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Neanderthal complex behaviour through the lens of faunal resources

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Neanderthal complex behaviour through the lens of faunal resources

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Table of contents

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Editorial: Neanderthal complex behaviour through the lens of faunal resources

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Neanderthal, zooarchaeology, subsistence, behavioural complexity, faunal resources

Editorial on the Research Topic
Neanderthal complex behaviour through the lens of faunal resources

The longstanding view of Neanderthals as ecologically inflexible and behaviourally limited hominins has been challenged in recent decades. Modern zooarchaeological and taphonomic research has revealed a variety of complex behaviours among Neanderthal populations across Europe and the Levant, decisively overturning the notion that advanced subsistence and technological strategies were exclusive to Anatomically Modern Humans (AMH). This Research Topic, *Neanderthal complex behaviour through the lens of faunal resources*, assembles innovative research that sheds light on the sophisticated ways Neanderthals procured, processed and used faunal resources. Collectively, these studies contribute to reframing Neanderthals as cognitively and behaviourally comparable to their African contemporaries, through the perspective of faunal exploitation.

Solano-García and Moigne's research at Cueva del Ángel in southern Spain focuses on the systematic exploitation of large ungulates across a long Middle Pleistocene sequence. Their evidence for targeted hunting, intensive marrow extraction and minimal carnivore interference supports a persistent pattern of high-yield, large-game hunting. This pattern, coupled with strategic carcass processing, places Neanderthals within a broader Eurasian tradition of flexible but large-game-focused subsistence, reiterating their sophisticated ecological adaptability.

Nabais and Zilhão's study of Gruta da Figueira Brava (Portugal) highlights Neanderthals' exploitation of diverse resources from a mosaic coastal and inland environment during the Last Interglacial. Their faunal analysis indicates a systematic, contextually flexible approach to red deer, ibex and larger species, such as aurochs and horses. The patterns of carcass transport and processing further suggest a strategic, adaptive use of local ecotones, reinforcing Neanderthals' capacity to integrate varied habitats and prey types into their subsistence systems.

Westbury et al. examine Neanderthal occupation of the Abric Pizarro site in the Pre-Pyrenees (Spain) during MIS 4, a period of pronounced climatic instability. Their zooarchaeological and taphonomic data reveal a diverse prey spectrum, systematic butchery practices and extensive evidence of fire use. These finds challenge entrenched ideas of Neanderthal ecological vulnerability, instead portraying them as resilient, organised and capable of sustaining long-term occupations in marginal environments through strategic planning and technological competence.

This is also clear in Carvalho et al. case-study from Lapa do Picareiro cave in Portuguese Estremadura, demonstrating Neanderthals' consistent targeting of red deer across multiple occupational phases. Despite environmental fluctuations during Heinrich Stadial 5, these communities maintained a remarkably stable, regionally adapted subsistence strategy, focused on predictable resources within a defined territory. Such evidence undermines any residual perception of Neanderthal ecological rigidity, instead highlighting their resilience and behavioural stability in the face of climatic perturbations.

Crezzini et al. take a nutritional and genetic perspective, revealing how Neanderthals in arid Late Mousterian Italy relied intensively on animal fats and proteins, notably from aurochs and horses. This work highlights the interplay between environmental stressors, genetic adaptations and subsistence practices. The authors suggest Neanderthals' ancestral FADS1/FADS2 haplotype constrained their endogenous fatty acid synthesis, necessitating dietary reliance on lipid-rich faunal resources and demonstrating a subtle, metabolically informed adaptive strategy.

Goffette et al. expand the faunal narrative beyond mammals, analysing avian remains from Scladina Cave in Belgium. They document anthropogenic modifications on several bird bones, suggesting consumption, tool use and potentially symbolic practices involving birds. These results decisively challenge the stereotype of Neanderthals as exclusively large-game hunters, revealing a broader and more complex subsistence and cultural repertoire than previously acknowledged in north-western Europe.

In a related vein, Nabais et al. employ experimental archaeology to replicate Neanderthal bird butchery and cooking practices. Their experiments reveal how cooking dramatically alters the archaeological visibility of avian remains, reducing cut-mark prevalence while increasing thermal damage and skeletal loss. This study provides a critical interpretive framework for evaluating bird exploitation in Palaeolithic contexts, cautioning that traditional zooarchaeological assemblages may underestimate the full extent of Neanderthal avian resource use.

Jallon et al. present a comparative study of faunal processing at Amud and Kebara caves in the Levant. Their microscopic and macroscopic cut-mark analyses uncover culturally distinct butchery strategies despite comparable faunal compositions and lithic technologies. Amud Neanderthals appear to have favoured an intensive butchery strategy that broke bones into many fragments and left dense cut-mark concentrations on small ungulates; while Kebara Neanderthals displayed more standardised, systematic carcass processing. These differences are best interpreted as evidence for cultural traditions and socially transmitted practices, rather than purely ecological responses, highlighting the social and cognitive complexity of these groups.

Finally, the contribution by Cobo-Sánchez et al. at Escoural Cave, located in Portugal, employs an innovative blend of traditional taphonomic methods and machine learning approaches to disentangle human from carnivore agency in faunal assemblages. Their analysis of leporid remains points convincingly to lynxes and other small carnivores as the primary accumulators, finding no clear evidence of Neanderthal small-game exploitation at this site. Beyond its finds, the study exemplifies how advanced computational models can enhance our understanding of complex site-formation processes, setting new methodological standards for zooarchaeological investigations.

Taken together, the papers assembled in this Research Topic demonstrate the rich potential of zooarchaeological research for better revealing the complex behavioural signatures of Neanderthals. From experimental archaeology to genetic dietary inferences and advanced computational modelling, the breadth of methodological innovation on display here reaffirms the central role of faunal studies in Palaeolithic archaeology. Crucially, the contributions show that Neanderthals were neither ecologically naïve nor behaviourally impoverished. Rather, they emerge as sophisticated, adaptable hominins whose interactions with faunal resources rivalled, and in some cases anticipated, patterns seen in their AMH contemporaries.

This Research Topic challenges us to transcend outdated evolutionary hierarchies that diminish Neanderthal capacities. It advocates instead for a perspective that recognises them as creative, resilient and contextually responsive members of the human lineage. We hope that this Research Topic stimulates further dialogue and research, encouraging scholars to continue exploring the zooarchaeological record as a window onto the subtle, diverse and complex worlds inhabited by Neanderthals.

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Conflict of interest

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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 biassed 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 review[1]). 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 ± 5,359 BP and level P at 62,602 ± 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 Behrensmeyer (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*).

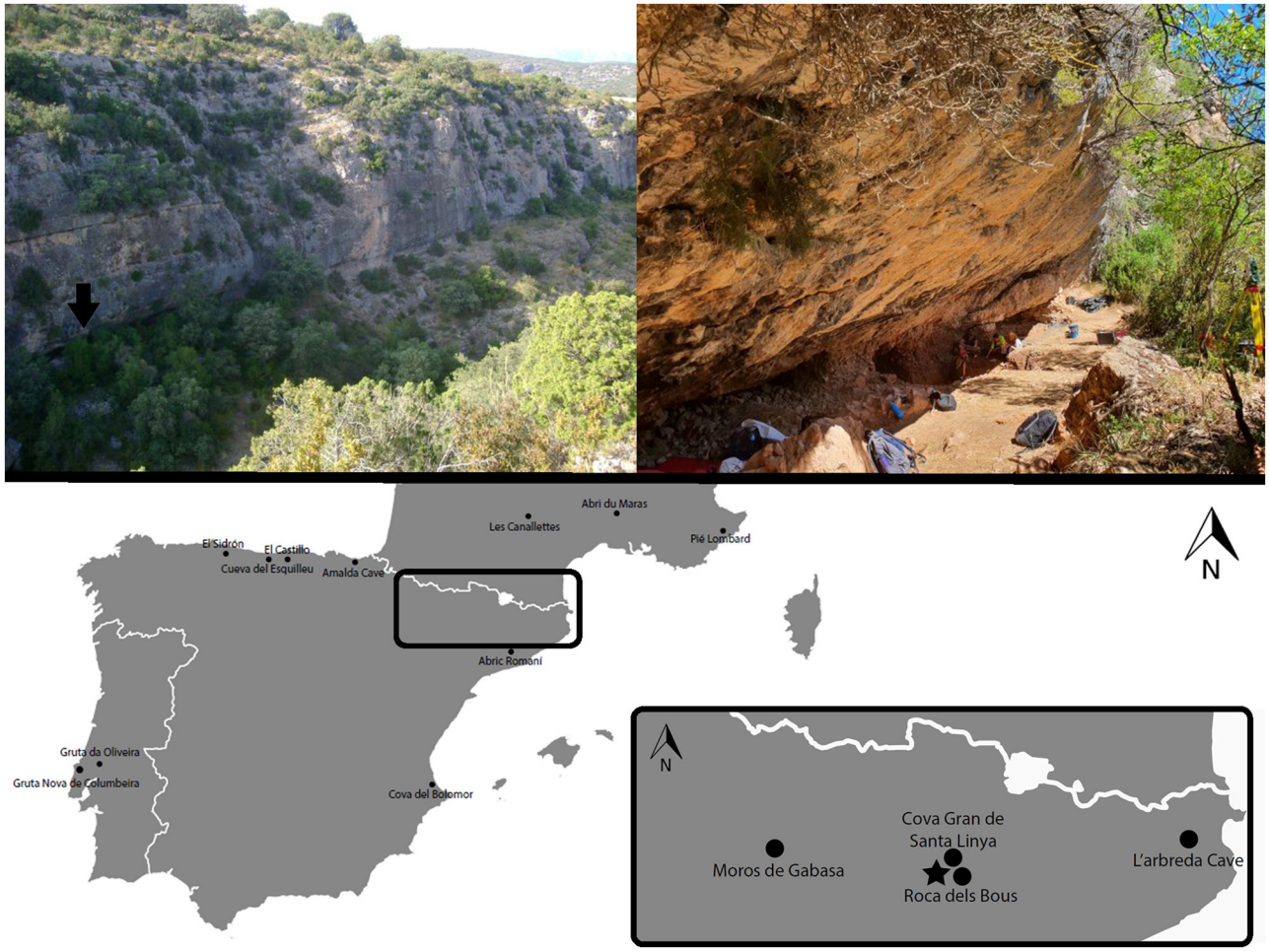

FIGURE 1
Location of Abric Pizarro rockshelter and other key temporally synonymous Middle Palaeolithic Neanderthal sites in the immediate Pre-Pyrenean region and broader Iberian Peninsula and southern France. The arrow in the top left photograph and ⋆ in the bottom map indicates the location of Abric Pizarro.

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 Arqueologic (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

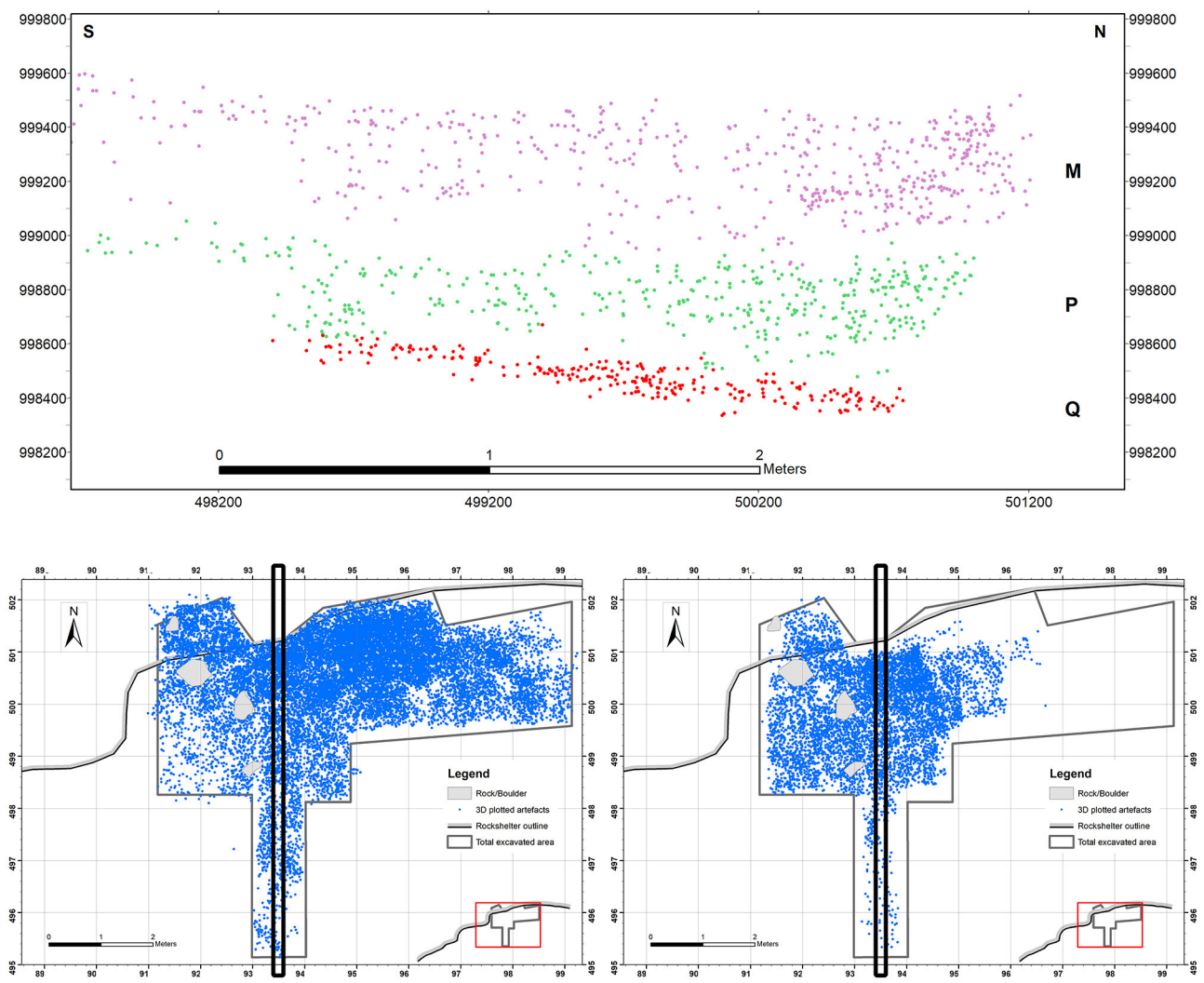

FIGURE 2
Vertical **(top)** and horizontal **(bottom)** distribution of 3D plotted cultural material recovered in units M **(bottom left)** and P **(bottom right)** from Abric Pizarro.

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
Rana rana	0	0	0	1	1	1
Testudinae	201	8	2	35	2	1
Talpa europaea	1	1	1	0	0	0
Rodentia	1	1	1	0	0	0
Oryctolagus cuniculus	31	23	3	56	39	10
Lepus europaeus	11	10	3	3	3	1
Lagomorpha	24	17	4	0	0	0
Lynx lynx	1	1	1	0	0	0
Felidae	1	1	1	0	0	0
Hyaenidae	2	2	1	0	0	0
Vulpes vulpes	1	1	1	0	0	0
Canis sp.	1	1	1	0	0	0
Ursidae	6	5	2	0	0	0
Carnivora	6	5	1	0	0	0
Sus scrofa	6	6	1	3	3	1
Cervus elaphus	421	183	13	72	36	5
Cervidae	839	207	16	165	31	2
Capra pyrenaica	14	12	1	5	3	1
Caprinae	204	77	7	52	11	1
Large Bovinae (*Bos* sp./Bison)	16	6	1	7	6	2
Rhinocerotidae	3	2	1	1	1	1
Equus ferus	186	105	9	32	15	2
Equus hydruntinus	161	101	6	16	15	3
Equus sp.	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 bovids 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
Capra pyrenaica	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	–	–
Cervus elaphus	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
Equus ferus	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
Equus hydruntinus	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	–	–
Equus 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

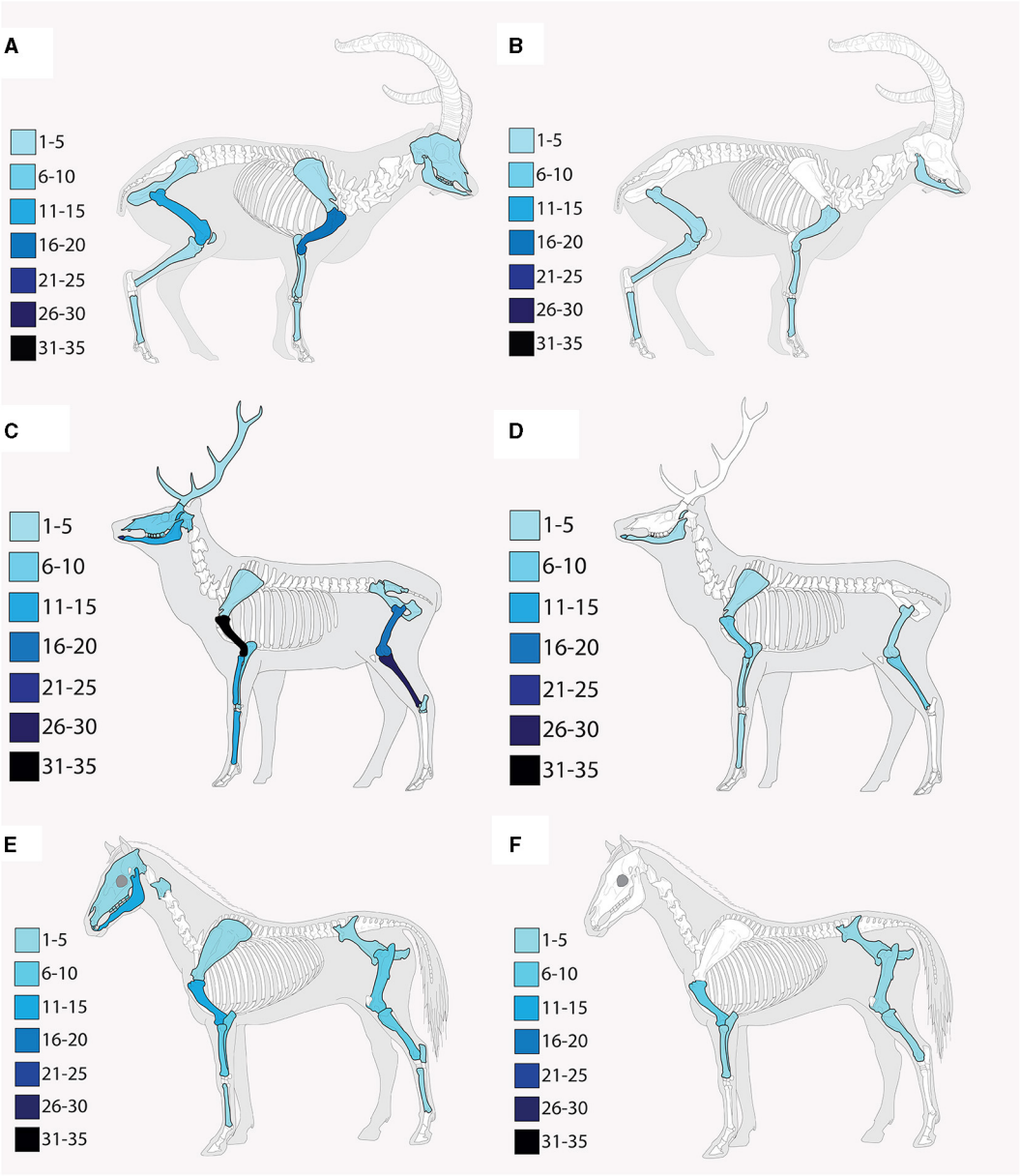

FIGURE 3
Skeletal profiles based on the MNE of the dominant hunted prey species at Abric Pizarro. **(A)** Level M caprines, **(B)** Level P caprines, **(C)** Level M cervids, **(D)** Level P cervids, **(E)** Level M equids, **(F)** Level P equids. Skeletal representations are based exclusively on identifiable 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 lone 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
Oryctolagus cuniculus	Cranium	Slicing	–	1
	Mandible	Slicing	1	1
		Scraping	–	1
	Tibia	Slicing	–	1
	Long bone	Slicing	–	1
Lepus europaeus	Dorsal vertebra	Slicing	1	–
Lagomorpha	Long bone	Slicing	1	–
Testudinae	Carapace	Slicing	9	3
		Scraping	3	–
		Impact point	5	–
		Notch	2	–
Sus scrofa	Second phalanx	Indirect percussion	1	–
Capra pyrenaica	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	–
Cervus elaphus	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	–
Equus asinus	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
Equus caballus	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
		Notch	2	–
Herb 1/2 herbivore	Long bone	Slicing	24	4
		Scraping	14	–
		Chop mark	3	–
		Impact point	4	2
		Notch	6	2
		Indirect percussion	27	–
Size 2/3 herbivore	Long bone	Slicing	6	1
		Scraping	3	–
		Chop mark	1	–
		Impact point	5	1
		Notch	3	–
		Indirect percussion	9	–
Size 3/4 herbivore	Long bone	Slicing	7	–
		Scraping	1	1
		Impact point	2	–
		Notch	1	–
		Indirect percussion	2	–
Mammal	Cranium	Slicing	4	1
		Notch	1	–
	Mandible	Indirect percussion	3	–
		Impact point	1	–
		Indirect percussion	3	1
	Scapula	Slicing	2	–
		Scraping	1	–
		Indirect percussion	5	–
	Long bone	Slicing	1	–
		Indirect percussion	1	–
	Rib	Slicing	5	5
		Scraping	1	1
		Chop mark	1	–
		Impact point	6	1
		Notch	1	–
		Indirect percussion	12	–
	Cervical vertebra	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
		Impact point	10	1
		Notch	5	5
		Indirect percussion	52	1
	Flat bone	Slicing	15	2
		Scraping	7	1
		Chop mark	2	–
		Impact point	10	2
		Notch	9	–
		Indirect Percussion	10	–
Unidentifiable	Unidentifiable	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

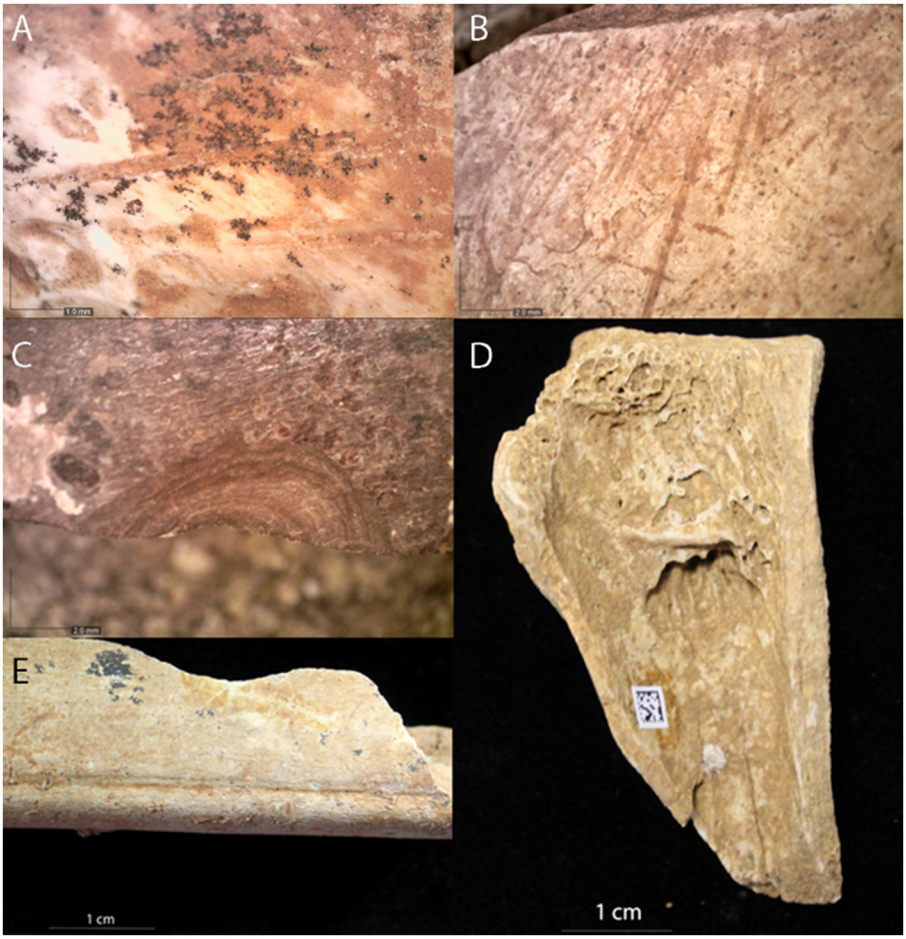

FIGURE 4
Examples of anthropogenic bone surface modifications identified within the Abric Pizarro faunal assemblage. **(A)** Slicing marks on *Cervus elaphus* radius, **(B)** scraping marks on size 2 herbivore long bone, **(C)** indirect percussion on Caprinae humerus, **(D)**, orthogonal bone breakage 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 Esquilleu (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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References

Alperson-Afil, N., Sharon, G., Kislev, M., Melamed, Y., Zohar, I., Ashkenazi, S., et al. (2009). Spatial organization of hominin activities at Gesher Benot Ya'aqov, Israel. *Science* 326, 1677–1680. doi: 10.1126/science.1180695

Baena Preysler, J., Carrión, E., Cuartero, F., and Fluck, H. (2012). A chronicle of crisis: the Late Mousterian in north Iberia (Cueva del Esquilleu, Cantabria, Spain). *Quat. Int.* 247, 199–211. doi: 10.1016/j.quaint.2011.07.031

Bargalló, A., Gabucio, M. J., Gómez de Soler, B., Chacón, M. G., and Vaquero, M. (2020). "A snapshot of a short occupation in the Abric Romaní rock shelter: archaeo-level Oa," in *Short-Term Occupations in Paleolithic Archaeology: Definition and Interpretation*, eds. J. Cascalheira and A. Picin (Cham: Springer), 217–235. doi: 10.1007/978-3-030-27403-0_9

Bar-Oz, G., Belfer-Cohen, A., Meshveliani, T., Djakeli, N., and Bar-Yosef, O. (2008). Taphonomy and zooarchaeology of the Upper Palaeolithic cave of Dzudzuana, Republic of Georgia. *Int. J. Osteoarchaeol.* 18, 131–151. doi: 10.1002/oa.926

Behrensmeyer, A. K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162. doi: 10.1017/S0094837300005820

Benito-Calvo, A., Arnold, L. J., Mora, R., Martínez-Moreno, J., and Demuro, M. (2020). Reconstructing Mousterian landscapes in the southeastern Pyrenees (Roca dels Bous site, Pre-Pyrenees range, Spain). *Quat. Res.* 97, 167–186. doi: 10.1017/qua.2020.29

Blanco, G., Sánchez-Marco, A., and Negro, J. J. (2021). Night capture of roosting cave birds by Neanderthals: an actualistic approach. *Front. Ecol. Evol.* 9:733062. doi: 10.3389/fevo.2021.733062

Blasco Sancho, M. F., and Montes Ramírez, L. (1997). Los hiénidos del yacimiento musteriense de Gabasa 1 (Huesca, España). *Bolskan* 14, 9–27.

Blasco, M. F. (1995). *Hombres, fieras y presas: studio arqueozoológico y tafonómico del yacimiento del paleolitico medio de la Cueva de Gabasa 1 (Huesca)* [PhD Thesis]. Universidad de Zaragoza, Zaragoza.

