandible (0.01%), ribs (0.29%), and unidentifiable long bones (0.15%). Scraping was primarily noted on unidentifiable long bones (0.75%), though was also observed on a single humerus (0.01%), a single radius (0.01%), metatarsals (0.11%), a single mandible (0.01%), a single rib (0.01%), a single unidentifiable flat bone (0.01%), and undiagnostic fragments (0.17%). No chop marks were identified in this level.

Direct percussion within level P was documented on 3.50% of bones, while indirect percussion was observed on a smaller proportion, affecting only 0.17% of bones. Mimicking the pattern observed throughout both archaeological strata, direct percussion primarily impacts unidentifiable long bones from size 1 through size 3 herbivores (1.38%) and non-diagnostic fragments (1.09%). Epiphyses and undiagnostic flat bones contribute 0.34 and 0.11%, respectively, to the modified identifiable assemblage. Directly percussed identifiable elements include humeri (0.29%), a single

femur (0.01%), a single tibia (0.01%), a single metatarsal (0.01%), a single rib (0.01%), and a single pelvis (0.01%). Indirectly percussed elements include an equid humerus (0.01%), a mammal mandible (0.01%), and a mammal epiphysis (0.01%).

4 Discussion

The Abric Pizarro rockshelter, situated in the Pre-Pyrenean region, presents a unique opportunity to investigate Neanderthal resilience and adaptability during the climatically challenging period of MIS 4. Traditionally, this period, characterised by extreme aridity and changing landscapes, has been considered unsuitable for Neanderthal occupation (d'Errico and Sánchez Goñi, 2003; Fernández-García et al., 2023). However, the zooarchaeological analysis of faunal remains from levels M and P at Abric Pizarro provides compelling data that challenge these assumptions and sheds light on Neanderthal hunting and butchery behaviours, as well as their ability to exploit diverse dietary resources.

4.1 Site formation and occupation processes

It is worth noting the disparity in the number of bones between levels M and P at Abric Pizarro. Level M represents a palimpsest with a depth of ~80 cm, contributing to a larger quantity of bones, whereas Level P constitutes a more discrete unit, with a depth of only 5–10 cm. Given the extensive deposition over thousands of years, it becomes challenging to formulate hypotheses regarding site use or seasonality. Observations from numerous other sites within the same spatiotemporal region, including Covalejos Cave (Sánchez-Hernández et al., 2019), Cova Gran de Santa Linya