Blasco, M. F. (1997). In the pursuit of game: the Mousterian cave site of Gabasa 1 in the Spanish Pyrenees. *J. Anthropol. Res.* 53, 177–217. doi: 10.1086/jar.53.2.3631276

Blasco, R. (2008). Human consumption of tortoises at level IV of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839–2848. doi: 10.1016/j.jas.2008.05.013

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Cambridge, MA: Academic Press), 123–206. doi: 10.1016/B978-0-12-821428-2.00010-X

Blasco, R., and Fernández Peris, J. (2009). Middle Pleistocene bird consumption at level XI of Bolomor cave (Valencia, Spain). *J. Archaeol. Sci.* 36, 2213–2223. doi: 10.1016/j.jas.2009.06.006

Blasco, R., and Fernández-Peris, J. (2012). Small and large game: human use of diverse faunal resources at level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus Pale* 1, 265–282. doi: 10.1016/j.crpv.2012.01.003

Brown, W. A. B., and Chapman, N. G. (1991). The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. *J. Zool.* 224, 519–536. doi: 10.1111/j.1469-7998.1991.tb03783.x

Bunn, H. T. (1986). Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690. doi: 10.1016/S0047-2484(86)80004-5

Busk, G. (1865). "On a very ancient human cranium from Gibraltar," in *Report of the British Association for the Advancement of Science 1864* (London), 91–92.

Carvalho, M., Peireira, T., and Manso, C. (2018). Rabbit exploitation in the Middle Paleolithic at Gruta Nova da Columbeira, Portugal. *J. Archaeol. Sci. Rep.* 21, 821–832. doi: 10.1016/j.jasrep.2018.09.003

Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., et al. (2019). Neanderthal selective hunting of reindeer? The case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011. doi: 10.1007/s12520-017-0580-8

d'Errico, F., and Sánchez Goñi, M. F. (2003). Neandertal extinction and the millennial scale climatic variability of OIS 3. *Quat. Sci. Rev.* 22, 769–788. doi: 10.1016/S0277-3791(03)00009-X

Estévez, J. (1987). La fauna de l'Arbreda (sector Alfa) en el conjunt de faunes del Plistocè Superior. *Cypsela* 6, 73–87.

Fa, J. E., Stewart, J. R., Lloveras, L., and Vergas, J. M. (2013). Rabbits and hominin survival in Iberia. *J. Hum. Evol.* 64, 233–241. doi: 10.1016/j.jhevol.2013.01.002

Fernández-García, M., Vidal-Cordasco, M., Jones, J. R., and Marín-Arroyo, A. B. (2023). Reassessing palaeoenvironmental conditions during the Middle to Upper Palaeolithic transition in the Cantabrian region (Southwestern Europe). *Quat. Sci. Rev.* 301, 1–18. doi: 10.1016/j.quascirev.2022.107928

Fernández-Jalvo, Y., and Andrews, P. (2016). *Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification*. Springer. doi: 10.1007/978-94-017-7432-1

Fernández-Laso, M. C., Rivals, F., and Rosell, J. (2010). Intra-site changes in seasonality and their consequences on the faunal assemblages from Abric Romaní (Middle Palaeolithic, Spain). Quaternaire. *Rev. Assoc. Fr. l'Étude Quaternaire* 21, 155–163. doi: 10.4000/quaternaire.5525

Fisher, J. W. (1995). Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theor*. 2, 7–68.

Garralda, M. D., Galván, B., Hernández, C. M., Mallol, C., Gómez, J. A., Maureille, B., et al. (2014). Neanderthals from El Salt (Alcoy, Spain) in the context of the latest Middle Palaeolithic populations from the southeast of the Iberian Peninsula. *J. Hum. Evol*. 75, 1–15. doi: 10.1016/j.jhevol.2014.02.019

Grant, A. (1982). "The use of tooth wear as a guide to the age of domestic animals," in *Ageing and Sexing Animal Bones from Archaeological Sites,* eds. B. Wilson, C. Grigson, and S. Payne (Oxford: B.A.R.), 91–108.

Greenfield, H. J., and Arnold, E. R. (2008). Absolute age and tooth eruption and wear sequences in sheep and goat: determining age-at-death in zooarchaeology using a modern control sample. *J. Archaeol. Sci*. 35, 836–849. doi: 10.1016/j.jas.2007.06.003

Hajdinjak, M., Mafessoni, F., Skov, L., Vernot, B., Hübner, A., Fu, Q., et al. (2021). Initial Upper Palaeolithic humans in Europe had recent Neanderthal ancestry. *Nature* 592, 253–257. doi: 10.1038/s41586-021-03335-3

Hardy, K. (2022). "The use of plant by Neanderthals as food, medicine, and raw materials," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Cambridge, MA: Academic Press), 145–162. doi: 10.1016/B978-0-12-821428-2.00004-4

Haynes, G. (1983). Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages. *Am. Antiq*. 48, 102–114. doi: 10.2307/279822

Hillson, S. (1991). *Mammal Bones and Teeth: An Introductory Guide to Methods of Identification*. London: Routledge.

Hillson, S. (2005). *Teeth*. New York, NY: Cambridge University Press. doi: 10.1017/CBO9780511614477

Hodgkins, J., Marean, C. W., Turq, A., Sandgathe, D., McPherron, S. J. P., Dibble, H., et al. (2016). Climate-mediated shifts in Neandertal subsistence behaviors at Pech de l'Azé IV and Roc de Marsal (Dordogne Valley, France). *J. Hum. Evol*. 96, 1–18. doi: 10.1016/j.jhevol.2016.03.009

Lemoine, X., Zeder, M. A., Bishop, K. J., and Rufolo, S. J. (2014). A new system for computing dentition-based age profiles in *Sus scrofa*. *J. Archaeol. Sci*. 47, 179–193. doi: 10.1016/j.jas.2014.04.002

Lloveras, L., Moreno García, M., and Nadal, J. (2009). Butchery, cooking and human consumption marks on rabbit (*Oryctolagus cuniculus*) bones: an experimental study. *J. Taphonomy* 7, 179–201.

Lloveras, L., Moreno-García, M., Nadal, J., Moroto, J., Soler, J., Soler, N., et al. (2010). The application of actualistic studies to assess the taphonomic origin of Musterian rabbit accumulations from Arbreda Cave (North-East Iberia). *Archaeofauna* 19, 99–119.

Lloveras, L., Moreno-García, M., Nadal, J., and Zilhão, J. (2011). Who brought in the rabbits? Taphonomical analysis of Mousterian and Solutrean leporid accumulations from Gruta do Caldeirão (Tomar, Portugal). *J. Archaeol. Sci*. 38, 2434–2449. doi: 10.1016/j.jas.2011.05.012

López-González, F., Grandal-d'Anglade, A., and Vidal-Romaní, J. R. (2006). Deciphering bone depositional sequences in caves through the study of manganese coatings. *J. Archaeol. Sci*. 33, 707–717. doi: 10.1016/j.jas.2005.10.006

Marean, C. W., and Kim, S. Y. (1998). Mousterian large-mammal remains from Kobeh Cave: behavioral implications for Neanderthals and Early Modern Humans. *Curr. Anthropol*. 39(S1), S79–S114. doi: 10.1086/204691

Marín Arroyo, A. B., Landete Ruiz, M. D., Vidal Bernabeu, G., Seva Román, R., González Morales, M. R., Straus, L. G., et al. (2008). Archaeological implications of human-derived manganese coatings: a study of blackened bones in El Mirón Cave, Cantabrian Spain. *J. Archaeol. Sci*. 35, 801–813. doi: 10.1016/j.jas.2007.06.007

Marín, J., Rodríguez-Hidalgo, A., Vallverdú, J., Gómez de Soler, B., Rivals, F., Rabuñal, J. R., et al. (2019). Neanderthal logistic mobility during MIS3: zooarchaeological perspective of Abric Romaní level P (Spain). *Quat. Sci. Rev*. 225:106033. doi: 10.1016/j.quascirev.2019.106033

Martínez-Polanco, M. F., Blasco, R., Rosell, J., Ibáñez, N., and Vaquero, M. (2017). Rabbits as Food at the end of the Upper Palaeolithic at Molí del Salt (Catalonia, Spain). *Int. J. Osteoarchaeol*. 27, 342–355. doi: 10.1002/oa.2541

Moncel, M.-H., Chacón, M. G., Vettese, D., Courty, M.-A., Daujeard, C., Eixea, A., et al. (2021). Late Neanderthal short-term and specialized occupations at the Abri du Maras (South-East France, level 4.1, MIS 3). *Archaeol. Anthropol. Sci*. 13, 1–28. doi: 10.1007/s12520-021-01285-5

Myers, T. P., Voorhies, M. R., and Corner, R. G. (1980). Spiral fractures and bone pseudotools at paleontological sites. *Am. Antiq*. 45, 483–490. doi: 10.2307/279863

Nabais, M. (2018). Neanderthal subsistence in Portugal: what evidence? *Archaeol. Int*. 21, 95–100. doi: 10.5334/ai-376

Nabais, M., Dupont, C., and Zilhão, J. (2023). The exploitation of crabs by Last Interglacial Iberian Neanderthals: the evidence from Gruta da Figueira Brava (Portugal). *Front. Environ. Archaeol*. 2:1097815. doi: 10.3389/fearc.2023.1097815

Nabais, M., and Zilhão, J. (2019). The consumption of tortoise among last interglacial Iberian Neanderthals. *Quat. Sci. Rev*. 217, 225–246. doi: 10.1016/j.quascirev.2019.03.024

Nicholson, R. A. (1993). A morphological investigation of burnt animal bone and an evaluation of its utility in archaeology. *J. Archaeol. Sci*. 20, 411–428. doi: 10.1006/jasc.1993.1025

Pales, L., and Garcia, M. A. (1981). *Atlas Ostéologique pour Servir à l'Identification des Mammifères du Quaternaire*. Paris: Editions du Centre National de la Recherce Scientifique.

Pelletier, M., Desclaux, E., Brugal, J.-P., and Texier, P.-J. (2019). The exploitation of rabbits for food and pelts by last interglacial Neandertals. *Quat. Sci. Rev*. 224, 1–20. doi: 10.1016/j.quascirev.2019.105972

Pike-Tay, A., Cabrera Valdés, V., and Bernaldo de Quirós, F. (1999). Seasonal variations of the Middle–Upper Paleolithic transition at El Castillo, Cueva Morín and El Pendo (Cantabria, Spain). *J. Hum. Evol*. 36, 283–317. doi: 10.1006/jhev.1998.0271

Pizarro, J., Roy, M., Roda, X., Vega, S., Samper, S., Plasencia, J., et al. (2013). Nous elements de reflexió al voltant del poblament del Prepirineu oriental: al llarg del plistocè superior i l'holocè. *Colloqui d'Arqueologia d'Odèn* 3, 17–26.

Real Margalef, C., Sanchís Serra, A., Morales Pérez, J. V., Bel Martínez, M. Á., Eixa Vilanova, A., Zilhão, J., et al. (2019). Estudio de la fauna del nivel IV del Abrigo de la Quebrada y su aportación al conocimiento de la economía y el comportamiento humano en el Paleolítico medio de la vertiente Mediterránea Ibérica. *SPAL* 28, 17–49. doi: 10.12795/spal.2019.i28.13

Real, C., Eixea, A., Sanchis, A., Morales, J. V., Klasen, N., Zilhão, J., et al. (2018). Abrigo de la Quebrada level IV (Valencia, Spain): interpreting a Middle Palaeolithic palimpsest from a zooarchaeological and lithic perspective. *J. Paleolit. Archaeol*. 3, 187–224. doi: 10.1007/s41982-018-0012-z

Rendu, W. (2022). "Selection versus opportunism: a view from Neanderthal subsistence strategies," in updating Neanderthals: understanding behavioural complexity in the late Middle Palaeolithic, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Cambridge, MA: Academic Press), 109–122. doi: 10.1016/B978-0-12-821428-2.00013-5

Rodríguez-Gómez, G., Pérez-Fernández, E., Fernandez, P., Arsuaga, J. L., Díez, C., Arceredillo, D., et al. (2022). Palaeoecology of the Southern chamois from Valdegoba Cave (Burgos, Spain) and its exploitation by the Neanderthals. *Lethaia* 55, 1–25. doi: 10.18261/let.55.4.3

Romagnoli, F., Rivals, F., and Benazzi, S. (2022). Updating Neanderthals: *Understanding Behavioural Complexity in the Late Middle Palaeolithic*. Cambridge, MA: Academic Press.

Rosell, J., Cáceres, I., Blasco, R., Bennàsar, M., Bravo, P., Campeny, G., et al. (2012). A zooarchaeological contribution to establish occupational patterns at Level J of Abric Romaní (Barcelona, Spain). *Quat. Int*. 247, 69–84. doi: 10.1016/j.quaint.2011.01.020

Rosell, J., Modesto-Mata, M., Fernández-Laso, M. C., Modolo, M., and Blasco, R. (2019). Refitting bones to reconstruct the diversity in Middle Palaeolithic human occupations: the case of the Abric Romaní site (Capellades, Barcelona, Spain). *Archaeol. Anthropol. Sci*. 11, 4601–4619. doi: 10.1007/s12520-019-00887-4

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., et al. (2011). Carcass transport decisions in *Homo antecessor* subsistence strategies. *J. Hum. Evol*. 61, 425–446. doi: 10.1016/j.jhevol.2011.05.012

Samper Carro, S. C., Martínez-Moreno, J., and Mora Torcal, R. (2020). Winds of change: zooarchaeological approach to the Middle - Upper Palaeolithic transition in Cova Gran of Santa Linya (Lleida, south-eastern Pre-Pyrenees). *J. Paleolit. Archaeol*. 3, 989–1031. doi: 10.1007/s41982-020-00066-1

Sánchez Goñi, M. F. (2022). "The climatic and environment context of the Late Pleistocene," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds F. Romagnoli, F. Rivals, and S. Benazzi (Cambridge, MA: Academic Press), 17–38. doi: 10.1016/B978-0-12-821428-2.00017-2

Sánchez-Hernández, C., Gourichon, L., Pubert, E., Rendu, W., Montes, R., Rivals, F., et al. (2019). Combined dental wear and cementum analyses in ungulates reveal the seasonality of Neanderthal occupations in Covalejos Cave (Northern Iberia). *Sci. Rep*. 9:14335. doi: 10.1038/s41598-019-50719-7

Sanchis Serra, A., Morales Pérez, J. V., Real Margalef, C., Eixea Vilanova, A., Zilhão, J., Villaverde Bonilla, V., et al. (2013). "Los conjuntos faunísticos del Paleolítico medio del Abrigo de la Quebrada (Chelva, Valencia): problemática de estudio, metodología aplicada y síntesis de los primeros resultados," in *Animals i Arqueologia Hui: I Jornades d'Arqueozoologia del Museu de Prehistòria de València*, eds. A. Sanchis and J. Ll. Pascual (Valencia: Museu de Prehistòria de València), 65–82.

Sankararaman, S., Mallick, S., Dannemann, M., Prüfer, K., Kelso, J., Pääbo, S., et al. (2014). The genomic landscape of Neanderthal ancestry in present-day humans. *Nature* 507, 354–357. doi: 10.1038/nature12961

Steele, T. E. (2004). Variation in mortality profiles of red deer (*Cervus elaphus*) in Middle Palaeoltihic assemblages from western Europe. *Int. J. Osteoarchaeol*. 14, 307–320. doi: 10.1002/oa.763

Stiner, M. C., Kuhn, S. L., Weiner, S., and Bar-Yosef, O. (1995). Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* 22, 223–237. doi: 10.1006/jasc.1995.0024

Texier, P.-J., Renault-Miskovsky, J., Desclaux, E., de Lumley, M.-A., Porraz, G., and Tomasso, A. (2011). L'abri Pié Lombard à Tourrettes-sur-Loup (Alpes-Maritimes): anciennes fouilles, nouvelles données. *Bull. Musée Anthropol. Préhistorique Monaco* 51, 19–49.

Trinkaus, E., and Shipman, P. (1993). *The Neanderthals: Changing the Image of Mankind*. New York, NY: Knopf.

Uzquiano, P., Yravedra, J., Ruiz Zapata, B., José Gil Garcia, M., Sesé, C., Baena Preysler, J., et al. (2012). Human behaviour and adaptations to MIS 3 environmental trends (>53-30 ka BP) at Esquilleu cave (Cantabria, northern Spain). *Quat. Int.* 252, 82–89. doi: 10.1016/j.quaint.2011.07.023

Vaquero, M. (2022). "The organisation of living spaces in Neanderthal campsites," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Cambridge, MA: Academic Press), 207–226. doi: 10.1016/B978-0-12-821428-2.00001-9

Vega Bolivar, S., Samper Carro, S. C., Pizarro Barberà, J., Mora, R., Martínez-Moreno, J., Benito-Calvo, A., et al. (2015). "Abric Pizarro (Àger, Lleida): un nou jaciment del Paleolític Mitjà al Prepireneu Oriental," in *Primeres Jornades d'Arqueologia i Paleontologia de Ponent* (Lleida), 32—39.

Villa, P., and Mahieu, E. (1991). Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48. doi: 10.1016/0047-2484(91)90034-S

Yravedra Sáinz de los Terreros, J., Gómez-Castanedo, A., Aramendi Picado, J., and Baena Preysler, J. (2014). Specialised hunting of Iberian ibex during Neanderthal occupation at El Esquilleu Cave, northern Spain. *Antiquity* 88, 1035–1049. doi: 10.1017/S0003598X00115303

Yravedra, J., and Gómez Castanedo, A. (2014). Taphonomic implications for the Late Mousterian of South-West Europe at Esquilleu Cave (Spain). *Quat. Int.* 337, 225–236. doi: 10.1016/j.quaint.2013.09.030

Zilhão, J., Angelucci, D. E., Igreja, M. A., Arnold, L. J., Badal, E., Callapez, P., et al. (2020). Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* 367:6485. doi: 10.1126/science.aaz7943ff

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Experimental replication of early human behaviour in bird preparation: a pilot-study focusing on bone surface modification and breakage patterns

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The origin of complex behaviour amongst early humans is a subject of heated debate within the scientific community, and the study of small prey remains has become a significant aspect when examining such modern behaviour. Nonetheless, the consumption of small prey by human populations poses analytical difficulties due to the often negligible, or entirely absent, traces on bone surfaces. To address this difficulty, an experimental study focusing on terrestrial avifauna has been prepared, and here we present a preliminary phase of this research. The aim is to distinguish potential modifications on bird bone surfaces and fracture patterns that might facilitate the recognition of human manipulation of avian skeletal remains. Building upon the challenges encountered in the study of archaeological findings recovered from recent excavations in Iberian Middle Palaeolithic sites, the experimental protocol was formulated to encompass the processing of two uncooked and three roasted birds; and the lithic use-wear analysis of the flint flake used in the processing of raw birds. The results showcase distinct patterns of bone surface modifications and breakage between cooked and uncooked birds. Higher numbers of cut marks and manual disarticulation breaks are found on raw animals, whereas roasted animals show no cut marks, local-specific burns and higher bone loss. This pilot-study provides a baseline for future research to further explore the role of avifauna in Neanderthal subsistence and food processing, which may help highlight cultural choices.

KEYWORDS

experimental archaeology, taphonomy, use-wear, cooked vs. raw meat processing, avifauna

1 Introduction

The investigation of human dietary behaviours has long been a central theme in palaeoanthropological research, offering crucial insights into the adaptive strategies and subsistence practices of early human populations. Among the various components of prehistoric diets, the consumption of birds by Neanderthals emerges as an interesting and, yet, scarcely studied facet. This dietary choice, involving the deliberate use of avian resources, represents a vital area of inquiry, as it holds the potential to illuminate essential aspects of Neanderthal culture, adaptation, and ecological interactions.

Neanderthals inhabited a diverse range of environments in Eurasia for over 200,000 years. Their ability to thrive across a broad geographical expanse has prompted investigations into the means by which these humans secured their sustenance. While the consumption of large game has received considerable attention (e.g., Smith, 2015; Weyrich et al., 2017; Gaudzinski-Windheuser et al., 2023), the role of birds in Neanderthal diet has been overshadowed. However, recent archaeological discoveries and advancements in analytical techniques have allowed the opportunity to reassess the importance of avian use by Neanderthals. Birds offer a complementary dietary resource that may have played an essential role in Neanderthal adaptation and survival (e.g., Rufà and Laroulandie, 2021; Blasco et al., 2022; Nabais et al., 2023). Additionally, the use of bird feathers and other bird products carries different implications, encompassing technological, social, and symbolic dimensions (e.g., Finlayson et al., 2012; Morin and Laroulandie, 2012; Radovcic et al., 2015; Rodríguez-Hidalgo et al., 2019).

To assess the importance of birds in Neanderthal lifeways, and diets in particular, it is imperative to have a multidisciplinary approach. Therefore, this study promotes the application of archaeological experimentation to investigate and document taphonomic alterations on avian remains through detailed examination of bird bone surface modifications. This experimental endeavour is essential for identifying human-related bone surface alterations—indicative of bird use, cooking, butchering and consumption—so they can be distinguished from natural processes and carnivore-induced damage. By simulating early human cooking and butchering techniques, this pilot-study will provide a baseline for further experimentation and research in the identification and understanding of the human-signatures of avian exploitation. It offers the potential to shed light on the technological capabilities, cultural choices and cognitive faculties of early humans' avian resource use.

2 Materials and methods

2.1 Bird taxa

Bird specimens were recovered from the Wildlife Ecology, Rehabilitation and Surveillance Centre (CERVAS), which is part of the ICNF Serra da Estrela Natural Park, located in Gouveia (Portugal). The birds died under natural conditions in this rehabilitation centre, following veterinary checks and then frozen in order to preserve for scientific research after death. Information regarding the bird species and date of death used were collected by Dr. Ricardo Brandão from CERVAS.

The selection of birds tried to represent species commonly associated with Neanderthal diets in the Iberian Peninsula (e.g., Blasco et al., 2014, 2016; Martínez Valle et al., 2016; Nabais et al., 2023). However, given that the obtainability of wild animals depends on their natural death and availability, the species used were the nearest equivalents to those discovered in archaeological sites—i.e., taxonomically close relatives, similar in size to other bird species consumed by Neanderthals. Hence, the species used were *Corvus corone* (carrion crow; Birds 2 and 4), *Columba palumbus* (common wood-pigeon; Bird 5), and *Streptopelia decaocto* (Eurasian collared-dove; Birds 1 and 3), with a total of five individuals used in the study (Table 1; Supplementary material 1). Bird specimens were let to defrost 24 h prior the start of the experimentation so that carcasses could resemble their original raw state and appearance.

2.2 Experimental protocol

The birds were photographed and measured prior to processing for experimental purposes (Table 1; Supplementary material 1). The archaeological experimentation was conducted at ICArEHB research centre (Faro, Portugal), in a controlled research environment designed to replicate Neanderthal techniques for the treatment and culinary preparation of avian species. Consequently, birds were prepared, cooked and processed according to archaeological evidence and ethnographic data (e.g., Osgood, 1971; Nicolaysen, 1980; Laroulandie, 2001; Blasco and Fernández Peris, 2009). To acquire a better understanding regarding diverse potential Neanderthal consumption practices, two individuals were butchered uncooked (*S. decaocto* and *C. corone*, corresponding to Birds 1 and 2), whereas the other three were butchered after cooking (*S. decaocto, C. corone,* and *C. palumbus*; or Birds 3, 4, and 5). All avian specimens started by being manually defeathered and then, in the case of the raw individuals, immediately butchered. The other three specimens were cooked by roasting in direct contact with the coals whenever the temperature reached 500°C; they were cooked defeathered and complete, without being broken before heat exposure (Figure 1). Temperature was permanently measured using an Infrared Thermometer HS 960D. Complete birds were initially roasted with their bellies on the coals for 4 min, and then turned around and cooked for another 3 min. Cooking durations were determined empirically, based on the assessment of the birds' meat's doneness, which occurs quickly when directly exposed to the coals.

The butchering techniques employed used manual handling, and movements such as flexion, twisting, pulling and overextension. Whenever needed, such actions were aided by an experimental flint flake (Supplementary material 1). The latter was produced by ICArEHB students during their practical sessions in lithic technology. Two of us (AR and MN) processed one raw bird specimen each (Birds 1 and 2, respectively). MN processed one roasted animal (Bird 5), and AR processed two (Birds 3 and 4). After processing, each bird's bones were placed in separate laundry bags to soak in Neutrase enzyme solution. This facilitates tissue

TABLE 1 Summary of bird specimens used in the experimental study detailing species name, corresponding rehabilitation centre (CERVAS) identifiers, date of death, physical measurements (body length and wingspan), state of conservation at the time of study, processing actions undertaken and duration of each experiment, and additional observations noted prior to and during the experimental procedure.

	Bird 1	Bird 2	Bird 3	Bird 4	Bird 5
Species	*Streptopelia decaocto*	*Corvus corone*	*Streptopelia decaocto*	*Corvus corone*	*Columba palumbus*
CERVAS number	U246/21/A	M456/23/A	V200/23/A	V191/20/A	V376/22/A
Date of death	18/06/2021	07/10/2023	22/06/2023	19/06/2020	13/08/2022
Body length	26 cm	40 cm	21 cm	30 cm	36 cm
Wingspan	46 cm	77 cm	37 cm	66 cm	62 cm
State of Conservation	Good preservation; all elements present	Good preservation; all elements present	Good preservation; all elements present	Good preservation; all elements present	Good preservation; all elements present
Actions	Raw	Raw	Roasted (for 7 min)	Roasted (for 7 min)	Roasted (for 7 min)
Manual processing duration	33 min	41 min	14 min	18 min	18 min
Observations	Young animal with feathers still forming	-	Young animal based on long bone epiphysis observation	Left tibiotarsus had a fracture	Several undigested corn grains were found in the bird's gut. Broken left wing

removal within a stable 34–55°C range over 3–12 h (Simonsen et al., 2011). Post-enzyme action, bones were cleaned, brushed, and sun-dried to deactivate the enzymes.

The birds' remains underwent macroscopic and microscopic analysis (using a Hirox HR 5000E in the LARC-Archaeosciences Laboratory, in Lisbon) to document modifications on bone surfaces. This included recording all marks such as cuts, their distribution, location, and orientation, as well as patterns of breakage like fragment size, fracture outlines, angles, and edges. Given that most avian skeletal remains unearthed from Palaeolithic contexts predominantly consist of appendicular elements (e.g., Mourer-Chauviré, 1983; Ericson, 1987; Blasco et al., 2016; Romero et al., 2017; Rufà et al., 2018), this pilot-study focused on these anatomical components, specifically the bones associated with the wings and legs.

All experimental actions were recorded with a Nikon D5300 camera, an iPhone 11 and an Android Pixel 4a, and the video files are archived at the CORA repository (https://dataverse.csuc.cat/dataset.xhtml?persistentId=doi%3A10.34810%2Fdata1216) for future reference and potential replication of this experimentation.

Finally, it is important to acknowledge that the experimental setting may not fully replicate the exact environmental conditions experienced by Neanderthals, and our butchering experience may not mimic the exact movements used by these early humans. Therefore, such limitations should be considered when interpreting our results.

2.3 Lithic use-wear analysis

Use-wear analysis refers to the study of traces present on the artefact's surfaces that result from the wear produced by human use. It takes into account the fact that repeated actions performed with a stone tool leave micro- and macroscopic evidence of friction. It heavily relies on experimental reference collections that aim to replicate past potential uses and understand the formation process of identifiable diagnostic traces, to which the archaeological material can be compared.

Based on experimental replication, researchers showed that these modifications are known to be the result of the interaction between different surfaces (i.e., tool and worked material), which causes a gradual removal or deformations of the natural surface. The character of the discipline is based on a pattern recognition method when assessing the typology, location, and distribution of the different types of wear traces (Semenov, 1964; Tringham et al., 1974; Kamminga, 1979; Keeley, 1980; Plisson, 1985; Gonzales Urquijo and Ibanez Estevez, 1994; Andrefsky, 2005; McPherron et al., 2014; Claud et al., 2019a,b). Comparing the use-wear observed on replicated tools used in experimental actions to use-wear found on archaeological artefacts, wear patterns found on artefacts have been successfully classified. It is a key discipline and currently the most reliable method for obtaining direct evidence on tool use.

Successful interpretations of stone tool use depend on as many lines of evidence as possible and must rely on the observation of both micro- and macroscopic use-wear. The present study combines the analysis of macroscopic features (scarring, edge rounding, and fractures) seen with low magnification with microscopic use-wear (such as polishes and striae) observed with high magnification microscopy and relies on comparisons with extensive experiments that have been previously completed on a wide range of rocks, including flint, and are broadly recognised as reliable references (Keeley, 1980; Gonzales Urquijo and Ibanez Estevez, 1994; Claud et al., 2019a).

The experimentally made flint flake (Supplementary material 1) used for processing the uncooked birds was submitted to macro- and microscopic analysis of tools' edges and probable use zones in LARC-Archaeosciences Laboratory (Lisbon, Portugal).

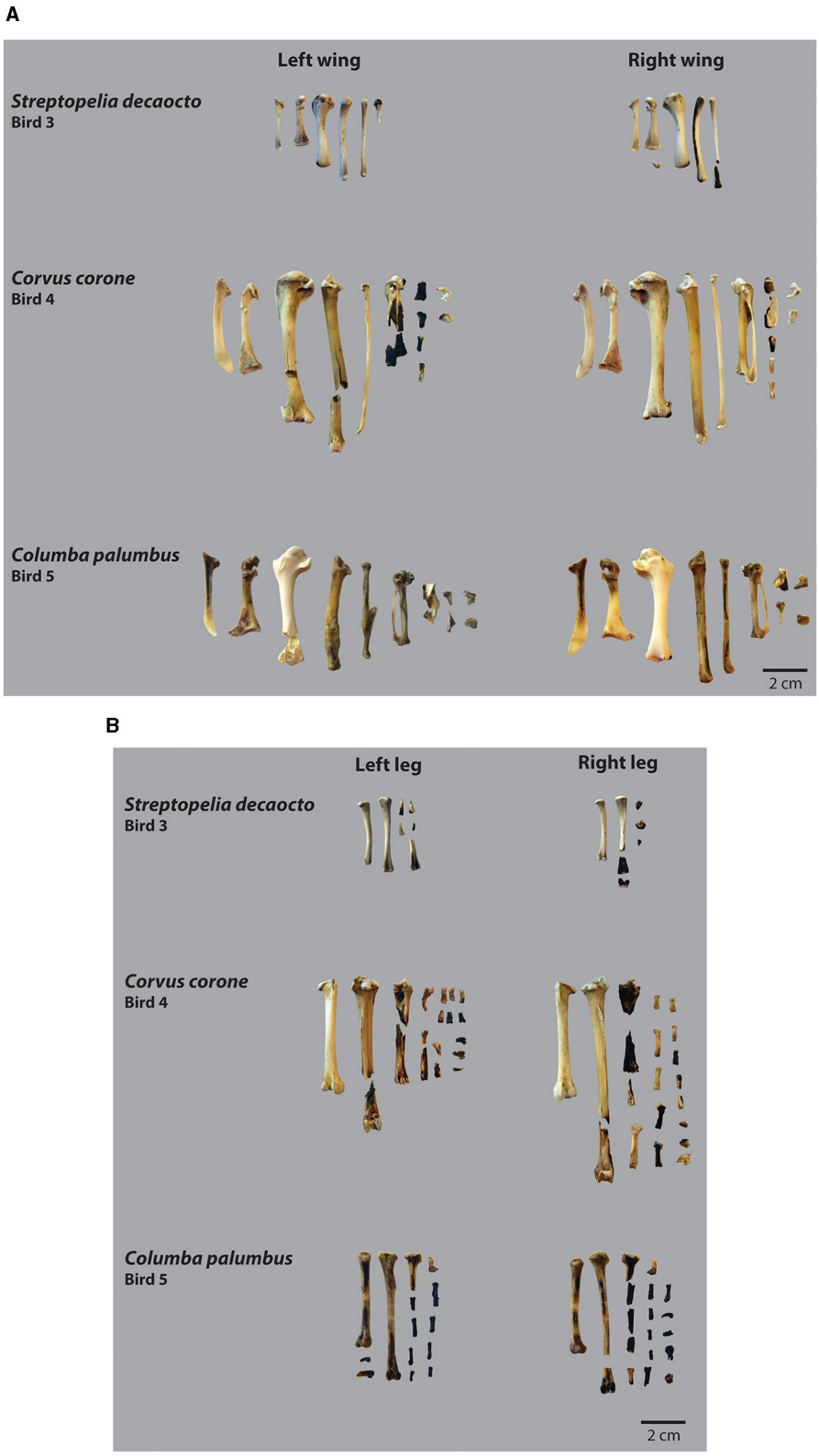

FIGURE 1
(A) Thermal alterations and impact of heat exposure on wing bones after experimental exposure to heat of three bird specimens, *Streptopelia decaocto, Corvus corone,* and *Columba palumbus*. **(B)** Thermal alterations and impact of heat exposure on leg bones after experimental exposure to heat of three bird specimens, *Streptopelia decaocto, Corvus corone,* and *Columba palumbus*.

Firstly, the flake was cleaned in order to remove any grease and residues that could adhere to it. Subsequently, the tool's edges and surfaces were examined under low and high magnifications by combining optical bright field reflected light and digital microscopy: the flake was first examined using an Olympus SZX12 and a Hirox HR 5000E, in order to macroscopically identify the used zones. Edges and surfaces were then analysed at high magnification with a Microscope Olympus BX60 for the observation and identification of the microscopic use-wear features indicative of specific materials worked and actions performed.

3 Results

3.1 Bird processing movements

All birds underwent initial manual plucking of feathers from the head, neck, and body by gripping the feathers at the skin joint and pulling them sharply away. Subsequently, the processing of both raw and roasted animals involved a similar sequence of actions. Manual handling was used for all, but roasted animals disarticulated more readily, without the need of a cutting tool. The birds' heads were manually detached by twisting and pulling them free from the cervical vertebra. The chest skin was then slit longitudinally with the flint flake along the sternum's centre line. Flesh was cut away and internal organs were carefully detached and removed intact.

Wings were detached by twisting, and for raw birds, a flint flake was used to sever tendons, which is particularly evident on the cuts found on the scapula, coracoid and humerus (Figure 2, Table 2). Regardless of whether the bird was raw or roasted, the scapula and coracoid stayed attached to the axial skeleton, separating from the wing bones. The humerus was disarticulated from the radius and ulna through flexion in a direction opposing the joint's natural movement. In some cases, this action resulted in minor fractures at the distal end of the humerus (Figure 2A–F) and the proximal end of the ulna (Figure 2A–I, L). Furthermore, the distal humerus occasionally exhibited a peculiar type of perforation (Figure 2B–D). These observations are consistent with the wrenching, squashing and notching previously documented by Laroulandie et al. (2008). A similar flexion motion was used to separate the radius and ulna from the carpometacarpus, resulting in wrenching observed on the proximal or distal joints of the bones (Figure 2B–E, G).

The legs were removed in a manner akin to the wings, using twisting motions and applying flexion and overextension to disarticulate the femur from the pelvis. On uncooked animals, tendons were cut using a flint flake, leaving cut marks on the proximal and mid-shaft of the femur (Figure 2A-N, P). Disarticulation from the tibiotarsus was achieved by flexing the femur against the joint's natural direction and through overextension, as well as with the aid of the flint flake resulting on marks on the proximal shaft of the tibiotarsus (Figure 2B–H, I). A similar technique was employed to separate the tibiotarsus from the tarsometatarsus without the necessity of using a flake. Flexion and overextension movements did not seem to cause any marks on the surface of leg bones, except for the wrenching identified on the roasted *Columba palumbus*' proximal tibiotarsus (Figure 1B, Table 2).

Through macroscopical observation, carrion crows were found to have minimal meat, in contrast to collared-doves, and wood pigeons in particular, which offered generous portions of breast filets and a significant amount of meat surrounding the femur. However, it is important to consider that the birds used were rescues and, as such, the meat yield from these animals might not accurately reflect that of birds in prime health. In roasted specimens, the meat fell away effortlessly, with no need for flint flakes. Conversely, processing raw specimens needed such tools for cutting the tendons, leaving cut marks on the long bones. Longitudinal cuts aimed at defleshing were made primarily on the humerus and femur, yet these did not imprint on bone surfaces. Therefore, only the transverse marks, indicative of tendon cutting or joint disarticulation, were observable.

3.2 Skeletal part representation and burning

A total of 265 bird bone remains, corresponding to complete and fragmented wing and leg elements, from five distinct individuals were collected following the experimental and cleaning procedures. Animals that underwent processing in their raw state retained the entirety of their skeletal representation, while those that were roasted exhibited a predisposition to bone fracture and loss (Table 2, Supplementary material 2). The roasted dove (Bird 3) presented a skeletal loss of 57.1%, corresponding to a total of 29 remains that disappeared during burning. Conversely, the roasted crow (Bird 4) had an increase in the number of remains, due to higher bone breakage (Figure 1, Supplementary material 2). Bones subjected to heat tend to fracture more readily even in the absence of burning marks. Observations indicate that the content of the inner cavity of the bone also combusts internally increasing its fragility. This phenomenon is particularly evident in the wing bones of the carrion crow and the wood pigeon (Figure 1A), where a dark longitudinal stain is commonly found inside the long bones.

Evidence of charring was found on nearly all the bird bones subjected to heat (Figure 1; Table 2). Exceptions included the two humeri of the *Columba palumbus*, the scapula, ulnar carpal, and femur of the *Streptopelia decaocto*, and eighteen skeletal parts of the *Corvus corone*, comprising the scapula, coracoid, humeri, ulnae, radii, both ulnar and radial carpals, the first phalanx of the minor digit, femora, and the second and third phalanges. Leg bones tend to be more frequently and intensively charred than wing bones. All thermal alterations are either brown or black burns. Long bones generally exhibit a brown discolouration from heat, with localised blackened areas, mainly on their epiphyses and along the shafts. While the majority of charred bones exhibit a single colouration from burning, instances of double-coloured charring have also been observed.

3.3 Use-wear on flint flake

The experimentally replicated flake used in the processing of the two uncooked bird specimens, *Streptopelia decaocto* and *Corvus corone*, shows micro- and macroscopic recognisable use-wear typical of cutting up meat in the scope of butchering.

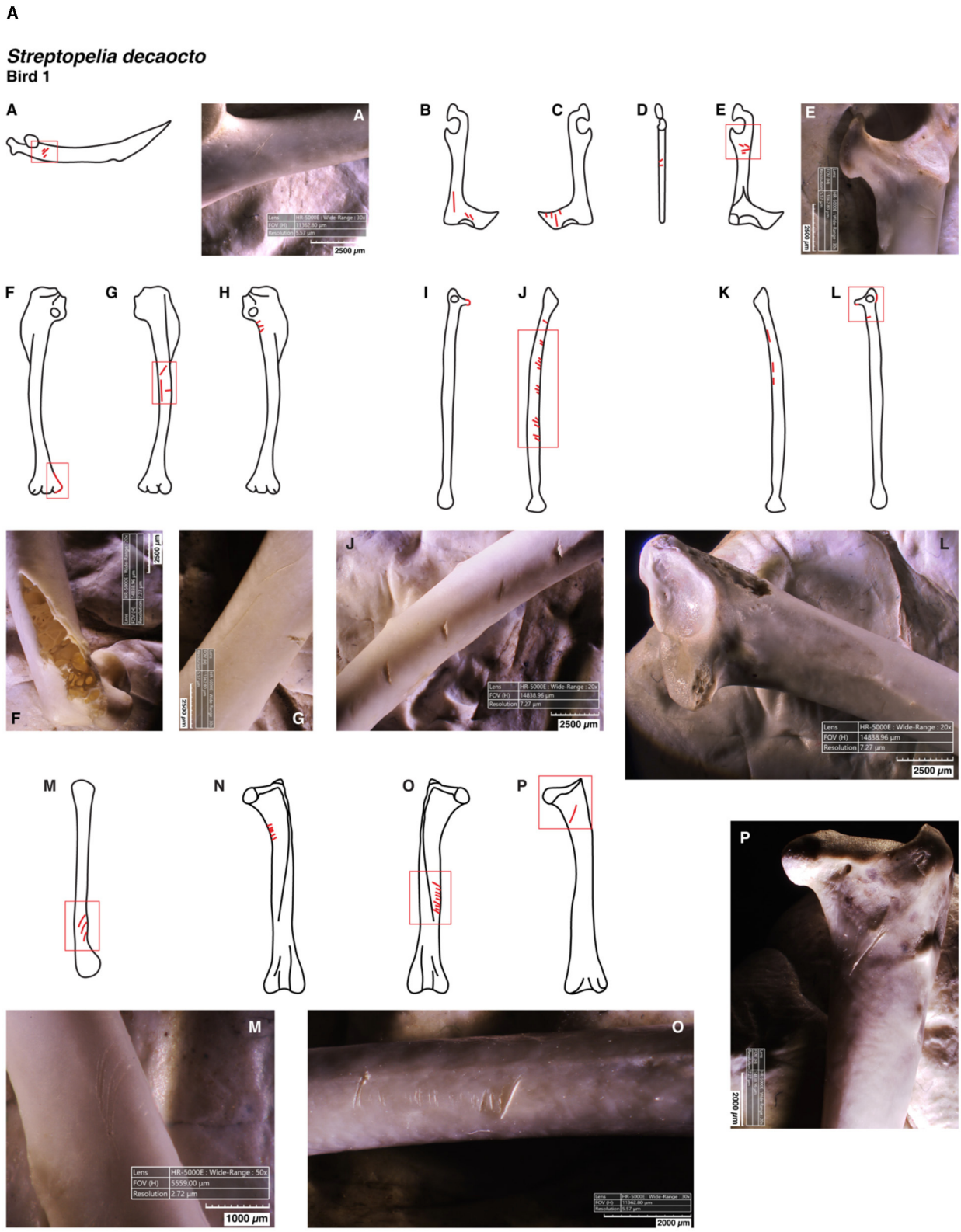

FIGURE 2
(A) Bone surface modifications on the appendicular skeleton of *Streptopelia decaocto* after being experimentally processed uncooked. Illustrations are not drawn to scale and should be interpreted as conceptual sketches; they are not suitable for species identification. A - Right scapula (lateral side): cut marks. B - Left coracoid (dorsal side): cut marks. C - Right coracoid (dorsal side): cut marks. D - Right coracoid (medial side): cut marks. E - Right coracoid (ventral side): cut marks. F - Left humerus (posterior side): notching. G - Left humerus (anterior side): cut marks. H - Right humerus (posterior side): cut marks. I - Left ulna (anterior side): wrenching mark. J - Left ulna (medial side): cut marks. K - Right ulna (medial side): cut marks. L - Right ulna (anterior side): wrenching and cut marks. M - Left radius (medial side): cut marks. N - Left femur (cranial side): cut marks. O - Right femur (cranial side): cut marks. P - Right femur (caudal side): cut marks.

(Continued)

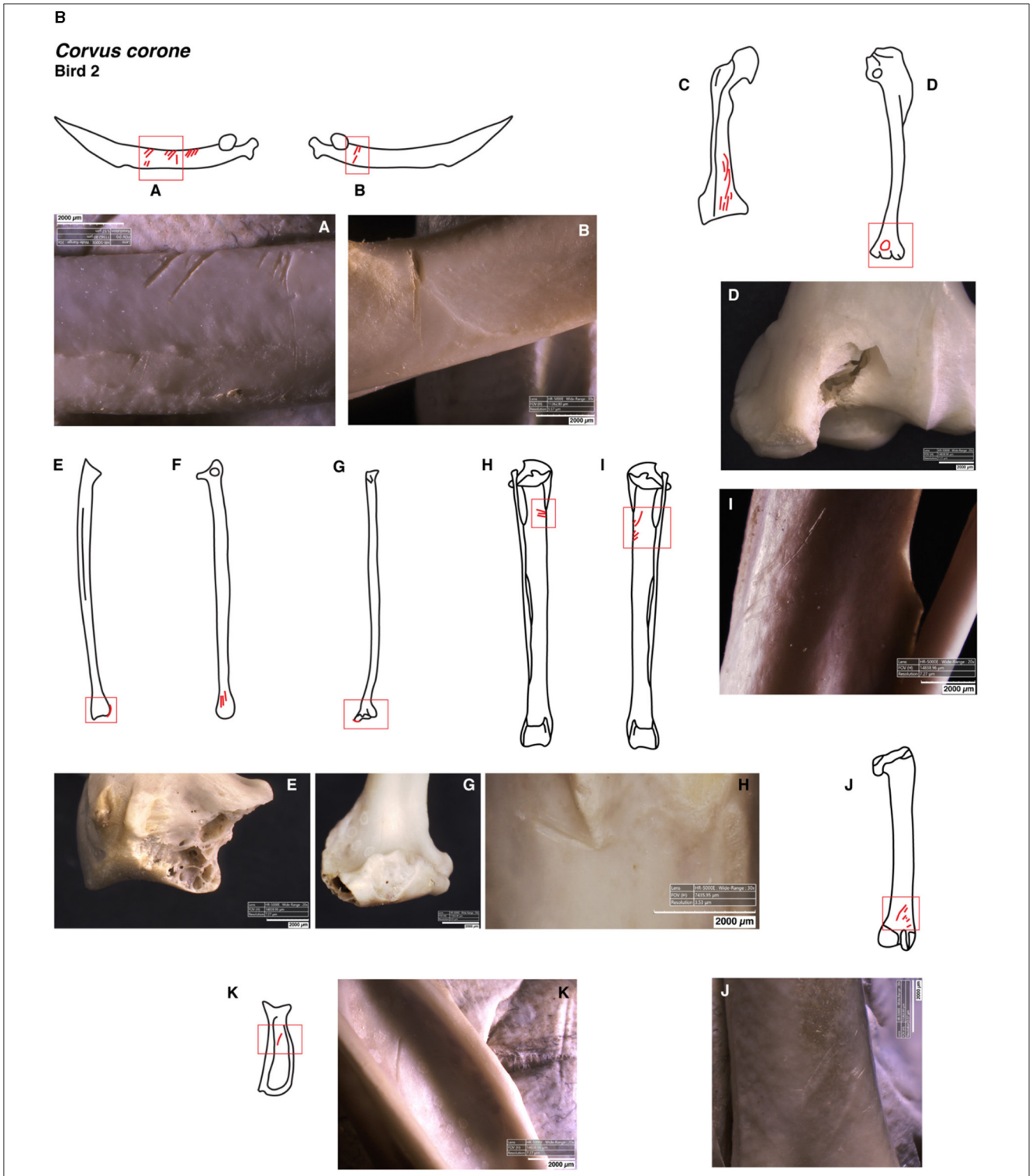

FIGURE 2 (Continued)
(B) Bone surface modifications on the appendicular skeleton of *Corvus corone* after being experimentally processed uncooked. Illustrations are not drawn to scale and should be interpreted as conceptual sketches; they are not suitable for species identification. A - Left scapula (lateral side): cut marks. B - Right scapula (lateral side): cut marks. C - Right coracoid (dorsal side): cut marks. D - Right humerus (posterior side): squashing mark. E - Right ulna (lateral side): wrenching mark. F - Right ulna (anterior side): cut marks. G - Right radius (lateral side): wrenching mark. H - Left tibiotarsus (caudal side): cut marks. I - Right tibiotarsus (caudal side): cut marks. J - Right femur (caudal side): cut marks. K - Right major digit phalanx 1: cut mark.

TABLE 2 Bone surface modifications of the five bird specimens following the experimental processing.

Streptopelia decaocto Bird 1 (raw)		*Corvus corone* Bird 2 (raw)		*Streptopelia decaocto* Bird 3 (roasted)		*Corvus corone* Bird 4 (roasted)		*Columba palumbus* Bird 5 (roasted)	
Cut		Cut		Cut		Cut		Cut	
Scapula	1	Scapula	2	None	27	None	66	None	55
Coracoid	2	Coracoid	1	% Cut	0	% Cut	0	% Cut	0
Humerus	2	Ulna	2						
Ulna	2	Major Digit Phalanx 1	1						
Radius	1	Femur	1						
Femur	2	Tibiotarsus	2						
None	46	None	52						
% Cut	**17.9**	**% Cut**	**14.8**						
Wrenching		Wrenching		Wrenching		Wrenching		Wrenching	
Humerus	1	Coracoid	1	None	27	None	66	Tibiotarsus	1
Ulna	2	Ulna	2	% Wrenching	0	% Wrenching	0	None	54
None	53	Radius	1					**% Wrenching**	**1.8**
% Wrenching	**5.4**	Carpal Ulnar	2						
		None	55						
		% Wrenching	**9.8**						
Squashing and notching		Squashing and notching		Squashing and notching		Squashing and notching		Squashing and notching	
None	56	Humerus	2	None	27	None	66	None	55
% Squashing and Notching	0	None	59	% Squashing and Notching	0	% Squashing and Notching	0	% Squashing and Notching	0
		% Squashing and Notching	**3.3**						
Burning		Burning		Burning		Burning		Burning	
None	56	None	61	Brown	7	Brown	14	Brown	11
% Burning	0	% Burning	0	Black	16	Black	25	Black	38
				None	4	Brown-Black	9	Brown-Black	4
				% Burning	**85.2**	None	18	None	2
						% Burning	**72.7**	**% Burning**	**96.4**

In the table, the designation "None" is used to indicate bone remains from the experiment that displayed no surface modifications.

Use-wear traces are tenuous, which is consistent to the working of a light butchery and over a short time. The set of use-wear features observed are similar to those mentioned by other authors on experimental pieces used in experimental butchery (Semenov, 1964; Keeley, 1980; Plisson, 1985; Gonzales Urquijo and Ibanez Estevez, 1994; Claud et al., 2019a; Costamagno et al., 2019).

Particularly noteworthy is the presence, on both sides, of the used edge of small isolated scars. These are "half-moon" shaped scars distributed along the edge and associated with a reticular shaped polish that can be observed at low and high magnifications. The edge removals result from the contact between the flake and the fibrous textures of avian muscle tissue that occasionally touched more resistant material, such as bone or cartilage (Figure 3).

No striations nor any edge rounding is observed. Edge rounding is usually associated with skin processing rather than with meat cutting (Keeley, 1980; Gonzales Urquijo and Ibanez Estevez, 1994).

4 Discussion

This pilot study reveals some initial patterns concerning the processing of bird remains that bear on archaeological interpretations of similar assemblages. We observed that when processing the carrion crow, it needed a longer processing time than the collared-dove, in particular when processed uncooked, which could be related to the larger size of this bird species. This aligns with the practical understanding of meat preparation, where cooked specimens provide easier meat access with, for instance, breast meat cutlets coming out effortlessly. However,

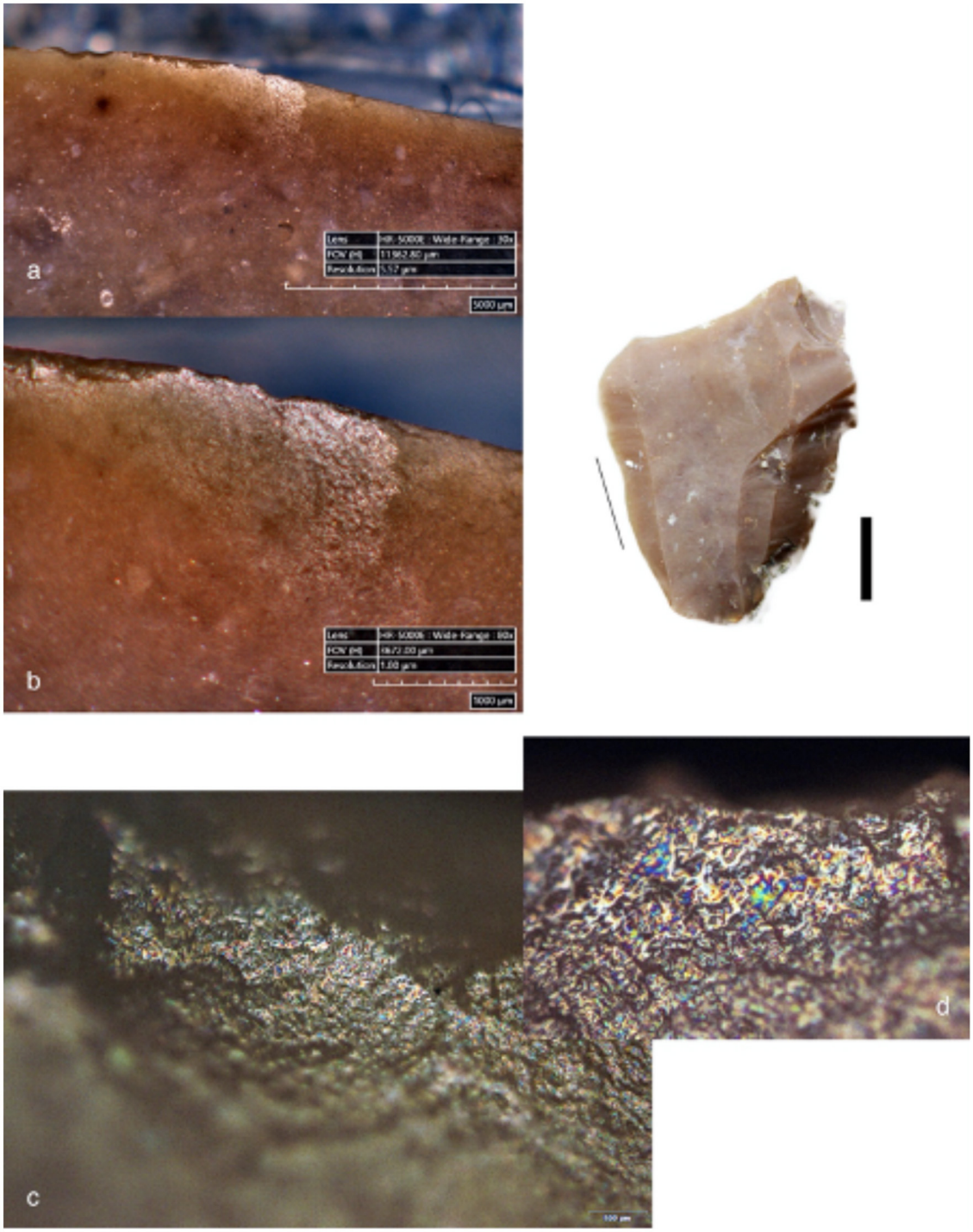

FIGURE 3
Microscopic use-wear patterns on a flint flake following experimental processing. The image highlights the scars and polish distributed along the used edge of the experimental flint flake visible at low magnification using a digital microscope Hirox HR500E **(a, b)**. Details of the same polish at high magnification (200x) using an Olympus BX60 optical microscope **(c, d)**.

larger birds, like the carrion crow, do not necessarily provide more substantial meat yields. The wood pigeon, noted for its ample meat quantity, especially around the breast filets and femur, supports the observations (1) that smaller birds can yield more edible meat than larger birds, and (2) that larger birds are not always sought after primarily for their meat content. This is consistent with findings from Gibraltar, where pigeons, and some corvids, were targeted for their meat (Blasco et al., 2014, 2016), while raptors were valued for their feathers (Finlayson et al., 2012). However, there are instances when raptors were also used for food (Gómez-Olivencia et al., 2018). Nonetheless, a growing body of Middle Palaeolithic research demonstrates that large birds were frequently sought for their

feathers, and also for their phalanges (e.g., Peresani et al., 2011; Morin and Laroulandie, 2012; Radovcic et al., 2015; Rodríguez-Hidalgo et al., 2019), even if some use for food is also suggested (see references in Gómez-Olivencia et al., 2018). These practices have been further substantiated by various experimental studies (e.g., Pedergnana and Blasco, 2016; Romandini et al., 2016; Rufà et al., 2023).