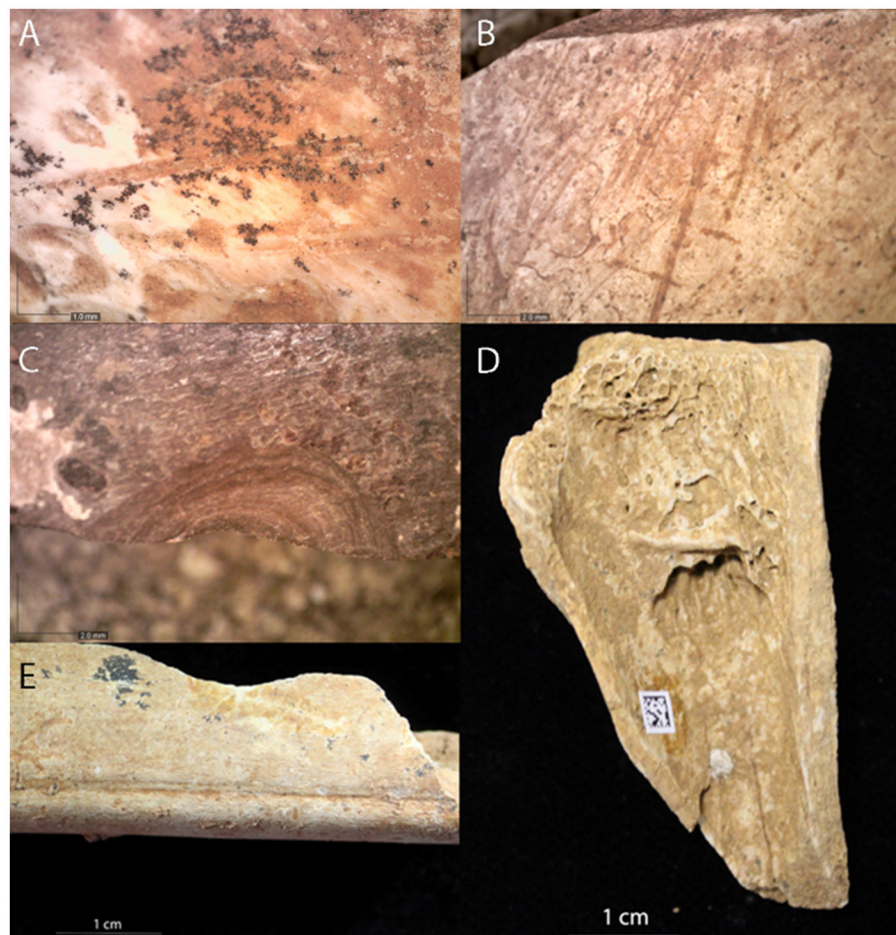


FIGURE 4

Examples of anthropogenic bone surface modifications identified within the Abric Pizarro faunal assemblage. (A) Slicing marks on *Cervus elaphus* radius, (B) scraping marks on size 2 herbivore long bone, (C) indirect percussion on Caprinae humerus, (D), orthogonal bone breakage of Cervidae radius, (E) direct percussion on *Cervus elaphus* metacarpal.

(Samper Carro et al., 2020), Abric Romaní (Fernández-Laso et al., 2010; Rosell et al., 2012), Cueva del Esquilieu (Yravedra Sáinz de los Terreros et al., 2014), El Castillo (Pike-Tay et al., 1999), Pié Lombard (Texier et al., 2011), and Abri du Maras (Daujeard et al., 2019; Moncel et al., 2021) indicate a general pattern of seasonal site use. However, the highly fragmented nature of the assemblage, along with potential biases in conducting age-at-death determinations, such as the greater ease in identifying very young individuals, presents challenges in confidently assessing occupation patterns at Abric Pizarro.

Levels M and P at Abric Pizarro exhibit a conspicuous abundance of Neanderthal-deposited prey species, coupled with a notably limited presence of carnivore remains. Moreover, these strata are delineated by culturally sterile layers. The conspicuous dearth of carnivore remains observed in comparison to other sites in Spain, such as Abric Romaní (Rosell et al., 2012, 2019), L'Arbreda Cave (Estévez, 1987; Lloveras et al., 2010), and Moros de Gabasa (Blasco, 1995, 1997; Blasco Sancho and Montes Ramírez, 1997), underscores the exceptional nature of the faunal assemblage at Abric Pizarro. In contrast to these sites, where the percentage of carnivore remains is considerably higher, Abric Pizarro and its neighbouring sites, including Cova Gran de Santa Linya and

Roca dels Bous (Benito-Calvo et al., 2020; Samper Carro et al., 2020), exhibit a significantly lower prevalence of carnivore remains. While the prevalence of carnivore remains at Moros de Gabasa is attributed to its general function as a hyena den (Blasco Sancho and Montes Ramírez, 1997), the relatively high number of carnivores at Abric Romaní and L'Arbreda Cave are attributable to alternating periods of occupation between carnivores and hominins (Estévez, 1987; Lloveras et al., 2010; Rosell et al., 2012). As such, the carnivore remains are often found independent of the archaeological levels in which the hominin prey species are observed (Estévez, 1987; Rosell et al., 2012). Moreover, the occurrence of bone surface modifications generated by carnivores is generally low, indicating that human occupations are responsible for primary deposition of faunal assemblages (Rosell et al., 2012). This pattern lends support to the interpretation that the faunal assemblages at Abric Pizarro were primarily accumulated through hominin activities rather than carnivore interactions.

Despite the limited occurrence of carnivore remains at Abric Pizarro, they offer valuable insights into the potential mechanisms by which they were introduced to the site. Absence of taphonomic indicators indicative of natural processes, such as bone abrasion and polishing, suggests that phenomena like water movement

or slope washes were not responsible for the deposition of carnivore remains. The predominance of isolated elements, such as teeth and phalanges, occasionally accompanied by larger post-cranial bones like ulnae, vertebrae, and pelvises, implies their introduction through secondary mechanisms, likely involving the activities of other fauna. Processes such as scavenging or predation events by other carnivores could have contributed to their presence. However, the culturally sterile layers and the absence of concentrated bone accumulations typical of carnivore dens suggest that carnivore-mediated deposition was not the primary mode of introduction. It is also plausible that the remains were transported to the site through the actions of other animals, such as burrowing species, capable of displacing carcasses. The absence of Neanderthal-mediated modifications on carnivore bones further supports the inference that Neanderthals did not bring the bones to the site, particularly as typically non-meat- and marrow-bearing bones are present. Nevertheless, the scarcity of carnivore remains complicates the determination of the mechanisms underlying their deposition, leaving open the possibility that they are the result of Neanderthal scavenging or the transportation of carnivore elements for alternate purposes, such as toolmaking. Further analyses, particularly of spatial distribution patterns, may yield additional insights into the intricate interactions between hominins and carnivores at Abric Pizarro.