In our experimentation, most bird specimens were processed by hand, without tools. The evidence of this manual processing is apparent in the form of twisting, crushing, and indenting marks, which were defined by Laroulandie et al. (2008) as wrenching, squashing and notching marks. These are evident on the distal humerus (Figure 2A–F, B–D), and on the ends of ulnas and radius (Figure 2A–I, L, B–E, G). Moreover, no tools were used to process the roasted specimens, other than cutting their chest line, indicating that cooking facilitated meat removal, thereby reducing/removing the need for their use. Additionally, the use of hammerstones was not required at any stage of our experimentation, which led to a total lack of percussion marks or breakage patterns associated with such actions (i.e., impact flakes or percussion notches).

Conversely, a lithic tool was necessary for processing raw birds. This is noted by the presence of cut marks on some uncooked appendicular skeleton bones. A flake was mainly used for cutting the tendons and to disarticulate bone joints. These actions are particularly visible by the transversal straight cuts that cluster on the scapulas' proximal and mid-shafts (Figure 2A–A, B–A, B), as well as on coracoids (Figure 2A–B–E, B–C). The same applies to the femurs and tibiotarsus from our uncooked sample, with predominance of oblique and transverse cuts in their shafts (Figure 2A–N–P, B–H–J). Although scapulas tend not to preserve well in archaeological contexts, the incisions found on coracoids, femurs and tibiotarsus agree with food provisioning actions, such as those found in Gorham's Cave (Blasco et al., 2016), for example.

The colouration of the burnt bones, exclusively brown and black, is consistent with the fact that these remains are associated with cooking activities (e.g., Nicholson, 1993). The absence of grey and white burns, which are characteristic of exposure to higher temperatures and longer burning times, supports the idea that the bird bones from the current experiment—which show brown and black burns—were subjected to controlled cooking rather than accidental or uncontrolled fire exposure. Notably, some bones, like the humerus, do not exhibit extensive burning marks, which is attributable to the thicker flesh surrounding them that may act as a barrier, insulating the bone from direct heat exposure. Conversely, bones with less surrounding meat, such as those in the limbs' extremities, display a greater propensity to burn, as evidenced by their charred appearance (as also noted by other studies, such as Cassoli and Tagliacozzo, 1997; Laroulandie, 2005; Blasco and Fernández Peris, 2009; Blasco et al., 2013, 2014).

The latter observation also highlights issues of skeletal loss. This is particularly evident in the roasted collared-dove (Bird 3), where the bird's extremities, especially the phalanges, became so fragile and brittle that they shattered into tiny, unrecoverable fragments. Similarly, higher bone breakage was noted in the roasted carrion crow (Bird 4), although this breakage did not lead to the complete disappearance of bones. Another observation made while handling the bones post-heat exposure was that some of the intact bones exhibited black staining on their inner surfaces. This occurred in instances where there appeared to be no direct contact between the bone's inner cavity and the heat source, since bones were not broken prior to heat exposure. Nonetheless, it seems that the inner structure of the bones, specifically the thin bar-like struts, had been burnt, rendering them more fragile and susceptible to breakage. These observations underscore the fact that bones from roasted birds tend to be underrepresented in archaeological assemblages. As burnt bird bones are prone to breakage and loss, roasting activities may therefore go undetected in archaeological sites.

The analysis of use-wear patterns on lithic artefacts provides invaluable insights into the technological behaviours and subsistence strategies of past human populations. Our use-wear results are consistent with the observations made by Pedergnana and Blasco (2016) during the defeathering of a *Circaetus gallicus* and a *Gyps fulvus*, since the use-wear observed on the flake that was used in our pilot experiment is under developed as well. This phenomenon may be attributed to the fact that we worked with less robust animals, which likely resulted in less damage to the flake used. Additionally, the flake shows few "half-moon" shaped scars distributed along the used edge, associated with polish.

All these observations not only have implications for the efficiency of food preparation but may also influence the archaeological visibility of butchery practices. Following the research line of this pilot study, future experimental approaches related to Neanderthal exploitation of birds are aimed to focus on expanding the variety of bird species examined in order to capture the range of avian life that early humans might have encountered and used. This would allow for a detailed comparison of processing times, meat yields, and bone preservation across species of different sizes and ecological roles. Nutritional analysis of the different bird species and preparation methods would also shed light on their contribution to Neanderthal diets. Additionally, amplifying the array of taphonomic studies, including human and other carnivores' bird bone chewing, as well as bird processing for the use of non-food elements (like feathers, tendons or some specific bones) could deepen our understanding of the role birds played within early human diets, but also beyond mere sustenance.

5 Conclusions

This pilot study has contributed to the growing body of experimental evidence providing insights into the replication of early human behaviour concerning the preparation and consumption of birds, focusing particularly on the implications of cooked vs. raw processing methods. Raw birds presented several cut marks, mainly associated with bone disarticulation and tendon cutting. The use of a flint flake for food processing was also detected by lithic use-wear observations. Conversely, cooked birds exhibited no cut marks and greater bone loss when compared to raw birds. This was due to heat exposure, which makes the disarticulation process and the removal of meat much easier and led to bone fragility and breakage. Such observations suggest that cooking methods significantly affect the preservation of skeletal remains in

archaeological contexts, potentially influencing the archaeological visibility of certain cooking practices.

Our study contributes to the broader discourse on Neanderthal subsistence strategies by offering experimental data that can help interpret cut mark patterns and cooking-related bone alterations found in archaeological assemblages. By simulating Neanderthal cooking and butchering techniques, this research provides a baseline for distinguishing human-related modifications from those caused by natural processes or other predators. However, acknowledging the limitations of our experimental setup, including the small sample size and a single cooking technique, this study calls for further research incorporating a wider range of avian species and different cooking methods. Such expansions are essential to fully understand the range of Neanderthal dietary practices, their complex interactions with their environment, and their adaptive strategies and cultural development across different ecological changes.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because these were animals recovered dead from a rehabilitation centre as well described in the methods section of the paper.

Author contributions

MN: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AR: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. MI: Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, 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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References

Andrefsky, W. (2005). *Lithics: Macroscopic Approaches to Analysis, Second edition* Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511810244

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Chapter 8 – Small animal use by Neanderthals," in *Updating Neanderthals. Understanding Behavioural Complexity in the Late Middle Palaeolithic,* eds. F. Romagnoli, F. Rivals, and S. Benazzi (New York: Elsevier Academic Press), 123–143. doi: 10.1016/B978-0-12-821428-2.00010-X

Blasco, R., and Fernández Peris, J. (2009). Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 36, 2213–2223. doi: 10.1016/j.jas.2009.06.006

Blasco, R., Finlayson, C., Rosell, J., Sánchez Marco, A., Finlayson, S., Finlayson, G., et al. (2014). The earliest pigeon fanciers. *Sci. Rep.* 4:5971. doi: 10.1038/srep05971

Blasco, R., Rosell, J., Fernández Peris, J., Arsuaga, J. L., and Bermúdez, de Castro, J. M., Carbonell, E. (2013). Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de

Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quat. Sci. Rev.* 70, 124–144. doi: 10.1016/j.quascirev.2013.03.008

Blasco, R., Rosell, J., Rufà, A., Sánchez Marco, A., and Finlayson, C. (2016). Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quater. Int.* 421, 62–77. doi: 10.1016/j.quaint.2015.10.040

Cassoli, P. F., and Tagliacozzo, A. (1997). Butchering and cooking of birds in the palaeolithic site of Grotta Romanelli (Italy). *Int. J. Osteoarchaeol.* 7, 303–320. doi: 10.1002/(SICI)1099-1212(199707/08)7:4<303::AID-OA380>3.0.CO;2-R

Claud, E., Thiébaut, C., Costamagno, S., Deschamps, M., Soulier, M. C., Brenet, M., et al. (2019b). The practices used by the Neanderthals in the aquisition and exploitation of plant and animal resources and the function of the sites studied: summary and discussion. *Palethnologie* 10:4179. doi: 10.4000/palethnologie.4179

Claud, E., Thiébaut, C., Coudenneau, A., Deschamps, M., Mourre, V., Brenet, M., et al. (2019a). Le référentiel des outils lithiques. *Palethnologie* 10:5142. doi: 10.4000/palethnologie.5142

Costamagno, S., Claud, E., and Thiébaut, C., Chacón-Navarro, M., Soulier, M. C. (2019). L'exploitation des ressources végétales et animales au Paléolithique: quels outils méthodologiques pour quelles questions? *Palethnologie* 10:3866. doi: 10.4000/palethnologie.3866

Ericson, G. P. (1987). Interpretations of archaeological bird remains: a taphponomic approach. *J. Archaeol. Sci.*14, 64–75. doi: 10.1016/S0305-4403(87)80006-7

Finlayson, C., Brown, K., Blasco, R., Roseli, J. N., J., Bortolotti, G., et al. (2012). Birds of a feather: neanderthal exploitation of raptors and corvids. *PLoS ONE* 7, 1–9. doi: 10.1371/annotation/5160ffc6-ec2d-49e6-a05b-25b41391c3d1

Gaudzinski-Windheuser, S., Kindler, L., Macdonald, K., and Roebroeks, W. (2023). Hunting and processing of straight-tusked elephants 125.000 years ago: implications for Neanderthal behavior. *Sci. Adv.* 9:eadd8186. doi: 10.1126/sciadv.add8186

Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garaizar, J., et al. (2018). First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* 8, 1–14. doi: 10.1038/s41598-018-28377-y

Gonzales Urquijo, J. E., and Ibanez Estevez, J. J. (1994). *Metodologia de analisis functional de instrumentos tallados en silex*. Bilbao: Universidad de Deusto, 301.

Kamminga, J. (1979). "The nature of use polish and abrasive smoothing on stone tools," in *Lithic Use-wear Analysis,* ed. B. Hayden (New York: Academic Press), 143–158.

Keeley, L. H. (1980). *Experimental Determination of Stone Tool Uses. A Microwear Analysis*. Chicago: University of Chicago Press.

Laroulandie, V. (2001). ≪ Les traces liées à la boucherie, à la cuisson et à la consummation d'oiseaux: apport de l'expérimentation," in *Préhistoire et approche expérimentale. Collection préhistoire 5,* eds. L. Bourguignon, I. Ortega, M.-C. Frère-Sautot (Montagnac : Monique Mergoual), 97–108.

Laroulandie, V. (2005). "Bird exploitation pattern: the case of *Ptarningan Lagopus* sp. in the Upper Magdalenian site of la Vache (Ardiège, France)," in *Feathers, Grid and Symbolism Birds and Humans in the Ancient Old and New Worlds*, eds. G. Grupe, J. Peters (Munich: Proceedings of the 5th. Meeting of the ICAZ), 165–178.

Laroulandie, V., Costamagno, S., Cochard, D., Mallye, J. B., Beauval, C., Castel, J. C., et al. (2008). When disarticulation causes bone damage. The case of the hyperextension of the elbow. *Ann. Paléontol.* 94, 287–302. doi: 10.1016/j.annpal.2008.09.002

Martínez Valle, R., Guillem Calatayud, P. M., and Villaverde Bonilla, V. (2016). Bird consumption in the final stage of Cova Negra (Xátiva, Valencia). *Quater. Int.* 421, 85–102. doi: 10.1016/j.quaint.2016.01.068

McPherron, S., Braun, D., DogandŽi,ć, T., Archer, W., and Desta, D. (2014). An experimental assessment of the influences on edge damage to lithic artifacts: a consideration of edge angle, substrate grain size, raw material properties, and exposed face. *J. Archaeol. Sci.* 49, 70–82. doi: 10.1016/j.jas.2014.04.003

Morin, E., and Laroulandie, V. (2012). Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE* 7:e32856. doi: 10.1371/journal.pone.0032856

Mourer-Chauviré, C. (1983). "Les oiseaux dans les habitats paléolithiques: gibier des hommes ou proies des rapaces?" in *Animals and Archaeology: 2. Shell Middens, Fishes and Birds*, eds. C. Grigson, J. Clutton-Brock (Oxford: BAR International Series 183), 111–124.

Nabais, M., Pimenta, C., and Zilhão, J. (2023). Human-bird interaction in last Interglacial Iberia: a combined approach using skeletal part analysis, bone surface modification, bird ethology and ethnography. *J. Archaeol. Sci.*49:104023. doi: 10.1016/j.jasrep.2023.104023

Nicholson, R. (1993). A morphological investigation of burnt animal bone and an evaluation of its utility in archaeology. *J. Archaeol. Sci.* 20, 411–428. doi: 10.1006/jasc.1993.1025

Nicolaysen, R. (1980). Arctic nutrition. *Perspect. Biol. Med.* 1980, 295–310. doi: 10.1353/pbm.1980.0061

Osgood, C. (1971). *The Han Indians: A Compilation of Ethnographic and Historical Data on the Alaska-Yukon Boundary Area*. Yale University Publications in Anthropology, Number 74. New Haven: Department of Anthropology Yale University.

Pedergnana, A., and Blasco, R. (2016). Characterising the exploitation of avian resources: An experimental combination of lithic use-wear, residue and taphonomic analyses. *Quater. Int.* 421, 255–269. doi: 10.1016/j.quaint.2015.07.025

Peresani, M., Fiore, I., Gala, M., Romandini, M., and Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc. Nat. Acad. Sci.* 108, 3888–3893. doi: 10.1073/pnas.1016212108

Plisson, H. (1985). *Etude fonctionnelle d'outillages lithiques prehistoriques par l'analyse des micro-usures: recherche méthodologique et archéologique.* Uni-versité Paris I, thèse doctorat, sciences humaines, 357.

Radovcic, D., Oros Srsen, A., Radovcic, J., and Frayer, D. W. (2015). Evidence for Neandertal Jewelry: Modified White-Tailed Eagle Claws at Krapina. *PLoS ONE* 10:e0119802. doi: 10.1371/journal.pone.0119802

Rodríguez-Hidalgo, A., Morales, J. I., Cebrià, A., Courtenay, L. A., Fernández-Marchena, J. L., García-Agudo, G., et al. (2019). The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. *Sci. Adv.* 5:eaax1984. doi: 10.1126/sciadv.aax1984

Romandini, M., Fiore, I., Gala, M., Cestari, M., Guida, G., Tagliacozzo, A., et al. (2016). Neanderthal scraping and manual handling of raptor swing bonés: Evidence from Fumane Cave. Experimental activities and comparison. *Quater. Int.* 421, 154–172. doi: 10.1016/j.quaint.2015.12.078

Romero, A. J., Díez, J. C., and Brugal, J. P. (2017). Aves de caza. Estudio tafonómico y zooarqueológico de los restos avianos de los niveles musterienses de Pié Lombard (Alps-Maritimes, Francia). *Munibe* 68, 73–84. doi: 10.21630/maa.2017.68.14

Rufà, A., Blasco, R., Roger, T., Rué, M., and Daujeard, C. (2018). A rallying point for different predators: the avian record from a Late Pleistocene sequence of Grotte des Barasses II (Balazuc, Ardèche, France). *Archaeol. Anthropol. Sci.* 10, 1459–1476. doi: 10.1007/s12520-017-0469-6

Rufà, A., and Laroulandie, V. (2021). Unravelling the taphonomic stories of bird bones from the middle pleistocene layer VIII of Grotte Vaufrey, France. *Quaternary* 4:30. doi: 10.3390/quat4040030

Rufà, A., Martin, C., and Laroulandie, V. (2023). "Searching for raptor feathers and talons: Results of an experimental approach," in *Hiatus, lacunes et absences: identifier et interpreter les vides archéologiques, Actes du 29e Congrès préhistorique de France, 31 mai – 4 juin 2021*, Toulouse, 25–40.

Semenov, S. A. (1964). *Prehistoric Technology: An Experimental Study of the Oldest Tools and Artefacts from Traces of Manufacture and Wear*. London: Cory, Adams and Mackay.

Simonsen, K. P., Rasmussen, A. R., Mathisen, P., Petersen, H., and Borup, F. (2011). A fast preparation of skeletal materials using enzyme maceration. *J. Foren. Sci.* 56, 480–484. doi: 10.1111/j.1556-4029.2010.01668.x

Smith, G. (2015). Neanderthal megafaunal exploitation in Western Europe and its dietary implications: a contextual reassessment of La Cotte de St Brelade (Jersey). *J. Hum. Evol.* 78, 181–201. doi: 10.1016/j.jhevol.2014.10.007

Tringham, R., Cooper, G., Odell, G., and Voytek, B. (1974). Experimentation in the formation of edge damage: a new approach to lithic analysis. *J. Field Archeol.* 1, 171–196. doi: 10.1179/jfa.1974.1.1-2.171

Weyrich, L., Duchene, S., Soubrier, J., Arriola, L., Llamas, B., Breen, J., et al. (2017). Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. *Nature* 544, 357–361. doi: 10.1038/nature21674

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Neanderthal exploitation of birds in north-western Europe: Avian remains from Scladina Cave (Belgium)

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For a long time, Neanderthals were considered hunters of large mammals, whereas the diversification of the exploited faunal spectrum to include smaller taxa, including birds, was assumed to be specific to anatomically modern humans. In recent decades, archeozoological analyses of faunal remains from layers associated with Middle Paleolithic lithic industries have revealed traces of human manipulation of small taxa, indicating the exploitation of a wider range of animals than previously thought. These new data have challenged the view that Neanderthals did not exploit small animals, thereby narrowing the behavioral gap with anatomically modern humans. Nevertheless, the information currently available comes almost exclusively from southern Europe and the nature of Neanderthal small fauna exploitation in northern Europe remains largely unknown. The present study aims to fill this gap by applying archeozoological methods, including detailed taphonomic and traceological analyses, to 119 bird remains recovered from layers containing Middle Paleolithic industries at Scladina Cave, Belgium. Analyses of proteomics were applied to clarify the taxonomic identity of two morphologically non-diagnostic elements. Modifications made by non-human predators or scavengers, suggest that mammalian carnivores are responsible for accumulating a considerable portion of the avian assemblage. In total, seven bird bones exhibit anthropogenic marks, and one element presents questionable marks. Various Galliformes taxa and a great cormorant were exploited likely for their meat. The talon of a likely lesser spotted eagle displays intense polishing possibly linked to human manipulation of this element, although this remains hypothetical. On the radius of a Western capercaillie, two deep incisions may indicate bone working, and intense use-wear indicates that the bone has been utilized, potentially on soft organic material. This study provides the first evidence of the exploitation of birds by Neanderthal in Belgium and constitutes the only detailed zooarchaeological analysis of Middle Paleolithic bird material in northwestern Europe. The likely modification and subsequent utilization of a bird bone is only the second example known from Neanderthal occupations in Eurasia. The novel taxa identified as Neanderthal prey highlight the plasticity of Neanderthal ecological

behavior, adapting to different landscapes and climates and exploiting a large spectrum of locally available prey.

KEYWORDS

archaeozoology, middle paleolithic, neanderthal-bird relationships, taphonomy, tool marks, traceology, use-wear analysis

1 Introduction

1.1 Historical background and archaeological perspective

Traditionally, Neanderthals were considered hunters of large mammals (Rabinovich and Tchernov, 1995; Hoffecker and Cleghorn, 2000; Speth and Tchernov, 2007; Gaudzinski-Windheuser and Niven, 2009; Delagnes and Rendu, 2011), whereas the diversification of the exploited faunal spectrum to include smaller, faster taxa was assumed to be specific to anatomically modern humans. Building on Flannery (1969)'s post-Paleolithic broad spectrum revolution (BSR), researchers suggested that the true diversification of dietary exploitation took place during the transition between the Middle to Upper Paleolithic (Stiner, 2001; Hockett and Haws, 2002; Stiner and Munro, 2002) driven by the alleged greater cognitive capacities of the anatomically modern humans moving out of Africa and into the Eurasian Neanderthal homelands.

However, in recent decades, multiple lines of evidence indicating complex cultural behavior in Neanderthals have emerged, demonstrating that they manufactured bone tools (Soressi et al., 2013; Abrams et al., 2014; Hutson et al., 2018), practiced hafting and hunted with stone projectiles (Rots, 2013, 2015), collected marine shells, stones, and pigment for aesthetic purposes (Soressi and d'Errico, 2007; Zilhão et al., 2010; Radovčić et al., 2016), produced abstract signs (Rodríguez-Vidal et al., 2014; Hoffmann et al., 2018), and engaged in mortuary practices (Maureille and Van Peer, 1998; Rendu et al., 2014; Maureille et al., 2016) at several sites across Europe predating the arrival of anatomically modern humans. Collectively, these studies have led to a shift in our perception of Neanderthals from archaic distant relatives to cognitively equal contemporaries of anatomically modern humans in the Pleistocene landscapes (Villa and Roebroeks, 2014; Romagnoli et al., 2022).

Archeozoological analyses of faunal assemblages from Middle Paleolithic sites, especially those focusing on the small mammal and avian components, have shed further light on the necessity for sophisticated hunting, and on dietary practices of Neanderthals. At several sites in southern Europe, traces of Neanderthal manipulation of small taxa are now relatively frequent, indicating the exploitation of a wider range of animals than previously thought, including small or fast-moving animals such as mollusks, leporids, marine mammals, and birds, some of which present challenges in their collection (Stiner et al., 2000; Speth and Tchernov, 2002; Stringer et al., 2008; Bonjean et al., 2012; Blasco et al., 2014, 2016, 2022; Morin et al., 2019; Zilhão et al., 2020).

Rock doves, corvids and Galliformes are the most commonly documented food bird species exploited by Neanderthals. Cutmarks and thermal modifications identified on bones from Middle Paleolithic contexts across Iberia and southern Europe, demonstrate butchery and cooking practices (Cova Negra IIIb, Spain—Martínez Valle et al., 2016; Gorham's, Vanguard, and Ibex Cave, Gibraltar, UK—Finlayson et al., 2012; Blasco et al., 2014, 2016; Arbreda Cave, Spain—Lloveras et al., 2018; Gruta da Oliveira and Gruta da Figueira Brava, Portugal—Nabais et al., 2023; La Crouzade, France—Garcia-Fermet et al., 2023; Pié Lombard, France—Romero et al., 2017; Fumane A9, Italy—Fiore et al., 2016). Ducks were a regular part of the Neanderthal diet during successive occupations at Bolomor Cave (Spain, 350–120 ka; Blasco and Fernández Peris, 2009; Blasco et al., 2013), while one swan bone has been recovered at the same location (Bolomor Cave XII, Spain—Blasco et al., 2008). Other species appear to also bear evidence of dietary exploitation, including Charadriiformes and diurnal raptors (Axlor, Spain—Gómez-Olivencia et al., 2018; La Crouzade Cave, France—Garcia-Fermet et al., 2023; Riparo del Broion, Italy—Romandini et al., 2023) while feather barbules reported on lithic tools at Payre and Abri du Maras in southern France suggest bird exploitation without direct evidence visible on any recovered bird remains (Hardy and Moncel, 2011; Hardy et al., 2013; Rufà et al., 2016). One feather barbule has also been recovered on a stone tool from the Middle Paleolithic layer A11 at Fumane (Cnuts et al., 2022).

A growing number of sites also report marks related to the harvest of feathers and talons, sometimes interpreted as having been used for cultural purposes such as personal decoration and pendants. A collection of cut-marked and polished white-tailed eagle pedal phalanxes from Krapina, Croatia (130 ka) have been interpreted as a part of a necklace (Radovčić et al., 2015), while cutmarks on the ulnae of raptors and dark-feathered species and/or cutmarks on talons were observed in Gibraltar (Finlayson et al., 2012), southern France (Combe Grenal and Les Fieux—Morin and Laroulandie, 2012; Laroulandie et al., 2016; Pech de L'Azé I and IV and Mandrin—Soressi et al., 2008; Dibble et al., 2009), and Italy (Fumane—Peresani et al., 2011; Romandini et al., 2016; Rio Secco—Romandini et al., 2014). Consequently, multiple lines of evidence now show that Neanderthals in southern Europe hunted a range of bird species for both utilitarian and non-utilitarian purposes. However, other than cutmarks on two Anseriformes elements from Salzgitter-Lebenstedt, Germany (Gaudzinski-Windheuser and Niven, 2009), cutmarks on a hare pelvis from Unit 5 at Scladina Cave, Belgium (Bonjean et al., 2012), and possible evidence of fishing at Walou Cave, Belgium (Van Neer and Wouters, 2011), the purpose of Neanderthal small fauna exploitation in northern Europe remains largely unknown.

Belgium is a particularly favorable ground for the study of the Paleolithic due to its ideal location in the plains of northwestern Europe and favorable geological parameters. In southern Belgium, the presence of deep valleys cutting through the limestone substrate creates conditions conducive to the formation of rock shelters or underground cavities, from small passages to complex cave networks. While most of these caves are of geological and ecological interest only, they regularly offer archaeological significance where, most of the time, excellent preservation of artifacts and osseous material provides information about past human societies (Di Modica et al., 2016). As part of the faunal record, bird bones also frequently preserve well, despite their fragile nature (Goffette et al., 2020, 2023; López-García et al., 2024). Over more than 150 years, thousands of bird bones have been recovered from rich archaeological sites in Belgium, including Middle Paleolithic occupations, but these have not yet been studied from a zooarchaeological point of view. As a result, the exploitation of birds by Neanderthals in Belgium is hitherto unknown.

The present study aims to fill in this gap by applying archeozoological and taphonomic methods to bird remains recovered from the archaeological site of Scladina Cave in southern Belgium. Scladina is an exceptional site because it is one of only two archaeological excavations from the end of the 20th century in Belgium that have yielded an extensive stratigraphic sequence covering at least the end of the Middle Pleistocene up to the Holocene, delivering Middle and Upper Paleolithic industries as well as Neanderthal remains (Pirson, 2007, 2011; Pirson et al., 2008; Toussaint et al., 2017). Scladina also contains several Neanderthal occupations (Di Modica and Bonjean, 2004), allowing us to investigate Neanderthal behavior at the same geographical location at two different intervals during the Middle Paleolithic (MIS 6 and MIS 3).

1.2 Scladina Cave

Scladina Cave was discovered by amateur archaeologists in 1971 and has been the subject of scientific excavations since 1978, initially under the leadership of the University of Liège and now under the direction of the Espace muséal d'Andenne with the support of various institutions such as the Walloon Heritage Agency, the Wallonia-Brussels Federation, and the City of Andenne. Since the mid-1980s, the excavations have become permanent and are now conducted in an interdisciplinary manner.

The cave is located between Andenne and Namur, on the right bank of the Meuse, in a secondary valley where the Ri de Pontainne, a small water stream, intermittently flows. Scladina is part of a complex network of caves that was partially excavated starting from the late 1940s (Dewez, 1981). These excavations have notably uncovered numerous artifacts and abundant fauna in the adjacent Saint-Paul Cave, as well as in the underlying Sous-Saint-Paul cave.

Initially, Scladina Cave was recognized for yielding archaeological remains from two major Middle Paleolithic occupations (Units 1A and 5), then later also from many smaller occupations (Loodts, 1998; Moncel, 1998; Otte, 1998a; Di Modica and Bonjean, 2004; Di Modica, 2010). Unit 5 yielded abundant and well-preserved fauna bearing anthropogenic modifications (Patou-Mathis, 1998) and bones used as retouchers, including cave bear remains (Abrams et al., 2014; Abrams, 2018). Unit 1A, although more recent, does not display the same state of preservation. The faunal remains are heavily altered, making it difficult to observe potential anthropogenic modifications (Bourdillat, 2008). However, nearly 200 burned bone fragments attest to their use as fuel (Abrams et al., 2010). Fragments of black coloring rocks, interpreted as pigment, have also been unearthed within this assemblage (Bonjean et al., 2015).

Starting from 1990, the discovery of dental and facial remains belonging to a Neanderthal juvenile individual bestowed Scladina with additional significance (Toussaint and Pirson, 2006; Toussaint et al., 2014). In Belgium, apart from a tooth unearthed at the Trou de l'Abîme in Couvin a few years earlier (Toussaint et al., 2010) and another tooth from Walou Cave (Toussaint et al., 2017), no Neanderthal remains had been found in stratigraphic context since the late 19th Century (Toussaint and Pirson, 2006; Toussaint et al., 2011).

Although the site is primarily known for its occupations by Neanderthal populations, more anecdotal evidence related to the Upper Paleolithic complements the cultural sequence (Otte, 1998b). Modified bones associated with an Upper Paleolithic end scraper on a blade have contributed to dating the emergence of the Upper Paleolithic in Belgium (Abrams et al., 2024).

1.3 Stratigraphy, sedimentary dynamics, paleoenvironment and chronostratigraphic framework

In the last 20 years, major interdisciplinary studies focusing on stratigraphy, sedimentary dynamics, paleoenvironmental reconstructions, and chronostratigraphy were conducted in Scladina. These recent studies complement and refine the numerous datasets already available for the site (Otte, 1992; Otte et al., 1998). With its sedimentary infill covering a long period from the Middle Pleistocene to the Holocene, Scladina appears as one of the most complete cave entrance sequences in Belgium (Pirson, 2007, 2014; Pirson et al., 2018, 2014). It is a reference site for cave entrance sedimentology and a key sequence for the study of paleoenvironments in northwestern Europe.

Since Scladina Cave is still under excavation, the stratigraphy meets the quality criteria of a modern excavation. Dozens of sedimentary profiles were studied in detail throughout the whole site (e.g., Gullentops and Deblaere, 1992; Haesaerts, 1992; Otte, 1992; Otte et al., 1998; Pirson, 2007, 2014), illustrating the complexity of the stratigraphy. Important lateral sedimentary variations were highlighted as well as complex geometries and varied lithologies. The 2007 stratigraphic reappraisal eventually led to the definition of the actual 15-m-thick Scladina stratigraphic sequence encompassing ca. 120 layers grouped in 30 major units (Pirson, 2007) (Figure 1). These field studies revealed the diversity of the sedimentary sources and a large variety of sedimentary dynamics dominated by slope processes, including debris flow, run-off, rock fall, solifluction, settling, torrential flow, and speleothem formation (Pirson, 2007, 2014). The stratigraphy of sediments accumulated under an aven, or sinkhole, opening in the cave ceiling

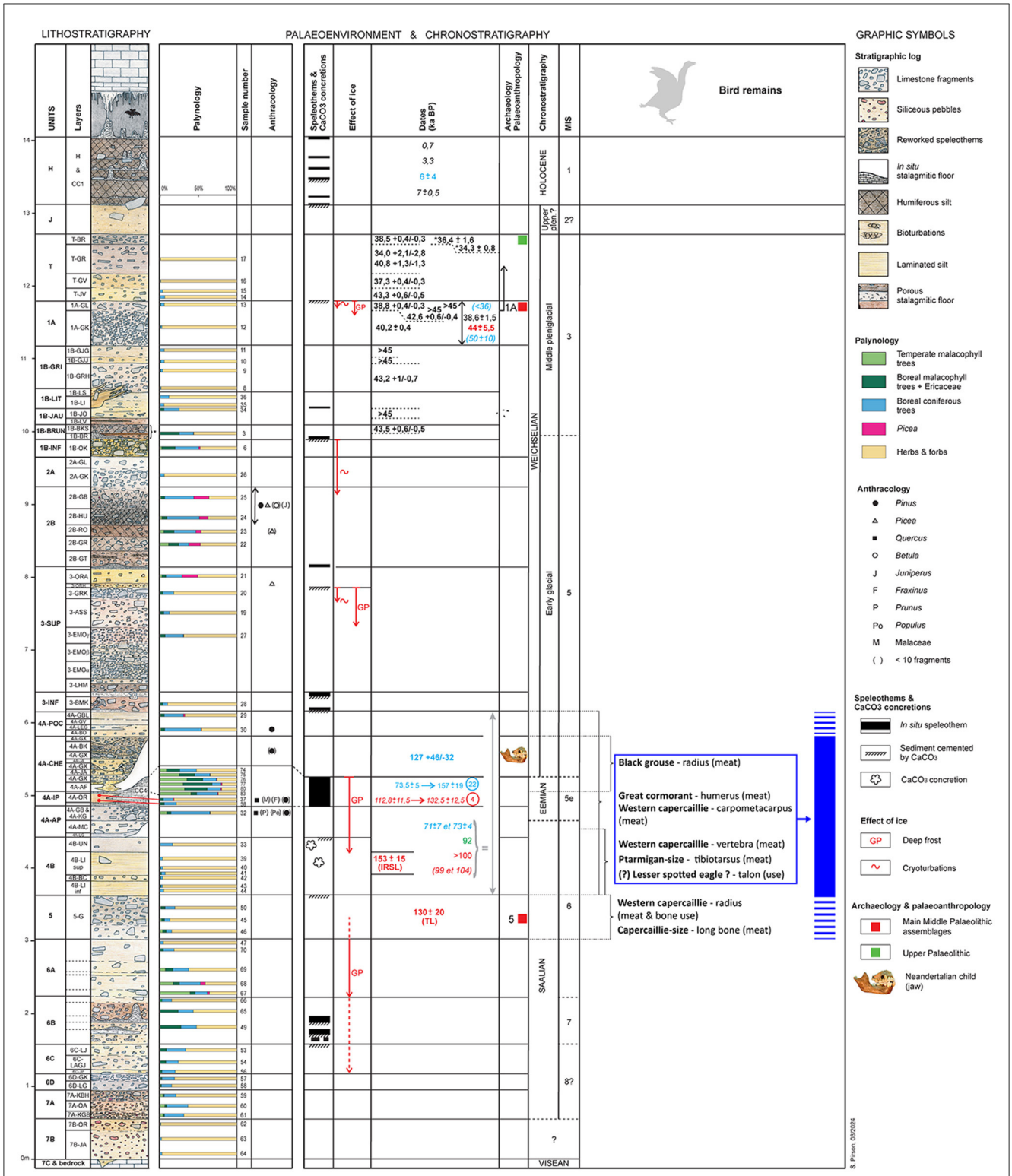

FIGURE 1
Scladina Cave stratigraphic sequence and chronostratigraphic interpretation, showing the stratigraphic position of bird remains with anthropogenic marks. (?) = uncertain anthropogenic marks. Black braces indicate the stratigraphic attribution. The blue bar indicates the potential stratigraphic origin of the bones discovered in sedimentary Complex 4, taking into account possible attribution errors and rearrangements (see text). Dates: synthesis of all reliable dates available for the Scladina Cave sequence (see Bonjean, 1998; Pirson, 2007; Bonjean et al., 2012; Pirson et al., 2014; Abrams et al., 2024). All the ^{14}C dates on this figure are uncalibrated. When an age interval is given, the number of dates concerned is indicated in a circle. Black = ^{14}C date on bone; *italic black* = ^{14}C date on calcite (*in situ* and reworked speleothems); **bold black** = ^{14}C date on teeth accurately positioned in the new stratigraphic system; * + **bold black** = ^{14}C date (hydroxyproline) on bone retoucher accurately positioned in the new stratigraphic system; blue = U/Th date on *in situ* speleothem; *italic blue* = U/Th date on reworked fragments of speleothems; **bold blue** = U/Th date (gamma spectrometry) obtained on the Neanderthal mandible; red = thermoluminescence date on sediment; *italic red* = thermoluminescence date on *in-situ* speleothem; **bold red** = luminescence date on burned flint (TL) and on sediment (IRSL); green = coupled U/Th–ESR dates on bone; circled numbers = number of dates for CC4 interval. () = problematic date.

was recorded separately. Complex diagenetic processes have also been recognized.

Scladina yielded one of the best interdisciplinary-studied cave entrance sequences in Belgium, together with Walou Cave, east of Liège (Draily et al., 2011; Pirson et al., 2011). The paleoenvironments have been documented through large and small mammals, amphibians, reptiles, palynological, anthracological, sedimentological, magnetic susceptibility, and pedological studies (e.g., Otte, 1992; Otte et al., 1998; Ellwood et al., 2004; Pirson, 2007; Pirson et al., 2008, 2014; Blain et al., 2014). More than twenty alternating climatic phases have been documented, including cold stadials, short interstadials, and longer temperate phases, either interglacial or early glacial. Scladina is also the most densely dated prehistoric site in Belgium, with more than 90 available dates (TL, IRSL, combined U/Th-ESR, U/Th, and radiocarbon). Recently obtained U/Th dates (Vonhof et al., 2024) led to refine the existing chronostratigraphic framework (see Pirson et al., 2014, 2008). The current chronostratigraphic interpretation of this complex sequence is based on climatostratigraphic, biostratigraphic, and mineralogical data, numerical dates, and comparison with the reference loess sequence from Central Belgium (Figure 1).

In this paper, we will focus on stratigraphic Unit 1A (MIS 3), the Sedimentary Complexes 3 and 4A (MIS 5), Unit 4B (MIS 6), and Unit 5 (MIS 6) encompassing in total more than 30 layers (Pirson, 2007, 2014). Unit 1A was mainly deposited by two sedimentary processes (debris flow and run-off). Complex of Units 3 is dominated by debris flow and run-off (locally torrential flow), with also rock fall and speleothem formation. Unit 4B mainly results from settling and run-off, while Unit 5 consists of a diamicton affected by solifluxion. The situation of 4A is special, as the stratigraphic reappraisal revealed a much more important complexity in this part of the stratigraphy than previously thought. Four distinct Units, each encompassing several layers, have been described in this sedimentary complex. Unit 4A-AP results from debris flow and wash processes. Palynological data suggests it records the first stage of a strong climatic improvement. Unit 4A-IP mainly consists of a thick stalagmitic floor (CC4) pointing to temperate conditions. Unit 4A-CHE is the result of an important erosional phase with cut-and-filled layers developed in a deep gully structure, resulting from a cold episode. Finally, Unit 4A-POC consists of fine-grained sediments mainly deposited by run-off and covering both underlying Units 4A-IP and 4A-CHE. This complexity was not fully understood before the stratigraphic reappraisal, therefore sometimes implying some uncertainty in the stratigraphic attribution of the material unearthed before 2007. This is especially the case for Unit 4B, which was supposed to lie below the stalagmitic floor CC4 in the original stratigraphy. Following the reappraisal, the recognition of the 4A-CHE gully, opening downwards from the surface of CC4, implies that in some situations Unit 4B corresponds in fact to 4A-CHE. It is also worth mentioning here that the gully erodes underlying Units 4A-IP, 4A-AP, and 4B, and locally also part of Unit 5.

The new U/Th dates recently obtained on speleothems led to reinterpret Sedimentary Complex 4 (Vonhof et al., 2024), as they indicate that the thick CC4 speleothem records the Eemian. As a result, underlying units 4B and 5 are now placed at the end of the Middle Pleistocene, in MIS 6.

Several modified bird bones have been recovered from the upper part of the Scladina sequence, but as they were unearthed before the stratigraphic reappraisal (Pirson, 2007), some uncertainties remain about their detailed stratigraphic position. This is mainly the case for Unit T, where early Upper Paleolithic material (Abrams et al., 2024) has been found alongside artifacts reworked from Middle Palaeolithic layer 1A. In this context, anthropologically modified bones excavated from Unit T before the stratigraphic reappraisal cannot be precisely attributed, therefore requiring radiocarbon dating. These are in progress and will be presented in another paper.

2 Materials and methods

Our study consisted of several steps. First, we selected the stratigraphic layers that had yielded testimonies of human activities, targeting the assemblages with the highest potential for traces of bird exploitation. We thus targeted 22 sedimentary assemblages from the Upper Paleolithic and Middle Paleolithic, from which we sorted all the bone remains to isolate the bird bones. The only exception was the avian remains from the layers of Unit 1A, that had been isolated by researchers from the Institut de Paléontologie Humaine (Paris) following the sorting of the faunal material from this assemblage. A new sorting of this assemblage was therefore not undertaken. Some bird bones had been isolated by the excavation team. This explains the presence of bones from units 3-SUP, 3-INF, and 6A to 6C, which we did not sort in the course of this work. This selection means that we have not studied certain units (2A, 2B, 6D, and 7A to 7C), while others are only partially studied (3-SUP, 3-INF, and 6A to 6C). Further bird bones may still be identified among the faunal remains of these layers, but the potential for finding remains with anthropogenic modifications is low given the low frequency of other archaeological material. All sediment was sieved to a maximum mesh size of 5 mm, except in the case of some specific research efforts (e.g., small mammals) when a 2.5 mm mesh was used.

For all the specimens, the attribution to a stratigraphic unit determined at the time of discovery has been retained in this manuscript, unless a stratigraphic reattribution in relation with the 2007 stratigraphic reappraisal could be carried out with certainty (e.g., based on the examination of existing neighboring stratigraphic sections). Then, the new stratigraphic attribution was used. This point is particularly important for unit 4B, to which bones were attributed before the stratigraphic reappraisal, although their attribution to unit 4B is questionable (see Discussion). However, due to the lack of possible reattribution, we retained the original attribution.

The sorting led to the recovery of 159 bird remains (Middle Paleolithic, $n = 119$; Upper Paleolithic, $n = 40$). All were subjected to an archeozoological study but here, the focus is on material recovered from Middle Paleolithic-related sedimentary units. Elements with uncertain stratigraphic attribution that potentially come from layers including Middle Paleolithic material were also retained. The stratigraphic details are given in Figure 1 and Supplementary Tables 1, 2. Bones associated with the Upper

Paleolithic have been analyzed but will not be presented in this article.

The zooarchaeological study includes detailed taphonomic and traceological analyses. First, we determined the anatomical part and the taxon present using reference collections held at the Institute of Natural Sciences (Brussels, Belgium), as well as reference manuals dedicated to the identification of certain taxonomic groups (Woolfenden, 1961; Bacher, 1967; Woelfle, 1967; Erbersdobler, 1968; Kraft, 1972; Langer, 1980; Bocheński et al., 2022; Wertz et al., 2022). The taxonomy used follows that of Gill et al. (2022). The nomenclature used to describe anatomic features of bones and soft tissues follows Baumel (1993). The side (left or right) of the bone was recorded. Where possible, measurements were taken according to von den Driesch (1976) or dedicated manuals. The calculation of the minimum number of individuals (MNI) was based on the minimum number of elements (MNE) completed by the laterality and the age of the individuals. Age estimation was made by examining the ossification stage to attribute each bone to one of the four age classes summarized in Serjeantson (2009). The sex of certain taxa was assessed based on measurements. The completeness or fragmentation of each element was recorded, as were the parts preserved and the morphology of the fracture edges (Fernández-Jalvo and Andrews, 2016; Romero et al., 2016). In addition, each bone was examined using a binocular microscope (magnification 6.5–50×) with oblique cold light, to record surface alterations, including color, root etching, erosion, thermal alterations, weathering, and gnawing or beak marks (Behrensmeyer, 1978; Lyman, 1994; Behrensmeyer et al., 2003; López-González et al., 2006; Bocheński et al., 2009, 2018; Fernández-Jalvo and Andrews, 2016). To create a workable dataset, while still preserving the integrity of the stratigraphy, we grouped the Middle Paleolithic remains into five samples according to sedimentary units and MIS (Supplementary Table 3).

To observe and illustrate some of the modifications in detail, two scanning electron microscopes were used and operated under low vacuum conditions to eliminate the need for a conductive coating, a FEI Quanta 200 (23 kV; Mineralogical Laboratory of the Geological Survey of Belgium) and a JEOL-IT300 (20 kV; TraceoLab of ULiège). In addition, a digital microscope Hirox HRX-01 equipped with an H-2500E attachment and an LED ring light was used (acquisition mode multi-focus or 3D; TraceoLab of ULiège). The works of Barisic (2006) and Domínguez-Rodrigo et al. (2009) have been used to help distinguish between cut and trampling marks, bearing in mind that it can be very difficult to differentiate between intentional cutmarks and trampling marks, particularly when bones are mixed with lithic pieces in the sediment (Barisic, 2006).

Analyses of proteomics (MALDI) were applied to clarify the taxonomic identity of two bird bones with anthropogenic modifications that did not preserve sufficient morphological characteristics to allow any taxonomic identification beyond the class level. The digestion of bones was described in Bray et al. (2023). Briefly, 1–5 mg of bones were deposited in 96 wells plate MultiScreenHTS-IP, 0.45 µm (MSIPS4510, Millipore, Billerica, MA, USA). The bone powder was demineralized, washed, gelatinized and digested in the 96 wells plate MultiScreenHTS-IP. The demineralization solution was digested in classical 96 well plates. The peptides form bones and demineralized solution were purified on C18 96 well plates (Affinisep, Petit-Couronne, France). Purification of peptides was performed by washing the plates once with 500 µL of acetonitrile (ACN) followed by a washing step with 80% ACN, H_2O 0.5% acetic acid repeated 3 times and a second washing repeated 3 times with H_2O alone 0.5% acetic acid. Tryptic peptides from bone powder were resuspended in 200 µL of a H_2O, 0.5% acetic acid solution. Tryptic peptides form both solutions were transferred to C18 96-well plate and eluted with a vacuum manifold. The plate was washed 3 times with 200 µL of H_2O, 0.5% acetic acid. Peptides were recovered in a V-bottom well collecting plate using 100 µL of a 80% ACN, 0.1% acetic acid solution followed by 100 µL of ACN. The plate was evaporated on TurboVap 96 Evaporator (Caliper LifeScience, Hopkinton, USA). For mass spectrometry analysis, the sample was dissolved again in 10 µl of H_2O 0.1% formic acid. Mass spectrometry analysis was performed by depositing desalted peptides (1 µL) on 384 massive MALDI plates (Bruker Daltonics, Bremen, Germany), then 1 µL of HCCA matrix at 10 mg/mL in ACN/H_2O 70:30 v/v 0.1% TFA was added for each sample. The spots were dried at room temperature. MALDI FTICR experiments were carried out on a Bruker 9.4 Tesla SolariX XR FTICR mass spectrometer (Bruker Daltonics, Bremen, Germany). The frequency of the laser was set to 1,000 Hz using the "Minimum" predefined shot pattern. MALDI FTICR spectra were generated in the *m/z* range from 693.01 to 5,000 by accumulating 10 scans. Two M data points were used per spectrum which corresponds to a transient duration of 5.0332 s. The transfer time to the ICR cell was set to 1.2 ms and the quadrupole mass filter set at *m/z* 600 was operated in RF-only mode. MS raw data from MALDI FTICR were processed using DataAnalysis 5.0. The identification is supported by all peptide markers presented in previous reports (Eda et al., 2020; Codlin et al., 2022). The mass spectrometry proteomics data have been deposited on the ProteomeXchange Consortium (https://proteomecentral.proteomexchange.org/) via the PRIDE partner repository with the data set identifier PXD051309.

3 Results

3.1 Taxonomic composition

The bird bone assemblage from Scladina Cave recovered from Middle Paleolithic stratigraphic units comprises a total of 119 remains representing at least 32 individuals from 16 taxa (Table 1; Supplementary Tables 1, 2). The assemblage does not appear highly taxonomically diverse. Most of the remains have been identified to genus or specific level, so taxonomic diversity is probably not underestimated due to identification issues. The bones present come mainly from medium- (such as ducks and ptarmigans), to large-sized taxa (such as goose and capercaillie). It is likely that conservation conditions within the sediment favored the preservation of the largest, most resistant bones, to the detriment of the smaller elements. If we consider the proportions of the different orders present, Galliformes largely dominate the assemblage both in terms of NISP and MNI, ahead of Anseriformes, while the other orders are less abundant.

TABLE 1 Inventory of the number of identified specimens (NISP) of bird remains from Scladina Cave, grouped by Units.

Area	Cave								Aven	Total
Units	1A	1B	3	4/4A	4B	5	5 + 6	6	Z1-4	
Anseriformes										
Goose (*Anser* cf. *albifrons*)	-	-	-	-	-	1	1	-	1	3
Anatinae size mallard	5	-	-	1	-	1	-	-	-	7
Anatinae size wigeon	-	-	-	-	-	1	-	-	-	1
Galliformes										
Gray partridge (*Perdix perdix*)	-	-	-	-	-	-	-	1	-	1
Ptarmigan (*Lagopus* sp.)	-	1	-	1	-	-	-		-	2
Black grouse (*Lyrurus tetrix*)	2	-	-	3	6	2	-	1	-	14
Western capercaillie (*Tetrao urogallus*)	-	2	8	6	17	-	2		-	35
Galliformes size ptarmigan	1	-	2	1	2	3	-	1	-	10
Galliformes size capercaillie	1	-	-	-	-	-	-	-	-	1
Columbiformes										
Wood pigeon? (*Columba* cf. *palumbus*)	1	-	-	-	-	-	-	-	-	1
Strigiformes										
Eurasian eagle/snowy owl (*Bubo* sp.)	-	-	-	2	1	-	-	-	-	3
Tawny owl (*Strix aluco*)	-	-	-	-	1	-	-	-	-	1
Short/long-eared owl (*Asio otus/flammeus*)	-	-	-	-	-	1	-	-	-	1
Suliformes										
Great cormorant (*Phalacrocorax carbo*)	-	-	-	1	-	-	-	-	-	1
Accipitriformes										
Eurasian sparrowhawk (*Accipiter nisus*)	1	-	-	-	-	-	-	-	-	1
Lesser spotted eagle? (*Clanga* cf. *pomarina*)	-	-	-	-	1	-	-	-	-	1
Eagle size golden eagle	1	-	-	-	-	-	-	-	-	1
Passeriformes										
Passeriformes size yellowhammer	3	-	-	-	-	-	-	-	-	3
Total identified bird remains	**15**	**3**	**10**	**15**	**28**	**9**	**3**	**3**	**1**	**87**
Unidentified bird remains	7	-	1	2	11	8	-	-	1	30
Unidentified bird size goose	-	-	-	-	-	2	-	-	-	2
Total unidentified bird remains	**7**	**0**	**1**	**2**	**11**	**10**	**0**	**0**	**1**	**32**
Total	**22**	**3**	**11**	**17**	**39**	**19**	**3**	**3**	**1**	**119**

Detailed inventories can be found in Supplementary Tables 1, 2.

Within the order Anseriformes, remains of geese were present alongside duck bones. The order Galliformes included almost exclusively remains belonging to the subfamily Tetraoninae and was chiefly dominated by the Western capercaillie. The black grouse and willow/rock ptarmigan were also present. Furthermore, one bone of gray partridge was identified. The order Strigiformes was represented by the tawny owl (Figure 2A), the long-eared/short-eared owl, and a large owl, possibly the Eurasian eagle owl in the case of a premaxillary of very large size (Figure 2C). In the order Accipitriformes, we noted the presence of a small species of raptor, the European sparrowhawk, and two species of eagle; one the size of a golden eagle, the other likely a lesser spotted eagle. In the order Passeriformes, three remains were from a passerine the size of the yellowhammer. Additionally, one bone of a great cormorant (Suliformes) and one of a pigeon, probably the wood pigeon (Columbiformes) were identified in the assemblage.

One radius fragment from a large bird with no taxonomically diagnostic morphological features (Sc1985-910-309) was identified through proteomics as Tetraoninae (Supplementary Figure 1 and Supplementary Table 4). The only Tetraoninae known to have occurred during the Middle Paleolithic in Western Europe large enough to match the size of this element is the Western capercaillie. This taxonomic identification has been retained on this basis. No morphometric criteria contradict the identification obtained through proteomic analyses. Proteomic analyses were also applied to another unidentified bone fragment

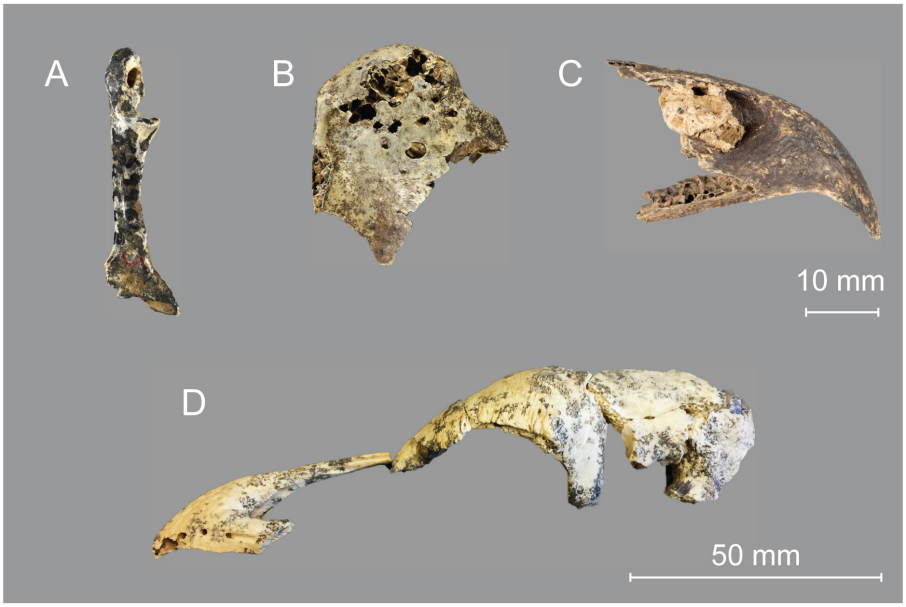

FIGURE 2
Scladina Cave. **(A)** Tawny owl, left coracoid (Sc1999-64-5; Unit 4B). **(B)** Western capercaillie, proximal right humerus with gnawing marks from carnivore (Sc1997-52-258-1; Unit 4B). **(C)** Eurasian eagle or snowy owl, premaxilla (Sc1993-192-194-6 and Sc1993-192-194-7; Unit 4A). **(D)** Western capercaillie, partial skull (Sc1995-397-94-1; Unit 4B).