The presence of black spots on the cortical surface of bones raises questions regarding site formation processes. This phenomenon may be attributed to post-depositional taphonomic processes impacting the bones, or alternatively, to the presence of manganese-rich sediments owing to the calcareous composition of the rockshelter (López-González et al., 2006; Marín Arroyo et al., 2008). Manganese deposition on bone surfaces can result from soil humification subsequent to anthropic occupation and the decomposition of organic matter, as observed in sites characterised by seasonal occupation, exemplified by the case of El Mirón Cave (Marín Arroyo et al., 2008). Yet, the evidence for seasonal occupation at Abric Pizarro remains limited, and therefore, it is conceivable that the black staining observed on bone surfaces predominantly stems from the intrinsic geological characteristics of the rockshelter.

The identification of burned bones at the Abric Pizarro site, in the absence of evident hearth-related features, poses intriguing questions. One plausible explanation for the lack of identifiable hearths may stem from preservation challenges. It is pertinent to note that despite the absence of conspicuous hearth features, the presence of concentrated black stains within the sediment matrix and the recovery of charcoal fragments from both levels M and P suggest past fire-related activities. If indeed hearths were integral to the Neanderthal occupation at Abric Pizarro, it would imply a level of spatial organisation consistent with other prehistoric sites of similar antiquity (e.g., Gesher Benot Ya'aqov in Israel, and Abric Romaní, Cova Gran de Santa Linya and Roca dels Bous in Spain; Alperson-Afil et al., 2009; Marín et al., 2019; Samper Carro et al., 2020). However, to substantiate assertions of spatial organisation, further investigations into the spatial distribution of bone fragments are imperative. Such inquiries represent a promising avenue for advancing our understanding

of site use dynamics and Neanderthal behavioural patterns at Abric Pizarro.

4.2 Diverse dietary resources and hunting efficiency

The faunal assemblage from Abric Pizarro reveals a diverse spectrum of dietary resources exploited by Neanderthals, ranging from smaller herbivorous prey like caprids to very large herbivores such as Bos/Bison. This rich array of dietary choices lends support to the hypothesis that the site was surrounded by a resource-rich environment. Notably, the prevalence of cervids and medium-sized herbivores, coupled with a notable abundance of meat-bearing bones (i.e., long bones and mandibles), suggests the implementation of methodical hunting and butchery practices.

The marked preference for deer among the faunal remains attests to a pattern of high hunting efficiency, underscoring the Neanderthals' adeptness at effectively exploiting the surrounding landscape. Comparative analyses with sites across the broader geographical region, encompassing locales from Portugal, Spain and southern France, highlight striking similarities in hunting preferences (Steele, 2004; Baena Preysler et al., 2012; Blasco and Fernández-Peris, 2012; Uzquiano et al., 2012; Yravedra and Gómez Castanedo, 2014; Nabais, 2018; Bargalló et al., 2020; Samper Carro et al., 2020; Rendu, 2022). Yet not all Middle Palaeolithic sites in the Iberian Peninsula demonstrate a preference for deer. For example, caprines are preferred at Cueva del Esquilleu (Uzquiano et al., 2012; Yravedra and Gómez Castanedo, 2014), Abrigo de la Quebrada (Sanchis Serra et al., 2013; Real et al., 2018; Real Margalef et al., 2019), El Salt (Garralda et al., 2014; Real et al., 2018), and Valdegoba Cave (Rodríguez-Gómez et al., 2022). Considering the mountainous topography of these sites, it is likely that the exploitation of caprines is related to their abundance within the local environment. As such, the preference for deer within biomes abundant with available prey and between sites across the broader geographic expanse hints at a level of choice and preference exercised by Neanderthals. This implies a degree of cognitive complexity in their subsistence strategies, encompassing ecological awareness, deliberate decision-making, and knowledge transmission. Overall, the preference for deer within diverse ecological settings and across different sites implies that Neanderthals were not simply reacting to immediate environmental conditions. This aspect of their behaviour provides valuable insights into the complexity of Neanderthal cognitive abilities and their capacity to adapt to a variety of ecological contexts.

It is pertinent to underscore that the present analysis has primarily concentrated on the examination of large vertebrates within the faunal assemblage. However, small vertebrates, including lagomorphs and turtles, are presently undergoing detailed study. The outcomes derived from this analysis of small vertebrates will be amalgamated and compared with the findings obtained from the investigation of large vertebrates. Such a holistic approach contributes to a more nuanced understanding of Neanderthal resource exploitation practices.