(Sc1985-783-196), but taxonomic identification was not successful (Supplementary Figure 2). Results showed that the specimen has been affected by unknown contaminants.

3.2 Age and sex

All bird bones collected are of adult individuals, with the exception of the European sparrowhawk which was a sub-adult.

The sparrowhawk bone came from a female individual. The sex ratio in the black grouse (NISP = 3 male; 1 female; 3 likely female) is balanced but in the capercaillie, practically all the bones identified come from males since only 3 bones out of 30 which could be sexed come from female birds. However, this is not significant because a detailed examination of the remains of capercaillie from layer 4B, which delivered most of the bones from this species, revealed the presence of two female individuals to one male individual.

3.3 Taphonomic analysis

The taphonomic sample totaled 99 specimens from 15 layers; 16 from Unit 1A, 10 from complex of Units 3, 18 from complex of Units 4A, 36 from Unit 4B, and 19 from Unit 5. Remains from other Middle Paleolithic contexts were also examined, but are excluded from this study due to uncertain provenance.

3.3.1 Post-depositional processes

Concreted sediments were observed on 75% of the specimens in Unit 1A (Figure 3; Supplementary Table 5), 60% of specimens in the complex of Units 3, and 52.7% of specimens in Unit 5. In the Sedimentary Complex 4A and in Unit 4B concretions were observed on 17.7% and 22.3% respectively. The modifications appeared as localized attached sediments covering between 0–75% of the bone surfaces. Modifications related to weathering (cracks, flaking, etc.) affected 100% of the bones in complex of Units 3, 75% of elements in Unit 1A, ca. 70% of remains in Unit 5 and complex of Units 4A, and 54.3% in Unit 4B. In line with observations made by Bocheński and Tomek (1997), only three stages of weathering were apparent on the material, not including stage 0 (no weathering).

Manganese dioxide deposits were observed at high frequencies in all five samples (Unit 1A = 87.5%, complex of Units 3 = 100%, complex of Units 4A = 88.3%, Unit 4B = 91.5%, Unit 5 = 89.5%), which may indicate high bacterial activities and/or high humidity levels within the cave. These processes are not mutually exclusive. Modifications ranged from small dark stains on the bone surface (grade 1) to covering the entire bone surface (grade 4). Irregular u-shaped striations from rooting were absent in Unit 4B and appeared infrequently in complex of Units 3 (10%) and Unit 1A (18.8%). Rooting marks were of a similar frequency in complex of Units 4A (35.2%) and Unit 5 (31.5%). Striations related to trampling were infrequent throughout the five samples, but most prominent in the occupation sediments of Unit 5 where 31.5% of the sample was affected. However, sample sizes were too small to interpret trampling frequencies beyond presence and absence.

3.3.2 Fragmentation

Fragmentation is significant throughout the entire Middle Paleolithic sequence: only 9 out of 100 long bones are complete (9%). The proportion of complete bones per taxon reflects the abundance of their bones within the site. The Western capercaillie, a species with large and robust bones, provides only one complete element. There does not seem to be any preferential conservation

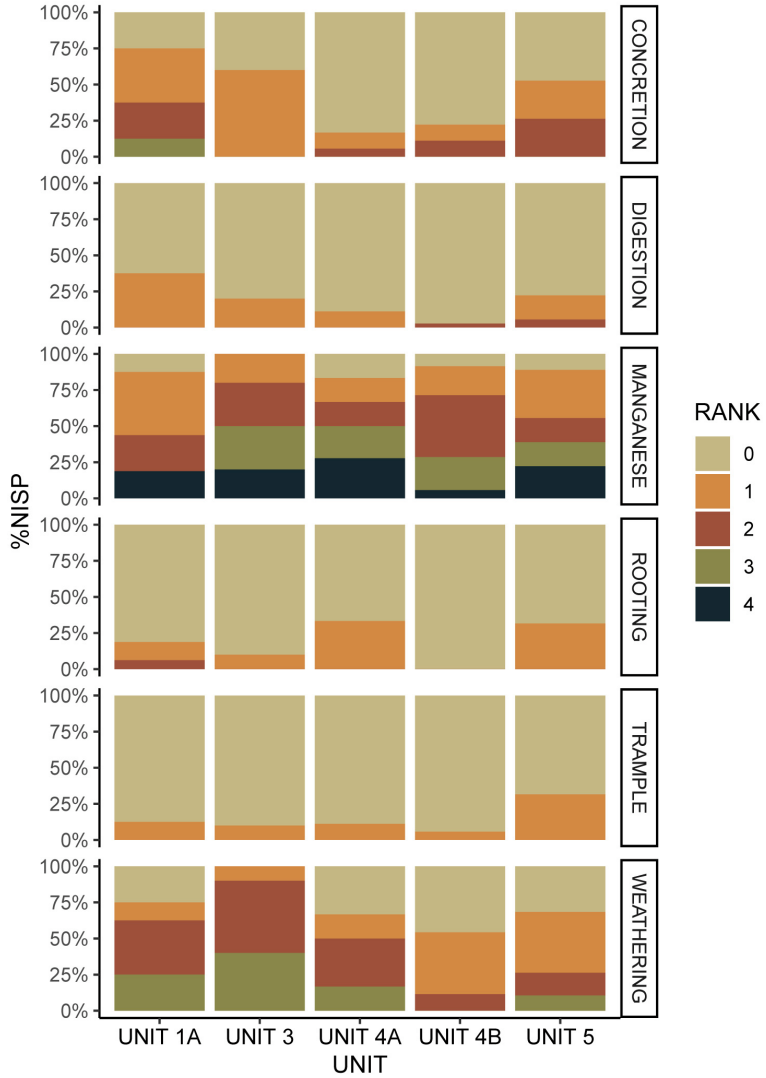

FIGURE 3
Bar charts showing the dispersal of natural taphonomic modifications and digestion modifications observed in the taphonomic samples ranked on a scale from 0 (= none) to 4 (= very high).

of a particular skeletal element. Strikingly, Unit 4B and Unit 5 yield no complete long bone despite being the richest in bird bones. This testifies to the intense fragmentation in these layers. On the contrary, complex of Units 4 delivered parts of two bird skulls, one of an owl of the genus *Bubo* (Figure 2C) and another of a Western capercaillie (Figure 2D). Although incomplete and fragmented, these fragile elements are quite well preserved, highlighting the complexity of the sedimentary dynamics within Scladina Cave.

3.3.3 Corrosive and mechanical predator modifications

Marks concurrent with digestion were identified in all five samples (Figure 3; Supplementary Table 5). In Unit 1A (37.5%), complex of Units 3 (20%), and complex of Units 4A (11.8%) all corrosion was of low level (grade 1). Two levels of corrosion were identified in Unit 5 (grade 1 = 16.7%, grade 2 = 5.6%), and a single element in Unit 4B exhibited grade 2 corrosion (2.8%). Along with low occurrences of polish (Unit 1A = 6.3%, complex of Units 3 = 10%, Unit 5 = 10.5%), these modifications could indicate bird of prey agency and mammalian carnivore agency.

Mechanical marks in the form of pitting, punctures, and crenulated edges add further information to the predator profile. 57.6% of the mechanical marks were concentrated on the articular ends of the bones. In Unit 1A, 37.5% of the remains bore modifications caused by mammalian carnivores (Figure 4; Supplementary Table 5). These included remains of Galliformes, ducks, and a rock dove-sized bird. A further 12.5% displayed marks that were likely produced by carnivores. Seven of 10 Galliformes bird remains from complex of Units 3 were predated by mammalian carnivores as attested by punctures, crenulated edges and tooth grooves. All but one of these remains were concentrated at the junction between Scladina and Saint-Paul caves, and may indicate carnivore denning activity. In the complex of Units 4A,

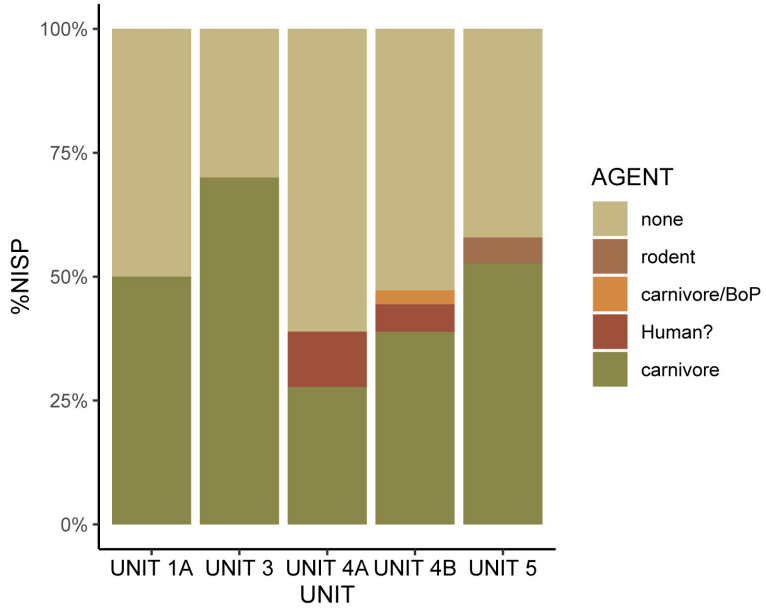

FIGURE 4
Bar chart showing the proportions of mechanical agency visible on the avian remains in the five taphonomic samples from Scladina Cave. Carnivore marks appear most frequently throughout the sample. BoP, bird of prey.

carnivore agency (29.4%) was observed in the remains of two species of Galliformes (black grouse and Western capercaillie) and one large owl of the genus *Bubo*. Two further specimens (11.8%), one great cormorant and one Western capercaillie, displayed pitting and puncture patterns that could be of human origin. Carnivore modifications affected 33.3% of the remains in Unit 4B (33.3%), all of which present on Galliformes. Unit 5 contained the highest frequency of mechanical modifications, with pitting and punctures from small carnivores visible on 47.4% of the remains of waterfowl and Galliformes. Rodent gnawing was observed on a single element (5.3%). No conclusive evidence of mechanical bird of prey modifications was observed in the samples.

3.3.4 Anthropogenic modifications

Marks interpreted as anthropogenic were recorded on 7 remains (6.7% of the Middle Paleolithic bird material from Scladina Cave) recovered from the complex of Units 4 (MIS 5 or 6; $n = 6$; 8.9%) and in Unit 5 (MIS 5 or 6; $n = 6$; 10.5%) while another specimen from the complex of Units 4 displays uncertain anthropogenic marks (Table 2). The stratigraphic position of these bones appears on the stratigraphic log (Figure 1).

3.3.4.1 Cutmarks

3.3.4.1.1 Complex of units 4 (MIS 5 or 6)

In Unit 4 *sensu lato*, the left humerus of a great cormorant displayed two double incisions on the anterior face as well as an area of scraping on the posterior face; these marks were located on the body of the bone, near the distal end (Figure 5A). The two double incisions were located at the level of the brachialis muscle insertion fossa, and penetrate into it (Figure 5A', arrow). This location is consistent with butchering activities (Laroulandie, 2001) and does not support interpretation as trampling. The scraping area on the posterior surface was likely linked to the removal of meat. Furthermore, a group of fairly superficial transverse striations was located near the fracture, on the proximal part of the body of the bone. These could be marks linked to the removal of meat but trampling cannot be excluded.

A right carpometacarpus of a Western capercaillie bears two incisions on the ventral side of the articular surface of the proximal condyle (Figure 5B), probably left during the disarticulation of the wrist (Laroulandie, 2001). Imprints of teeth with a bilobed appearance on the processus extensorius suggest the action of a small carnivore (Figure 5B, arrow).

3.3.4.1.2 Unit 4A-CHE (MIS 5 or 6)

The complete right radius of a black grouse found in Unit 4A-CHE exhibited several deep, oblique incisions on the posterior side at the level of the proximal joint, as well as a scraped area on the ventral side (Figure 5C). These tool marks were concentrated near the facies articularis ulnaris and were probably produced during the disarticulation of the radius and ulna during meat recovery (Laroulandie, 2001).

3.3.4.1.3 Unit 4B (MIS 5 or 6)

Unit 4B provided two Galliformes bones with anthropogenic marks. The first was a thoracic vertebra of a Western capercaillie bearing a deep incision on one of the lateral faces accompanied by a second, more superficial incision, both aligned and most likely resulting from the same movement (Figure 6A). A left distal tibiotarsus of a ptarmigan-sized taxon showed longitudinal and oblique scraping marks on the posterior and medial surfaces of the body of the bone (Figure 6B). They are partly under the varnish applied to accommodate the archaeological marking. Their purpose

TABLE 2 Inventory of bird remains showing marks interpreted as anthropogenic in origin.

Unit	Inventory number	Figure number	MIS	Taxon	Element	Human modification	
						N	Proposed use
4, 4A-CHE, 4B							
4	Sc1986-72-3368	Figure 5A	5 or 6	Great cormorant (*Phalacrocorax carbo*)	Humerus	1	Meat
4	Sc1985-30-1	Figure 5B	5 or 6	Western capercaillie (*Tetrao urogallus*)	Carpometacarpus	1	Meat
4A-CHE	Sc2008-21-1	Figure 5C	5 or 6	Black grouse (*Lyrurus tetrix*)	Radius	1	Meat
4B	Sc2001-269	Figure 6A	5 or 6	Western capercaillie (*Tetrao urogallus*)	Thoracic vertebra	1	Meat
4B	Sc1999-55-47	Figure 6B	5 or 6	Galliformes size of ptarmigan	Tibiotarsus	1	Meat?
4B	Sc1997-135-10-6	Figure 6C	5 or 6	Lesser spotted eagle? (*Clanga* cf. *pomarina*)	Terminal posterior phalanx	1?	Claw use?
5							
5	Sc1985-910-309	Figure 7A	6	Western capercaillie (*Tetrao urogallus*) - P	Radius	1	Meat, bone industry?
5	Sc1985-783-116	Figure 7B	6	Unidentified bird size of capercaillie	Long bone	1	Meat
Total						7+ 1?	

Questionable specimens are marked with a "?". "P" next to a taxon indicates that it has been identified by proteomic analyses.

is unclear, and may have been produced during the harvesting of the meat.

3.3.4.1.2 Unit 5 (MIS 6)

In Unit 5, anthropogenic marks were identified on two bones of large birds (10.5% of the bones from Unit 5). The first was analyzed by proteomics and identified as a Western capercaillie (see above). It is a fragment of the body of a radius fractured at both ends (Figure 7A). One of these fractures displays a modern aspect and is associated with residues left by a metal tool. This fracture was likely produced during the excavation. The fracture on the other side of this element is strongly polished and associated with two deep incisions. The absence of metal particles close to the incisions and the presence of black manganese deposits on the inside exclude that they were produced recently, during the excavation or later. Particular attention was paid to this bone, especially to reconstruct the sequence of actions responsible for the marks observed.

First, the two deep incisions were produced. These marks could bear witness to butchery practices, but their location, far from a joint, is inconsistent with the disarticulation of the carcass, and their depth is unusual in the context of meat removal. Instead, they could be associated with a form of bone work and may have been intended to facilitate the fracture of this radius. The depth and breadth of the largest incision, in particular, suggests a repeated "sawing" type movement, which supports the hypothesis that these incisions were produced to help fracture the bone. Second, the bone has been broken transversally by flexion, which produced a flaking of the bone surface. The fracture progression was stopped by the incisions. Third, the bone has been used for a prolonged time, which resulted in the development of a strong polish on the broken edge (see Section 3.3.4.2.2.).

The second specimen is a small fragment of the body of a long bone from an unidentified large bird the size of a Western capercaillie. The specimen displays fine longitudinal incisions and several scraped areas in the form of groups of oblique striae (Figure 7B). The marks observed suggest different finalities. The longitudinal incisions probably relate to the action of cutting, and oblique striae are likely scraping marks left during butchering activities. Trampling is probably responsible for the fragmentation of the original bone into this tiny fragment and for the production of faint, randomly oriented striae observed at the surface of this specimen.

3.3.4.2 Polish

Two bones show strong polish.

3.3.4.2.1 Unit 4B (MIS 5 or 6)

A claw (phalanx 3) of the second digit of a likely lesser spotted eagle has very fine polish on the reliefs of the articular surface as well as on the area underlying the keratinous sheath of the phalanx (Figure 6C). These polishes are associated with micro-striations (visible at 800×), which could suggest human intervention. The absence of polish in the hollow parts of the affected areas tends to exclude digestion or post-depositional processes such as polishing by movements in the sediments, but further research on talon polish is required to ascertain this assumption. The fractured distal end does not show rounding nor polish. No tool marks were observed. The attribution of these modifications to human activities remains uncertain.

3.3.4.2.2 Unit 5 (MIS 6)

The incised Western capercaillie radius fragment described above shows a highly developed polish (Figure 7A). This polish is located at the apical part of one of the two fractured ends and does not affect the entire surface of the bone. The polish is spread over the area where the peeling is observed, which excludes that the fracture and the flaking of the bone surface occurred after the development of the polish. At high magnification (800×), a few fine streaks are visible. It was not possible to determine if the polish resulted from the use of this element as a tool dedicated to a specific action, or if the polish was produced unintentionally during the prolonged transport of the

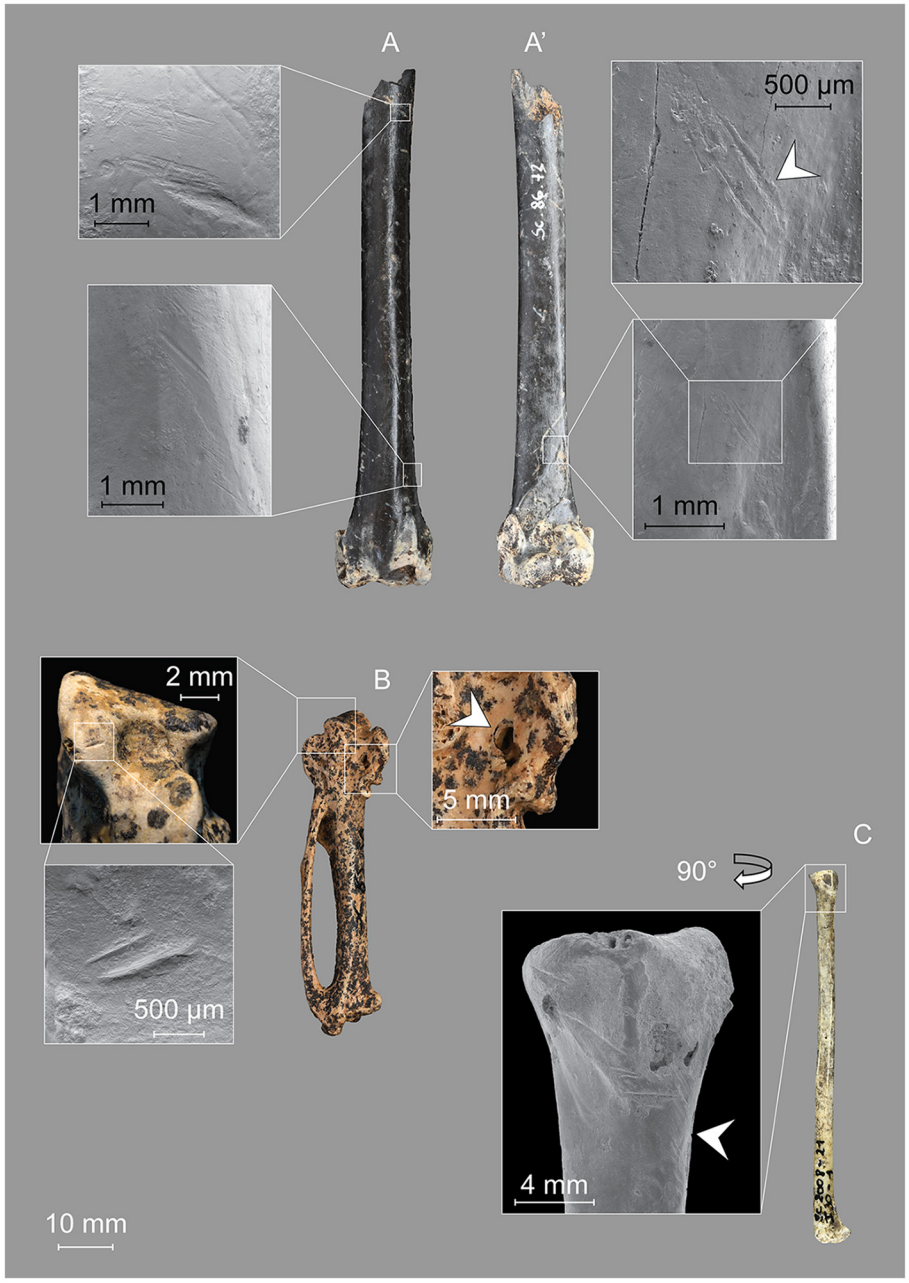

FIGURE 5
Units 4 and 4A-CHE. **(A)** Great cormorant, left distal humerus showing incisions and scraped areas (Sc1986-72-3368; Unit 4). Two double incisions enter the brachialis muscle insertion fossa (arrow). **(B)** Western capercaillie, right carpometacarpus with two short incisions at the proximal joint (Sc1985-30-1; Unit 4). Two tooth impressions, or one with a bilobed appearance, are present (arrow). **(C)** Black grouse, right radius with several deep incisions and a scraped area (arrow) in the proximal part (Sc2008-21-1; Unit 4A-CHE).

object. Anyway, the use of this specimen produced very fine micro-wear associated with short and multiple orientations micro-striations located close to the edge. These characteristics exclude that it was used on strongly abrasive materials such as stone or dry skin, but instead suggest a use on soft material such as fresh skin or plants. However, more comparative research is needed to determine the kind of material which generated the polish observed.

3.4 Spatial distribution

The bird bones bearing anthropogenic modifications were plotted onto a map of the cave (Supplementary Figures 3–6). Their location was based on the square of origin only, as the exact location within the square is not always known. We also examined the spatial distribution for Unit 1A because it constitutes one of the two main archaeological assemblages from the Middle

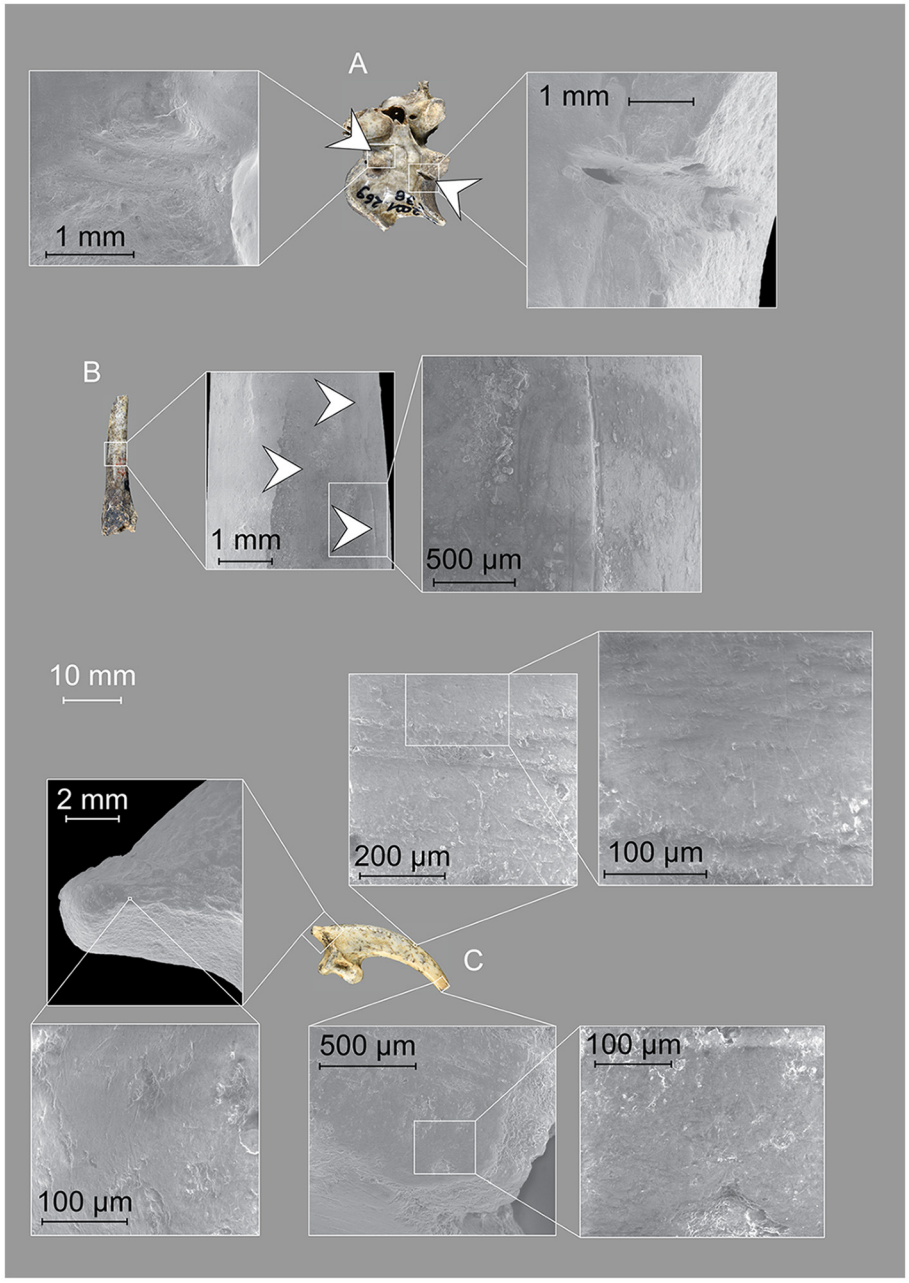

FIGURE 6
Unit 4B. **(A)** Western capercaillie, thoracic vertebra bearing a deep incision accompanied by a second, more superficial incision, in the same alignment (Sc2001-269; Unit 4B). **(B)** Ptarmigan-sized Galliformes, left distal tibiotarsus with fine longitudinal and oblique incisions on the body of the bone probably resulting from the removal of meat (Sc1999-55-47; Unit 4B). **(C)** Lesser spotted eagle (?), terminal posterior phalanx of the second toe showing areas of intense polish (Sc1997-135-10-6; Unit 4B).

Paleolithic, although it delivered no bird bones with anthropogenic modifications. Until now, evaluations of spatial distribution have hardly been attempted for the Scladina Cave, all types of remains combined. This limited the possibility of comparisons with other remains.

The spatial distribution of all avian remains should be interpreted with caution because the sediments were all reworked and none of the remains are in primary position. This is especially the case in 4A-CHE (very dynamic erosion and transport). Therefore, the spatial distribution of avian remains in no way represents the pattern of deposition of bird bones within the cave, and cannot inform us about behavior, be it Neanderthal or non-human predators.

3.4.1 Unit 1A (MIS 3)

In Unit 1A, the provenance square of 15 out of 16 avian remains is known. The remains were distributed evenly throughout the cave and do not appear to be deposited in any organized concentration (Supplementary Figure 3). Some fragments were

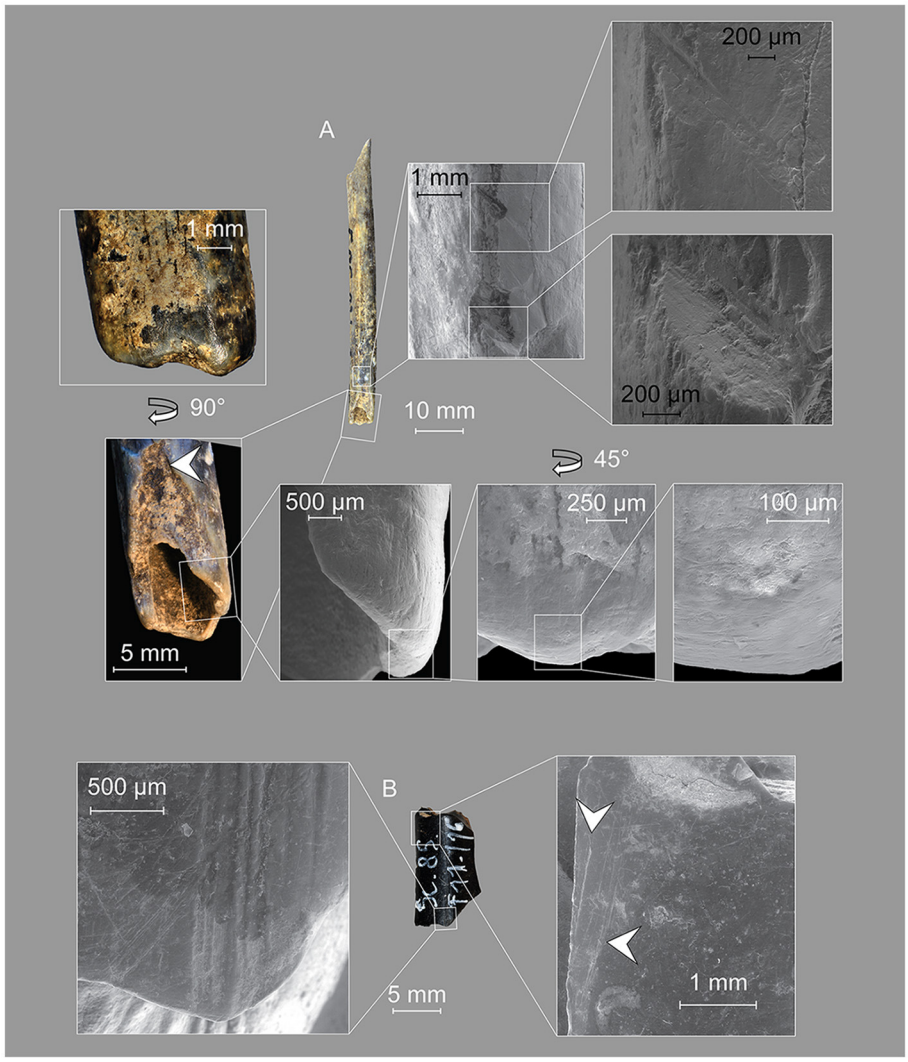

FIGURE 7
Unit 5. **(A)** Western capercaillie, right radius shaft presenting a very deep incision accompanied by a second parallel, more superficial incision (Sc 1985-910-309). One of the fractures shows a mark of peeling (arrow). The fracture edge is strongly rounded and shows a very developed polish (detail view). **(B)** Large bird, unidentified bone fragment with longitudinal incisions and superficial scraped areas (Sc1985-783-116).

found close to, and even within, a spread of burned mammal bones described by Abrams et al. (2010). However, there is no greater evidence of a concentration of avian remains here than elsewhere in the cave. Mechanical predator marks were identified throughout the cave, while digestion modifications were only identified in specimens located toward the back of the cave.

3.4.2 Complex of Units 4, Unit 4A-CHE and Unit 4B (MIS 5 and 6)

The bird bones from these units are presented on the same map, despite each sedimentary unit originating from a different set of processes (Supplementary Figure 4). The map shows the spatial position of the remains of the Neanderthal child within Unit 4A-CHE. There is a relative proximity between the bird bones with anthropogenic modifications and the human remains but they are not from the same grid squares and the sedimentary unit itself represents an erosion gully.

3.4.3 Unit 5 (MIS 6)

The bird bones from Unit 5 are mainly present within the first 25 meters from the cave opening (Supplementary Figures 5, 6). Specimens found in this area also bear marks made by small carnivores. Two concentrations can be distinguished in the distribution of avian remains: one closer to the entrance of the cave (10–13 m), and a second further into the cave (18–23 m). Both concentrations contain a specimen bearing anthropogenic modifications and are located close to numerous lithic artifacts and anthropogenically modified mammal remains. Analysis of the spatial distribution of lithics and faunal remains did not reveal any conclusive concentrations, and indicates instead that the archaeological remains in this unit were widely dispersed,

perhaps due to the post-depositional disturbance by mammals frequenting the cave when Neanderthals were not present (Bonjean, 1998; Patou-Mathis and Lopez-Bayon, 1998). However, the main sedimentary process responsible for the deposition of Unit 5, i.e., solifluction (Pirson, 2007, 2014), is also at least partly responsible for the spatial distribution of the material. Two bird bones bearing evidence of non-human predators were recovered from a natural alcove within the rock where the Scladina Cave joins with Saint-Paul Cave (30–33 m). A further specimen bearing digestion marks also appeared at this depth, isolated from other avian remains.

4 Discussion

4.1 Exploitation of birds by Neanderthals

The analysis of the avifauna of Scladina Cave provides the first testimonies of bird exploitation by Neanderthals in Belgium, extending the geographic area of dietary bird exploitation more than 600 km to the north. In total, 6 bird bones from MIS 5 or 6 (including 1 uncertain), and 2 from MIS 6 bear anthropogenic modifications.

The initial stratigraphic position of the bones unearthed from Unit 4A-CHE is uncertain, because they were reworked by the gully from other layers. In some situations, the stratigraphic position of the bones excavated from former Units 4 (4A and 4B) can also be uncertain, because of the complexity of this part of the sequence deciphered during the 2007 stratigraphic reappraisal (in former layers 4A and 4B, the new system implies 21 layers grouped into 5 Units). This is particularly true for bones initially attributed to Unit 4B. Given (1) the scarcity of bone remains in the whole Unit 4B, (2) the sedimentary dynamic of this unit (dominated by decantation in a pool covering a large surface inside the cave), and (3) the discrepancy between the environmental signal of certain bird taxa identified and that reconstructed by palynology for Unit 4B (see Section 4.3), it is unlikely that these objects truly came from Unit 4B. It seems plausible that they were mistakenly assigned to sedimentary unit 4B, as they were unearthed before the stratigraphic reappraisal which pointed to the existence of a deep gully (Unit 4A-CHE) eroding Unit 4B, and therefore lying at the same altitude. This hypothesis is all the more plausible because a bird bone initially attributed to Unit 4B has been reattributed to Unit 4A-CHE, thanks to careful re-examination of the available section drawings and pictures of the area, and thanks to the coordinates of the piece. This proves that at least some of the elements originally attributed to Unit 4B actually come from the gully, which seems much more consistent with the environmental significance of forest taxa identified as 4A-CHE reworked the temperate Sub-Units 4A-AP and 4A-IP, which correspond to MIS 5e (Eemian). However, we cannot exclude that some of these bones truly came from Unit 4B, or that some specimens unearthed from 4A-CHE come from Unit 5 (MIS 6), which delivered one of the two main Middle Paleolithic assemblages, as it was sporadically eroded by the 4A-CHE gully. This latter hypothesis nevertheless appears unlikely for the tawny owl bone, since this species favors temperate climate while palynology reconstructs cold environmental conditions in Unit 5. For all these reasons, for some of the studied specimens, we will only mention former Units 4, 4A or 4B, implying a chronostratigraphic attribution to the end of MIS 6 and/or the first part of MIS 5.

In Units 4, 4A-CHE, and 4B (MIS 5 or 6) the exploited taxa are the Western capercaillie, the great cormorant, the black grouse, another species of small grouse, and possibly the likely lesser spotted eagle. The exploitation of the great cormorant indicates predation at the edge of a waterbody or a watercourse of a given breadth, perhaps located at the level of the current Meuse Valley. The two grouse species may have been captured in woodlands, or an open environment in the case of the black grouse. The striae observed denote butchery activities, except for the lesser spotted eagle talon which exhibits a strong polish possibly related to manipulation by hominins. Two bones of large birds from Unit 5 (MIS 6) bear marks of tools also compatible with the removal of meat. However, the two deep incisions observed on the radius of a Western capercaillie suggest a sawing action which implies possible working of the bone. In addition, this element presents a highly developed polish on a broken edge which indicates that the bone was utilized for an unknown purpose.

Several Middle Paleolithic sites from southern Europe have revealed features of disarticulation and/or flesh removal on meat-bearing avian elements, suggesting consumption of the flesh. It is possible that some of these marks were produced during the recovery of other products such as tendons (Blasco et al., 2019), in particular when bones bearing little meat are affected. In general, remains of birds bearing marks of butchery activities are rare within the same site (Blasco et al., 2022), and this is confirmed in the case of Scladina. However, the sites of Bolomor, Cova Negra, Gorham's cave, Pié Lombard, and Fumane yielded more substantial assemblages (Peresani et al., 2011; Blasco and Fernández Peris, 2012; Finlayson et al., 2012; Blasco et al., 2013, 2014, 2016; Fiore et al., 2016; Romero et al., 2017). From a geospatial point of view, Blasco et al. (2022) indicated regional variations in the taxa exploited: the use of pigeons and partridges of the genus *Alectoris* seems to be specific to the Mediterranean Region, while diurnal birds of prey, corvids, and birds from the Anatidae family are exploited elsewhere in Europe. The consumption of the Western capercaillie by Neanderthals at Scladina proves to be the first direct evidence of exploitation of this species of the Galliformes order, unlike the black grouse that has been identified in Neanderthal contexts previously.

The assemblage from the Scladina Cave mainly includes birds from the order Galliformes. This does not stand out in comparison with other Middle Paleolithic sites where species of the Galliformes genus *Alectoris* are frequently exploited (Martínez Valle et al., 2016; Romero et al., 2017). Rather it suggests that *Alectoris* exploitation in the Mediterranean region is part of an overall dietary trend toward the exploitation of Galliformes in general, and that the exploitation of certain genera was constrained only by species distribution. Neanderthals exploited whichever species were available in the Pleistocene landscape whatever the latitude band.

The exploitation of the riparian great cormorant emphasizes the Neanderthals' ability to exploit a large range of game available to them in the vicinity of Scladina Cave. Indeed, despite being less useful as a proxy for paleoclimatic reconstruction, the ecological information from exploited taxa still informs us about the presence of a variety of habitats close to Scladina Cave at the time of original

deposition. This aligns well with established preferences in human habitat choice (Finlayson et al., 2011). The presence of cormorants, among several other aquatic bird species, has also been reported as the result of Neanderthal activities at Gruta da Figueira Brava (Nabais et al., 2023). The avian contribution to the human diet at Scladina Cave indicates that Neanderthals in MIS 5 and MIS 6 exploited woodland and wetland environments close to the cave. While some wetland species identified amongst the assemblage, like ducks, might be found in the small river valley close to the cave, others such as the great cormorant were more likely to frequent the larger waters running at the location of today's river Meuse. Extensive forested areas with large openings in the surroundings hosted Western capercaillie and black grouse. Knowledge and understanding of prey availability in this diverse ecotonal habitat testifies to Neanderthal cognitive complexity in regard to hunting and subsistence strategies.

Some sites have yielded phalanges of birds bearing marks of tools. The phalanges, especially the distal phalanx carrying the keratinous sheath of the talon, are devoid of nutritional value, implying an objective other than food (Morin and Laroulandie, 2012; Radovčić et al., 2015; Rodríguez-Hidalgo et al., 2019; Romandini et al., 2014). All phalanges modified during the Middle Paleolithic or Middle-to-Upper Paleolithic transition are of large diurnal birds of prey, at the exception of an incised swan phalanx unearthed from a Mousterian context at Baume de Gigny (Mourer-Chauviré, 1975) and an eagle owl phalanx found in the Châtelperronian layers of the Grotte du Renne (Vanhaeren et al., 2019). The possible manipulation of a talon from a likely lesser spotted eagle at Scladina Cave fits well into this pattern, although it remains hypothetical at this stage.

Examples of the use of hard materials from mammals by Neanderthals in tool-making are multiplying, with examples intended for working with skin, wood or lithic materials (for example, Gaudzinski, 1999; Burke and d'Errico, 2008; Mallye et al., 2012; Soressi et al., 2013; Tartar and Costamagno, 2016; Baumann et al., 2020, 2022). On the other hand, the shaping and use of bird bones has only been very rarely demonstrated for the Middle Paleolithic. The deep incision on the radius of a Western capercaillie from Scladina Cave presents a morphology reminiscent of incisions observed on the radius of a common raven discovered at the site of Zaskalnaya, Crimea (Majkić et al., 2017). The Zaskalnaya specimen shows marks of cutting on the anterior surface and seven parallel notches on the posterior surface of the bone, distributed over a length of approximately 1 cm. These notches are considered to have decorative value, although their production may have initially been utilitarian in purpose, such as ensuring a good grip on the bone. Indeed, the notches were produced in a series of events, some having been added to fill a void, which is interpreted as aesthetic desire (Majkić et al., 2017). Currently, there is no argument to suggest any decorative intention in the incisions on the Scladina Cave specimen, but it is interesting to note the morphological similarities. The Scladina radius also shows strong polish associated with micro-striations that resembles those identified on the fracture edge of an incised black vulture carpometacarpus at Fumane Cave and interpreted as possible use-wear produced during the utilization of the bone (Peresani et al., 2011).

4.2 Non-human accumulating agents

All bird remains in the occupationally scant complex of Units 3 displayed some indication of carnivore agency. It is also the only context group where all types of carnivore modification were visible on the bone surfaces. The remains were of Galliformes (MNI = 2; a Western capercaillie and a black grouse-sized bird) that were likely predated close to the cave. The remains were limited to an area with an alcove at the point where Scladina and Saint-Paul caves merge. The bird remains from complex of Units 3 were accumulated by a small to medium carnivore and indicated denning behavior through their distribution. The mammalian fauna identified in Scladina Cave is rich in carnivores, including large mammals such as cave bears (*Ursus spelaeus*), wolves (*Canis lupus*), and cave hyenas (*Crocuta crocuta spelea*) (Simonet, 1992; Patou-Mathis, 1998; Daujeard et al., 2016; Table 6.3). However, taphonomy indicates that the carnivores responsible for the partial accumulation of bird remains in Scladina were smaller. Smaller carnivores such as dhole (*Cuon* sp.), red fox (*Vulpes vulpes*), badger (*Meles meles*), wild cat (*Felis silvestris*), and mustelid remains in the sequence are prime candidates for the agent behind the mechanical and digestive marks identified on bone surfaces in complex of Units 3 (Daujeard et al., 2016; Marin-Monfort et al., 2019; Royer et al., 2021). However, this is inconsistent with the majority of digestion recorded in the avian assemblage of Scladina, which is more indicative of bird of prey action.

Though small carnivores hunted birds, they may also have scavenged the discarded remains of human meals. This behavior may be surmised from the presence of both cutmarks and subsequent carnivore tooth marks on the bone of a Western capercaillie in Sedimentary Complex 4A. In Unit 5, avian remains with carnivore marks accounted for 52.6% of the sample, but there was no evidence of carnivores scavenging Neanderthal leftover bird carcasses. Instead, rodent gnawing was present on the discarded bone of a grouse-sized bird. In the natural alcove utilized by carnivores in complex of Units 3, a co-occurrence of remains suggests its use as a den at some point during the deposition of Unit 5. The mammalian record shows the presence of canids and bears during this phase (Patou-Mathis, 1998; Daujeard et al., 2016), but the bird bones do not reflect predation by large mammalian carnivores. This is not unexpected as larger carnivores would eat the whole carcass and digest all the bones (Andrews, 1990).

The spatial proximity of certain owl (Strigiformes) remains with the main arch of the cave in Unit 5 (MIS 6) might suggest that these were the result of attritional accumulation in connection to roosts and nests. They were unlikely to have roosted when the cave was occupied by Neanderthals (Bocheński, 2005; Bocheński et al., 2018). There is no mechanical evidence of raptors catching birds in the recovered material, but a study of digestion marks on the molars of micromammals from MIS 5 and MIS 3 determined that two classes of Strigiform predator were responsible for their accumulation (López-García et al., 2017). Digestion profiles found on the avian remains, along with the presence of three species of owl remains (*Bubo* sp., *Strix aluco*, *Asio* sp.) in the assemblage align well with their findings, however digestion traces are infrequent in the avian sample, suggesting that avian predators were not the main

accumulation agent at Scladina. There are also clear taphonomic traces pointing toward small carnivore agency in complex of Units 3. Diurnal raptor remains in Unit 1A ($n = 2$) were found in an area between 35 and 40 meters from the cave entrance. Neither the large eagle (*Aquila* sp.) nor the sparrowhawk (*Accipiter nisus*) specimen exhibited identifiable marks of human agency, and sedimentary dynamics could easily explain their position in the cave and they are therefore not considered likely agents of accumulation.

4.3 Environment and climate

The bird remains reflect the presence of both open and wooded environments throughout the deposition of the Middle Paleolithic sediments (MIS 6–MIS 3) with intermittent wetland signals in the form of Suliformes and Anseriformes. This could indicate the presence of an ecotonal, mosaic type landscape in the vicinity of Scladina Cave during the Middle Paleolithic, and/or a dynamic shifting of habitats throughout time. Western capercaillie and black grouse would have frequented boreal forest environments around the cave, while the less arboreal ptarmigans would have occupied a more open, tundra-like environment (Cramp and Simmons, 1977-1994). Waterfowl such as ducks and geese could have exploited the nearby water bodies. Depending on the species, ducks can be highly adaptable and exploit any water body available. Geese however may have been drawn to the islands on the River Meuse for breeding and inland water bodies. The islands along the Meuse also provide a nesting habitat for the great cormorant (*Phalacrocorax carbo*). This insular nesting behavior is seen in the species today, which is still nesting on islands in the Meuse Valley nowadays.

These observations are supported by pollen analyses (Pirson, 2007; Pirson et al., 2008, 2014) and studies of various authors on the small and large mammals (Cordy, 1992; Simonet, 1992; Moncel, 1998; Patou-Mathis, 1998; Daujeard et al., 2016; López-García et al., 2017). Herbs and forbs are most frequent, in both Unit 1A (MIS 3) and Unit 5 (MIS 6), signaling open areas. However, these signals are highly variable between sedimentary units. The presence of boreal conifers in both stages also alludes to patches of forest (Pirson, 2007; Pirson et al., 2008). Micromammals from MIS 3 (Unit 1A) indicate cold and dry conditions (*Lagurus lagurus*, *Lemmus lemmus*, *Dicrostonyx torquatus*, *Microtus arvalis,* and *Chionomys nivalis*). In MIS 6 the species representation indicated sporadic peaks in aquatic local environments (*Microtus agrestis*, *Talpa europaea*, *Sorex gr. araneus*, and *Microtus gregalis*) (López-García et al., 2017).

However, despite the seeming correlation between proxies, it is important to note that some of the avian remains may have been reworked into their current position by sedimentary and/or post-depositional processes. In Unit 1A, the presence of a European sparrowhawk and a probable wood pigeon, both forest-dwelling taxa, could be due to more recent intrusions given that converging signals document the deposition of this unit in a cold steppe environment (Pirson et al., 2008). However, as mentioned above, pollen signals do attest to the presence of boreal conifers in this period, and both the wood pigeon and Eurasian sparrowhawk are multi-latitudinal semi-generalist to generalist species that can adapt to dynamic bioclimatic parameters (Finlayson et al., 2011).

The numerous remains of Western capercaillie ($n = 23$) and a single bone of a tawny owl (Figure 2A) attributed to Unit 4B are also forest-dwelling taxa. However, this unit records one of the harshest climate conditions in the entire sequence (Pirson et al., 2008, 2014). Therefore, as stated before, these remains were most likely erroneously attributed to Unit 4B and come from the gully, which reworked temperate layers characterized by a forest environment more compatible with these woodland taxa, especially the tawny owl (see Section 4.1).

5 Conclusion

Despite complex sedimentogenesis along with small sample size, the bird assemblage from Scladina Cave has proven highly informative as a proxy for Neanderthal behavior. Results demonstrate that Neanderthals navigating the dynamic Pleistocene landscapes of northwestern Europe in MIS 6 and 5 exploited birds as part of their diet. Additionally, they utilized bird bones as tools and may have collected talons for symbolic purposes. The avian prey spectrum at Scladina indicates a Neanderthal population with a profound understanding of available habitats and the avian game available to them with prey-species representing woodland and semi-open habitats, as well as wetlands. Our results from Scladina Cave contribute two novel species to the spectrum of known prey species during the Middle Paleolithic, and provide new geospatial data from northwestern Europe to the growing number of sites reporting bird exploitation by Neanderthals.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Author contributions

QG: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. VR: Conceptualization, Investigation, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. GA: Conceptualization, Data curation, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. SP: Conceptualization, Data curation, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. KD: Conceptualization, Data curation, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. FB: Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. DC: Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. DB: Data curation, Investigation, Resources, Writing – original draft, Writing – review & editing. LA: Conceptualization, Data curation, Formal

analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, 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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2024.1441926/full#supplementary-material

References

Abrams, G. (2018). "Palaeolithic bone retouchers from Belgium: a preliminary overview of the recent research through historic and modern bone collections", in *The Origins of Bone Tool Technologies,* eds. J.M. Hutson, A. García-Moreno, E.S. Noack, E. Turner, A. Villaluenga and S. Gaudzinski-Windheuser (Mainz: Verlag des Römisch-Germanisches Zentralmuseums - Leibniz-Forschungsinstitut für Archäologie), 197–214.

Abrams, G., Bello, S. M., Di Modica, K., Pirson, S., and Bonjean, D. (2014). When Neanderthals used cave bear (*Ursus spelaeus*) remains: Bone retouchers from unit 5 of Scladina Cave (Belgium). *Quarter. Int.* 326, 274–287. doi: 10.1016/j.quaint.2013.10.022

Abrams, G., Bonjean, D., Di Modica, K., Pirson, S., Otte, M., and Patou-Mathis, M. (2010). Les os brûlés de l'ensemble sédimentaire 1A de Scladina (Andenne, Belgique): apports naturels ou restes de foyer(s) néandertalien(s)? *Notae Praehistor.* 30, 5–13.

Abrams, G., Devièse, T., Pirson, S., De Groote, I., Flas, D., Jungels, C., et al. (2024). Investigating the co-occurrence of Neanderthals and modern humans in Belgium through direct radiocarbon dating of bone implements. *J. Hum. Evol.* 186:103471. doi: 10.1016/j.jhevol.2023.103471

Andrews, P. (1990). *Owls, Caves and Fossils.* London: British Museum of Natural History.

Bacher, A. (1967). *Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Schwäne und Gänse.* PhD thesis, München, Universität München.

Barisic, M. (2006). *Étude de l'effet du piétinement humain sur des ossements de faune mélangés à un amas de taille.* PhD thesis, Bordeaux, Université Bordeaux 1, UMR PACEA 5199.

Baumann, M., Plisson, H., Rendu, W., Maury, S., Kolobova, K., and Krivoshapkin, A. (2020). The Neandertal bone industry at Chagyrskaya cave, Altai Region, Russia. *Quater. Int.* 559, 68–88. doi: 10.1016/j.quaint.2020.06.019

Baumann, M., Ready, E., Plisson, H., Maury, S., Vanderesse, N., Coqueugniot, H., et al. (2022). Not so unusual Neanderthal bone tools: new examples from Abri Lartet, France. *Archaeol. Anthropol. Sci.* 14:200. doi: 10.1007/s12520-022-01674-4

Baumel, J. J. (1993). *Handbook of Avian Anatomy: Nomina Anatomica Avium.* Cambridge: Publications of the Nuttall Ornithological Club 23.

Behrensmeyer, A. K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162. doi: 10.1017/S0094837300005820

Behrensmeyer, A. K., Stayton, C. T., and Chapman, R. E. (2003). Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology* 29, 52–70. doi: 10.1666/0094-8373(2003)029<0052:TAEOMA>2.0.CO;2

Blain, H.-A., López-García, J. M., Cordy, J.-M., Pirson, S., Abrams, G., Di Modica, K., et al. (2014). Middle to late Pleistocene herpetofauna from Scladina and Sous-Saint-Paul caves (Namur, Belgium). *Comptes Rendus Palevol.* 13, 681–390. doi: 10.1016/j.crpv.2014.03.006

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals: understanding behavioural complexity in the Late Middle Palaeolithic,* eds F. Romagnoli, F. Rivals and S. Benazzi. (London: Academic Press, Elsevier), 123–143. doi: 10.1016/B978-0-12-821428-2.00010-X

Blasco, R., and Fernández Peris, J. (2009). Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 36, 2213–2223. doi: 10.1016/j.jas.2009.06.006

Blasco, R., and Fernández Peris, J. (2012). Small and large game: Human use of diverse faunal resources at Level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus Palevol.* 11, 265–282. doi: 10.1016/j.crpv.2012.01.003

Blasco, R., Fernández Peris, J., and Rosell, J. (2008). Estrategias de subsistencia en los momentos finales del Pleistoceno medio: el nivel XII de la Cova del Bolomor (La Valldigna, Valencia). *Zephyrvs* 62, 63–80.

Blasco, R., Finlayson, C., Rosell, J., Marco, A. S., Finlayson, S., Finlayson, G., et al. (2014). The earliest pigeon fanciers. *Sci. Rep.* 4, 1–7. doi: 10.1038/srep05971

Blasco, R., Rosell, J., Domínguez-Rodrigo, M., Lozano, S., Past,ó, I., Riba, D., et al. (2013). Learning by heart: cultural patterns in the faunal processing sequence during the middle pleistocene. *PLoS ONE* 8:e55863. doi: 10.1371/journal.pone.0055863

Blasco, R., Rosell, J., Rufà, A., Sánchez Marco, A., and Finlayson, C. (2016). Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quater. Int.* 421, 62–77. doi: 10.1016/j.quaint.2015.10.040

Blasco, R., Rosell, J., Sánchez-Marco, A., Gopher, A., and Barkai, R. (2019). Feathers and food: Human-bird interactions at Middle Pleistocene Qesem Cave, Israel. *J. Hum. Evol.* 136:102653. doi: 10.1016/j.jhevol.2019.102653

Bocheński, Z. M. (2005). "Owls, diurnal raptors and humans: signatures on avian bones," in Biosphere to Lithosphere: new studies in vertebrate taphonomy, ed. (Oxford: Oxbow Books), 31–45. doi: 10.2307/j.ctt1kw294s.8

Bocheński, Z. M., and Tomek, T. (1997). Preservation of bird bones: erosion versus digestion by owls. *Int. J. Osteoarchaeol.* 7, 372–387. doi: 10.1002/(SICI)1099-1212(199707/08)7:4<372::AID-OA355>3.0.CO;2-W

Bocheński, Z. M., Tomek, T., and Wertz, K. (2009). The state of preservation of bird remains in a cave environment: a case study from Ciemna Cave (Poland). *Acta Zool. Cracov.* 52, 1–16.