4.3 Nutritional stress and complex butchery

The predominance of spiral fracturing observed in both level M and level P, affecting a significant majority of long bones and epiphyses, suggests a consistent pattern in Neanderthal butchery actions at the Abric Pizarro site. Spiral fractures, particularly in the relative absence of carnivore remains and taphonomic indicators of trampling, are typically associated with intentional, systematic bone breakage aimed at accessing the nutrient-rich marrow contained within the bones (Myers et al., 1980; Haynes, 1983; Villa and Mahieu, 1991; Bar-Oz et al., 2008; Rosell et al., 2012). This technique indicates a deliberate and skilful approach to carcass processing, wherein Neanderthals likely used stone tools such as hammerstones to create these distinctive fracture patterns. The marginal occurrence of other fresh or “green” breakages (i.e., V-shaped and irregular) further supports the interpretation of intentional butchery practices, likely focused on marrow extraction, with these variations possibly resulting from occasional differences in tool use or butchery techniques (Villa and Mahieu, 1991; Bar-Oz et al., 2008; Rosell et al., 2012). Minimal transversal morphology suggests a lack of accidental or incidental dry bone damage, reinforcing the notion of purposeful and controlled processing of faunal resources by Neanderthal populations at the site. It is imperative to note that while the fracture data elicits discernible patterns within the identifiable assemblage, the non-diagnostic assemblage (i.e., fragments <2 cm) was not subject to detailed taphonomic analysis. As such, it is possible that incidences of dry bone damage are more common in the non-diagnostic assemblage.

The presence of distinctive orthogonal bone morphology on meat and marrow-bearing bones (i.e., long bones, phalanges, and epiphyses) further provides compelling evidence of intensive Neanderthal utilisation of edible animal portions for nutritional purposes. The relative scarcity of carnivore remains and carnivore-induced modifications within the assemblage further suggests that these breakages are likely the result of Neanderthal activities, possibly involving the percussion of short bones using stone tools like hammerstones. Analogous patterns of intense faunal processing in response to nutritional stress have been observed at Roc de Marsal and Pech IV in France during colder glacial periods (Hodgkins et al., 2016). Considering the relatively warm and stable environmental conditions indicated by preliminary paleoenvironmental analysis at the Abric Pizarro site (see text footnote 1) and the abundance of temperate taxa such as deer, it is plausible that Neanderthals favoured habitation in the region. The pronounced intensity of butchery activities at Abric Pizarro, aimed at maximising caloric extraction from prey, even during periods of relative climatic stability, suggests that Neanderthals regularly engaged in intensive faunal processing of carcasses. This possibly indicates that nutritional stress commonly affected Neanderthals throughout glacial and interglacial periods (see also Hodgkins et al., 2016). Through the examination of these zooarchaeological indicators and their contextual associations, valuable insights can be gained into the adaptive behaviours and dietary practises of Neanderthal groups during MIS 4.

Evidence of systematic butchery practises is additionally substantiated by the notably high proportion of meat-bearing bones, particularly long bones and mandibles, displaying characteristic anthropic surface modifications such as incisions, scrapes, chop marks, and percussion. The analysis of skeletal

profiles suggests that the butchery activities took place away from the site, with a preference for prime, meat-bearing bones being selectively transported back to the rockshelter. This pattern is consistent across various prey species and is likely attributed to the challenging accessibility and topographical constraints of Abric Pizarro. These observations collectively underscore a level of technological sophistication in the Neanderthals' approach to processing animal remains, reflecting a deliberate and skilful methodology employed in the extraction of valuable resources from their prey.

To gain a more comprehensive understanding of the specific butchery practises and behaviours employed by Neanderthals, further investigation is currently underway. This involves the incorporation of spatial analysis of bone surface modifications, using the method proposed by Westbury and Samper Carro (under review)². This ongoing research endeavour holds the potential to provide valuable comparative insights that will complement the findings of this study. It is anticipated to contribute to a more nuanced exploration of Neanderthal subsistence strategies and technological adaptations during the MIS 4 period at Abric Pizarro.

5 Concluding remarks

The zooarchaeological investigation at the Abric Pizarro rockshelter provides valuable insights into Neanderthal adaptability and resource exploitation capabilities. The diverse fauna, methodical hunting practices, and deliberate butchery behaviours offer a comprehensive understanding of Neanderthal subsistence and behaviours during the Middle Palaeolithic in the southeast Pre-Pyrenees region. These findings enrich the broader narrative of human evolution, reaffirming the intricate nature of Neanderthal behaviours and cognitive capabilities. The research at Abric Pizarro contributes significantly to the ongoing scholarly discourse on Neanderthals, highlighting their complexity and significance within the context of human evolution. This study provides important insights into the activities and strategies employed by Iberian Neanderthals at the Abric Pizarro site, shedding light on their adaptive behaviours during the critical MIS 4 epoch.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

EW: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. SS: Funding acquisition, Project administration, Supervision, Validation, Writing – review & editing. SV: Project administration, Resources, Software, Writing – review & editing.

² Westbury, E., and Samper Carro, S. (under review). A new open-access method applying GIS techniques to the study of bone surface modifications. *Int. J. Osteoarchaeol.*

JP: Project administration, Resources, Software, Writing – review & editing. JM-M: Project administration, Resources, Software, Writing – review & editing. RM: Project administration, Resources, Software, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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