Bocheński, Z. M., Tomek, T., and Wertz, K. (2022). Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey. *Int. J. Osteoarchaeol.* 33, 1–17. doi: 10.1002/oa.3165

Bocheński, Z. M., Wertz, K., and Tomek, T. (2018). What happens to dead birds left in a cave and its vicinity for a quarter of a century? A taphonomic experiment. *Histor. Biol.* 30, 855–867. doi: 10.1080/08912963.2017.1335721

Bonjean, D. (1998). "Répartition spatiale de l'industrie lithique," in *Recherches aux grottes de Sclayn. Volume 2. L'archéologie,* eds. M. Otte, M. Patou-Mathis, and D. Bonjean (Liège : Études et Recherches archéologiques de l'Université de Liège 79), 340–376.

Bonjean, D., Abrams, G., and Di Modica, K. (2012). Grotte Scladina, une preuve de la chasse au lièvre au Paléolithique moyen. *Chronique de l'Archéologie Wallonne* 19, 209–211.

Bonjean, D., Vanbrabant, Y., Abrams, G., Pirson, S., Burlet, C., Di Modica, K., et al. (2015). A new Cambrian black pigment used during the late Middle Palaeolithic discovered at Scladina Cave (Andenne, Belgium). *J. Archaeol. Sci.* 55, 253–265. doi: 10.1016/j.jas.2014.11.040

Bourdillat, V. (2008). *Hommes, carnivores? Caractériser l'action de l'hyène des cavernes: de l'utilisation des données fossiles pour l'interprétation des sites mixtes.* PhD thesis, Paris, Muséum national d'Histoire naturelle.

Bray, F., Fabrizi, I., Flament, S., Locht, J. L., Antoine, P., Auguste, P., et al. (2023). Robust high-throughput proteomics identification and deamidation quantitation of extinct species up to pleistocene with ultrahigh-resolution MALDI-FTICR mass spectrometry. *Anal. Chem.* 95, 7422–7432. doi: 10.1021/acs.analchem.2c03301

Burke, A., and d'Errico, F. (2008). A middle palaeolithic bone tool from crimea (Ukraine). *Antiquity* 82, 843–852. doi: 10.1017/S0003598X00097611

Cnuts, D., Peresani, M., and Rots, V. (2022). The contribution of stone tool residues in reconstructing Late Pleistocene hominin stone tool behaviour at Grotta di Fumane, Italy. *Quat. Sci. Rev.* 297:107829. doi: 10.1016/j.quascirev.2022.107829

Codlin, M. C., Douka, K., and Richter, K. K. (2022). An application of zooms to identify archaeological avian fauna from Teotihuacan, Mexico. *J. Archaeol. Sci.* 148:105692. doi: 10.1016/j.jas.2022.105692

Cordy, J.-M. (1992). "Bio- et chronostratigraphie des dépôts quaternaires de la grotte Scladina (province de Namur, Belgique) à partir des micromammifères," in *Recherches aux grottes de Sclayn, Volume 1.* Le contexte, ed M. Otte (Liège: Études et Recherches archéologiques de l'Université de Liège 27), 79–125.

Cramp, S., and Simmons, K.E.L. (1977-1994). *The Birds of the Western Palearctic.* Oxford, New York: Oxford University Press.

Daujeard, C., Abrams, G., Germonpré, M., Le Pape, J. M., Wampach, A., Di Modica, K., et al. (2016). Neanderthal and animal karstic occupations from southern Belgium and South-eastern France: Regional or common features? *Quater. Int.* 411, 179–197. doi: 10.1016/j.quaint.2016.02.009

Delagnes, A., and Rendu, W. (2011). Shifts in Neandertal mobility, technology and subsistence strategies in western France. *J. Archaeol. Sci.* 38, 1771–1783. doi: 10.1016/j.jas.2011.04.007

Dewez, M. (1981). Les grottes de Sclayn: ensemble rituel moustérien ou repaire d'ours? *Activités SOS Fouilles* 2, 79–83.

Di Modica, K. (2010). *Les productions lithiques du Paléolithique moyen de Belgique: variabilité des systèmes d'acquisition et des technologies en réponse à une mosaïque d'environnements contrastés.* PhD thesis, Liège, Université de Liège and Muséum d'Histoire Naturelle de Paris.

Di Modica, K., and Bonjean, D. (2004). Scladina (Sclayn, province de Namur): ensembles lithiques moustériens méconnus. *Notae Praehistoricae* 24, 5–8.

Di Modica, K., Toussaint, M., Abrams, G., and Pirson, S. (2016). The Middle Palaeolithic from Belgium: Chronostratigraphy, territorial management and culture on a mosaic of contrasting environments. *Quater. Int.* 411, 77–106. doi: 10.1016/j.quaint.2015.12.072

Dibble, H. L., Berna, F., Goldberg, P., Mcpherron, S.-P., Mentzer, S., Niven, L., et al. (2009). A preliminary report on Pech de l'Azé IV, Layer 8 (Middle Paleolithic, France). *Paleoanthropology* 2009, 182–219. doi: 10.4207/PA.2008.ART30

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B., and Rodríguez, M. (2009). A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654. doi: 10.1016/j.jas.2009.07.017

Draily, C., Toussaint, M., and Pirson, S. (2011). "La grotte Walou à Trooz (Belgique)," in *Fouilles de 1996 à 2004. Volume 2. Les sciences de la vie et les datations. Namur, Service public de Wallonie* (Études et documents – Archéologie 21).

Eda, M., Morimoto, M., Mizuta, T., and Inoué, T. (2020). ZooMS for birds: Discrimination of Japanese archaeological chickens and indigenous pheasants using collagen peptide fingerprinting. *J. Archaeol. Sci.* 34:102635. doi: 10.1016/j.jasrep.2020.102635

Ellwood, B. B., Harrold, F. B., Benoist, S. L., Thacker, P. T., Otte, M., Bonjean, D., et al. (2004). Magnetic susceptibility applied as an age-depth-climate relative dating technique using sediments from Scladina Cave, a Late Pleistocene cave site in Belgium. *J. Archaeol. Sci.* 31, 283–293. doi: 10.1016/j.jas.2003.08.009

Erbersdobler, K. (1968). *Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender mittelgroßer Hühnervögel.* PhD thesis, München, Universität München.

Fernández-Jalvo, Y., and Andrews, P. (2016). *Atlas of Taphonomic Identifications. 1001+ Images of Fossil and Recent Mammal Bone Modification.* The Netherlands: Springer. doi: 10.1007/978-94-017-7432-1

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., Bortolotti, G. R., et al. (2012). Birds of a feather: neanderthal exploitation of raptors and corvids. *PLoS ONE* 7:e45927. doi: 10.1371/journal.pone.0045927

Finlayson, C., Carrión, J., Brown, K., Finlayson, G., Sánchez-Marco, A., Fa, D., et al. (2011). The Homo habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quat. Sci. Rev.* 30, 1525–1532. doi: 10.1016/j.quascirev.2011.01.010

Fiore, I., Gala, M., Romandini, M., Cocca, E., Tagliacozzo, A., and Peresani, M. (2016). From feathers to food: reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane cave, unit A9. *Quater. Int.* 421, 134–153. doi: 10.1016/j.quaint.2015.11.142

Flannery, K. V. (1969). "Origins and ecological effects of early domestication in Iran and the Near East," in *The Domestication and Exploitation of Plants and Animals,* eds. P. J. Ucko and G. W. Dimbleby (Chicago: Aldine), 73–100. doi: 10.4324/9781315131825-7

Garcia-Fermet, T., Testu, A., Moigne, A., Saos, T., and Grégoire, S. (2023). The bird remains from La Crouzade Cave (Gruissan, Aude): the mixed origin of a Middle Palaeolithic bone accumulation. *Quarter. Environ. Hum.* 1:100001. doi: 10.1016/j.qeh.2023.100001

Gaudzinski, S. (1999). Middle Palaeolithic bone tools from the open-air site Salzgitter-Lebenstedt (Germany). *J. Archaeol. Sci.* 26, 125–141. doi: 10.1006/jasc.1998.0311

Gaudzinski-Windheuser, S., and Niven, L. (2009). "Hominin subsistence patterns during the middle and late Paleolithic in Northwestern Europe," in *The Evolution of Hominin Diets.* Vertebrate Paleobiology and Paleoanthropology, eds J. J. Hublin, M. P. Richards (Dordrecht: Springer). doi: 10.1007/978-1-4020-9699-0_7

Gill, F., Donsker, D., and Rasmussen, P. (2022). *IOC World bird list (v 12.1).* Available at: https://www.worldbirdnames.org/new/ioc-lists/master-list-2/ (accessed March 23, 2022).

Goffette, Q., Germonpré, M., Lefèvre, C., Brecko, J., Goemaere, E., and Rots, V. (2020). Bird bones from Trou de Chaleux and the human exploitation of birds during the late Magdalenian in Belgium. *J. Archaeol. Sci.* 29:102096. doi: 10.1016/j.jasrep.2019.102096

Goffette, Q., Lepers, C., Jadin, I., and Rots, V. (2023). A handful of duck radiuses: Peculiarities of the avifaunal exploitation at the Gravettian site of Maisières-Canal (Belgium). *Int. J. Osteoarchaeol.* 33, 668–682. doi: 10.1002/oa.3194

Gómez-Olivencia, A., Sala, N., Sanchis, A., and Arlegi, M. (2018). First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* 8, 1–14. doi: 10.1038/s41598-018-28377-y

Gullentops, F., and Deblaere, C. (1992). "Érosion et remplissage de la grotte Scladina," in *Recherches aux grottes de Sclayn, Volume 1. Le contexte,* ed. M. Otte (Liège, Études et Recherches archéologiques de l'Université de Liège 27), 9–31.

Haesaerts, P. (1992). "Les dépôts pléistocènes de la terrasse de la grotte Scladina à Sclayn (province de Namur, Belgique)," in *Recherches aux grottes de Sclayn, Volume 1. Le contexte,* ed. M. Otte (Liège, Études et Recherches archéologiques de l'Université de Liège 27),33–55.

Hardy, B. L., and Moncel, H. (2011). Neanderthal use of fish, mammals, birds, starchy plants and wood 125-250,000 years ago. *PLoS ONE* 6:e23768. doi: 10.1371/journal.pone.0023768

Hardy, B. L., Moncel, M., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., et al. (2013). Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). *Quat. Sci. Rev.* 82, 23–40. doi: 10.1016/j.quascirev.2013.09.028

Hockett, B., and Haws, J. A. (2002). Taphonomic and methodological perspectives of leporid hunting during the Upper Paleolithic of the Western Mediterranean Basin. *J. Archaeol. Method Theory* 9, 269–302. doi: 10.1023/A:1019503030246

Hoffecker, J. F., and Cleghorn, N. E. (2000). Mousterian hunting patterns in the Northwestern Caucasus and the ecology of the Neanderthals. *Int. J. Osteoarchaeol.* 10, 368–378. doi: 10.1002/1099-1212(200009/10)10:5<368::AID-OA555>3.0.CO;2-H

Hoffmann, D. L., Angelucci, D. E., Villaverde, V., Zapata, J., and Zilhão, J. (2018). Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* 107, 1023–1028. doi: 10.1126/sciadv.aar5255

Hutson, J. M., García-Moreno, A., Noack, E. S., Turner, E., Villaluenga, A., and Gaudzinski-Windheuser, S. (2018). *The Origins of Bone Tool Technologies.* Mainz: Verlag des Römisch-Germanisches Zentralmuseum - Leibniz-Forschungsinstitut für Archäologie.

Kraft, E. (1972). *Vergleichend morphologische Untersuchungen an Einzelknochen nord- und mitteleuropäischer kleinerer Hünhervögel.* PhD thesis, München, Universität München.

Langer, G. (1980). *Vergleichend morphologische Untersuchungen an Einzelknochen in Mitteleuropa vorkommender mittelgrosser Eulenarten.* PhD thesis, München, Universität München.

Laroulandie, V. (2001). ≪ Les traces liées à la boucherie, à la cuisson et à la consommation d'oiseaux. Apport de l'expérimentation, ≫ in *Préhistoire et approche expérimentale,* eds L. Bourguignon, I. Ortega, and M.-C. Frère-Sautot, (Montagnac: Éditions Monique Mergoil), 97–108.

Laroulandie, V., Faivre, J., Gerbe, M., and Mourre, V. (2016). Who brought the bird remains to the Middle Palaeolithic site of Les Fieux (Southwestern, France)? Direct evidence of a complex taphonomic story. *Quater. Int.* 421, 116–133. doi: 10.1016/j.quaint.2015.06.042

Lloveras, L., Garcia, L., Maroto, J., Soler, J., and Soler, N. (2018). The bird assemblage from the Middle Palaeolithic level I of Arbreda Cave: a taphonomic story. *J. Archaeol. Sci.* 21, 758–770. doi: 10.1016/j.jasrep.2018.08.040

Loodts, I. (1998). "Une approche comportementale de l'Homme de Neandertal. L'industrie lithique de la couche 1A de la grotte Scladina, économie des matières premières et coexistence des chaînes opératoires au Paléolithique moyen récent," in *Recherches aux grottes de Sclayn. Volume 2. L'archéologie,* eds M. Otte, M. Patou-Mathis, and D. Bonjean (Liège : Études et Recherches archéologiques de l'Université de Liège 79), 69–71.

López-García, J. M., Blain, H., Cordy, J.-M., Pirson, S., Abrams, G., Di Modica, K., et al. (2017). Palaeoenvironmental and palaeoclimatic reconstruction of the Middle to Late Pleistocene sequence of Scladina Cave (Namur, Belgium) using the small-mammal assemblages. *Histor. Biol.* 29, 1125–1142. doi: 10.1080/08912963.2017.1288229

López-García, J. M., Blain, H.-A., Goffette, Q., Cousin, C., and Folie, A. (2024). Environmental and climatic inferences for Marine Isotope Stage 2 of southern Belgium (Meuse valley, Namur Province) based on rodent assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 636:111976. doi: 10.1016/j.palaeo.2023.111976

López-González, F., Grandal-d'Anglade, A., and Vidal-Romaní, J. R. (2006). Deciphering bone depositional sequences in caves through the study of manganese coatings. *J. Archaeol. Sci.* 33, 707–717. doi: 10.1016/j.jas.2005.10.006

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9781139878302

Majkić, A., Evans, S., Stepanchuk, V., Tsvelykh, A., and d'Errico, F. (2017). A decorated raven bone from the Zaskalnaya VI (Kolosovskaya) Neanderthal site, Crimea. *PLoS ONE* 12:e0173435. doi: 10.1371/journal.pone.0173435

Mallye, J.-B., Thiébaut, C., Mourre, V., Costamagno, S., Claud, É., and Weisbecker, P. (2012). The Mousterian bone retouchers of Noisetier Cave: experimentation and identification of marks. *J. Archaeol. Sci.* 39, 1131–1142. doi: 10.1016/j.jas.2011.12.018

Marin-Monfort, M. D., García-Morato, S., Olucha, R., Yravedra, J., Piñeiro, A., Barja, I., et al. (2019). Wildcat scats: taphonomy of the predator and its micromamal prey. *Quat. Sci. Rev.* 225:106024. doi: 10.1016/j.quascirev.2019.106024

Martínez Valle, R., Guillem Calatayud, P. M., and Villaverde Bonilla, V. (2016). Bird consumption in the final stage of Cova Negra (Xátiva, Valencia). *Quater. Int.* 421, 85–102. doi: 10.1016/j.quaint.2016.01.068

Maureille, B., Bayle, P., and Balzeau, A. (2016). *Néandertal et ses morts. Néandertal à la loupe*. Les Eyzies-de-Tayac: Musée National de Préhistoire 120–130.

Maureille, B., and Van Peer, P. (1998). A little known element concerning the burial of the first adult at La Ferrassie (Savignac-de-Miremont, Dordogne). *Paléo* 10, 291–301. doi: 10.3406/pal.1998.1141

Moncel, M.-H. (1998). "L'industrie lithique de la grotte Scladina (Sclayn). La couche moustérienne 1A," in *Recherches aux grottes de Sclayn. Volume 2. L'Archéologie,* eds. M. Otte, M. Patou-Mathis, and D. Bonjean (Liège: Université de Liège) 103–112.

Morin, E., and Laroulandie, V. (2012). Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE* 7:e32856. doi: 10.1371/journal.pone.0032856

Morin, E., Meier, J., El Guennouni, K., Moigne, A. M., Lebreton, L., Rusch, L., et al. (2019). New evidence of broader diets for archaic *Homo* populations in the northwestern Mediterranean. *Sci. Adv.* 5 :eaav9106. doi: 10.1126/sciadv.aav9106

Mourer-Chauviré, C. (1975). Faunes d'oiseaux du pléistocène de France: Systématique, évolution et adaptation, interprétation paléoclimatique. *Geobios* 8, 333–352. doi: 10.1016/S0016-6995(75)80048-9

Nabais, M., Pimenta, C., and Zilhão, J. (2023). Human-bird interaction in last Interglacial Iberia: A combined approach using skeletal part analysis, bone surface modification, bird ethology and ethnography. *J. Archaeol. Sci.* 49:104023. doi: 10.1016/j.jasrep.2023.104023

Otte, M. (1992). *Recherches aux grottes de Sclayn. Volume 1: Le contexte.* Liège: Études et Recherches Archéologiques de l'Université de Liège.

Otte, M. (1998a). "Industrie lithique de la couche 5," in *Recherches aux grottes de Sclayn. Volume 2. L'archéologie,* eds. M. Otte, M. Patou-Mathis, and D. Bonjean (Liège : Études et Recherches archéologiques de l'Université de Liège 79), 277–278.

Otte, M. (1998b). "Le Paléolithique supérieur," in *Recherches aux grottes de Sclayn. Volume 2. L'archéologie,* eds M. Otte, M. Patou-Mathis, and D. Bonjean (Liège : Études et Recherches archéologiques de l'Université de Liège 79), 63–68.

Otte, M., Patou-Mathis, M., and Bonjean, D. (1998). *Recherches aux grottes de Sclayn. Volume 2. L'archéologie.* Liège: Études et Recherches Archéologiques de l'Université de Liège 79.

Patou-Mathis, M. (1998). "Les espèces chassées et consommées par l'homme en couche 5," in *Recherches aux grottes de Sclayn, Volume 2. L'archéologie,* eds. M. Otte, M. Patou-Mathis, and D. Bonjean (Études et Recherches archéologiques de l'Université de Liège 79), 297–310.

Patou-Mathis, M., and Lopez-Bayon, I. (1998). "Analyse spatiale des ossements de la couche 5," in *Recherches aux grottes de Sclayn. Volume 2. L"archéologie,* eds. M. Otte, M. Patou-Mathis, and D. Bonjean (Études et Recherches archéologiques de l'Université de Liège 79), 377-395.

Peresani, M., Fiore, I., Gala, M., Romandini, M., and Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc. Nat. Acad. Sci.* 108, 3888–3893. doi: 10.1073/pnas.1016212108

Pirson, S. (2007). *Contribution à l'étude des dépôts d'entrée de grotte en Belgique au Pléistocène supérieur. Stratigraphie, sédimentogenèse et paléoenvironnement.* PhD thesis, Liège, Université de Liège.

Pirson, S. (2011). "Contextes paléoenvironnemental et chronostratigraphique du remplissage de la grotte Walou: apport de la géologie et comparaison avec les autres disciplines," in *La grotte Walou à Trooz (Belgique). Fouilles de 1996-2004. Volume 1. Les sciences de la terre,* eds S. Pirson, C. Draily, and M. Toussaint (Namur: Institut du Patrimoine Wallon), 170–206.

Pirson, S. (2014). "The stratigraphic sequence of Scladina Cave," in *The Scladina I-4A Juvenile Neandertal (Andenne, Belgium). Palaeoanthropology and Context,* eds. M. Toussaint, and D. Bonjean (Liège: Études et Recherches archéologiques de l'Université de Liège 134), 49–68.

Pirson, S., Court-Picon, M., Damblon, F., Balescu, S., Bonjean, D., and Haesaerts, P. (2014). "The palaeoenvironmental context and chronostratigraphic framework of the Scladina Cave sedimentary sequence (units 5 to 3-SUP)," in *The Scladina I-4A Juvenile Neandertal (Andenne, Belgium). Palaeoanthropology and Context,* eds. M. Toussaint, and D. Bonjean (Liège: Études et Recherches archéologiques de l'Université de Liège 134), 69–92.

Pirson, S., Court-Picon, M., Haesaerts, P., Bonjean, D., and Damblon, F. (2008). New data on geology, anthracology and palynology from the Scladina Cave pleistocene sequence: preliminary results. *Mem. Geol. Surv. Belgium* 55, 71–93.

Pirson, S., Draily, C., and Toussaint, M. (2011). *La grotte Walou à Trooz (Belgique). Fouilles de 1996 à 2004. Volume 1. Les sciences de la terre.* Namur, Service public de Wallonie (Études et documents – Archéologie 20).

Pirson, S., Toussaint, M., Bonjean, D., and Di Modica, K. (2018). "Spy and Scladina caves: A Neandertal's story," in *Landscapes and landforms of Belgium and Luxemburg,* ed. A. Demoulin (Cham: Springer, World Geomorphological Landscapes), 357–383. doi: 10.1007/978-3-319-58239-9_21

Rabinovich, R., and Tchernov, E. (1995). Chronological, paleoecological and taphonomical aspects of the Middle Paleolithic site of Qafzeh, Israel. *Archaeozool. Near East* 2, 5–44.

Radovčić, D., JapundŽić, D., Sršen, A. O., Radovčić, J., and Frayer, D. W. (2016). An interesting rock from Krapina. *Comptes Rendus Palevol.* 15, 988–993. doi: 10.1016/j.crpv.2016.04.013

Radovčić, D., Sršen, A. O., Radovčić, J., and Frayer, D. W. (2015). Evidence for neandertal jewelry: modified white-tailed eagle claws at krapina. *PLoS ONE* 10:e0119802. doi: 10.1371/journal.pone.0119802

Rendu, W., Beauval, C., Crèvecœur, I., Bayle, P., and Balzeau, A., Bismuth, et al. (2014). Evidence supporting an intentional Neandertal burial at La Chapelle-aux-Saints. *Proc. Nat. Acad. Sci.* 111, 81–86. doi: 10.1073/pnas.1316780110

Rodríguez-Hidalgo, A., Morales, J. I., Cebrià, A., Courtenay, L. A., Fernández-Marchena, J. L., García-Argudo, G., et al. (2019). The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. *Sci. Adv.* 5:eaax1984. doi: 10.1126/sciadv.aax1984

Rodríguez-Vidal, J., d'Errico, F., Pacheco, F. G., Blasco, R., Rosell, J., Jennings, R. P., et al. (2014). A rock engraving made by Neanderthals in Gibraltar. *Proc. Nat. Acad. Sci.* 111, 13301–13306. doi: 10.1073/pnas.1411529111

Romagnoli, F., Rivals, F., and Benazzi, S. (2022). *Updating Neanderthals: understanding behavioural complexity in the Late Middle Palaeolithic*. London: Academic Press, Elsevier.

Romandini, M., Fiore, I., Gala, M., Cestari, M., Guida, G., Tagliacozzo, A., et al. (2016). Neanderthal scraping and manual handling of raptors wing bones: evidence from Fumane Cave. Experimental activities and comparison. *Quater. Int.* 421, 154–172. doi: 10.1016/j.quaint.2015.12.078

Romandini, M., Peresani, M., Laroulandie, V., Metz, L., Pastoors, A., Vaquero, M., et al. (2014). Convergent evidence of eagle talons used by late neanderthals in europe: a further assessment on symbolism. *PLoS ONE* 9:e101278. doi: 10.1371/journal.pone.0101278

Romandini, M., Silvestrini, S., Real, C., Lugli, F., and Tassoni, L., Carrera, et al. (2023). Late Neanderthal "menu" from northern to southern Italy: freshwater and terrestrial animal resources. *Quat. Sci. Rev.* 315:108233. doi: 10.1016/j.quascirev.2023.108233

Romero, A. J., Díez, J. C., and Brugal, J. P. (2017).. Aves de caza. Estudio tafonómico y zooarqueológico de los restos avianos de los niveles musterienses de

Pié Lombard (Alpes-Maritimes, Francia). *Munibe* 68, 73–84. doi: 10.21630/maa.2017.68.14

Romero, A. J., Díez, J. C., Rodríguez, L., and Arceredillo, D. (2016). Anthropic fractures and human tooth marks: an experimental approach to non-technological human action on avian long bones. *Quater. Int.* 421, 219–227. doi: 10.1016/j.quaint.2015.10.005

Rots, V. (2013). Insights into early Middle Palaeolithic tool use and hafting in Western Europe. The functional analysis of level IIa of the early Middle Palaeolithic site of Biache-Saint-Vaast (France). *J. Archaeol. Sci.* 40, 497–506. doi: 10.1016/j.jas.2012.06.042

Rots, V. (2015). "Hafting and site function in the European Middle Paleolithic," in *Settlement Dynamics of the Middle Palaeolithic and Middle Stone Age (Vol. 4),* eds. N.J. Conard and A. Delagnes (Tübingen: Kerns Verlag), 383–410.

Royer, A., Mallye, J.-B., Pelletier, M., and Griselin, S. (2021). Who killed the small mammals of ittenheim? An integrative approach and new taphonomic data for investigating bone assemblages accumulated by small carnivores. *Quaternary* 4:41. doi: 10.3390/quat4040041

Rufà, A., Blasco, R., Roger, T., and Moncel, M. (2016). What is the taphonomic agent responsible for the avian accumulation? An approach from the Middle and early Late Pleistocene assemblages from Payre and Abri des Pêcheurs (Ardèche, France). *Quater. Int.* 421, 46–61. doi: 10.1016/j.quaint.2015.05.016

Serjeantson, D. (2009). *Birds*. Cambridge: Cambridge University Press.

Simonet, P. (1992). "Les associations de grands mammifères du gisement de la grotte Scladina à Sclayn (Namur, Belgique)," in *Recherches aux grottes de Sclayn, Volume 1. Le contexte,* ed. M. Otte (Liège: Études et Recherches archéologiques de l'Université de Liège 27), 9–31.

Soressi, M., and d'Errico, F. (2007). "Pigments, gravures, parures: les comportements symboliques controversés des Néandertaliens," in *Néandertaliens: biologie et cultures,* eds. B. Vandermeersch, B. Maureille, and Y. Coppens (Paris: CTH, Documents Préhistoriques 23), 297–309.

Soressi, M., McPherron, S. P., Lenoir, M., DogandŽić, T., Goldberg, P., Jacobs, Z., et al. (2013). Neandertals made the first specialized bone tools in Europe. *Proc. Nat. Acad. Sci.* 110, 14186–14190. doi: 10.1073/pnas.1302730110

Soressi, M., Rendu, W., Texier, P.-J., Claud, É., and D'Errico, F., Laroulandie, et al. (2008). "Pech-de-l'Azé I (Dordogne, France): nouveau regard sur un gisement moustérien de tradition acheuléenne connu depuis le XIXe siècle," in *Les sociétés Paléolithiques dans un Grand Sud-Ouest: nouveaux gisements, nouvelles méthodes, nouveaux résultats - Actes des journées décentralisées de la SPF des 24-25 novembre 2006*, eds. J. Jaubert, J. G. Bordes and I. Ortega (Paris: Société Préhistorique française), 95–132.

Speth, J. D., and Tchernov, E. (2002). Middle Paleolithic tortoise use at Kebara cave (Israel). *J. Archaeol. Sci.* 29, 471–483. doi: 10.1006/jasc.2001.0740

Speth, J. D., and Tchernov, E. (2007). The Middle Paleolithic occupations at Kebara Cave: a faunal perspective. Kebara Cave, Mt. Carmel, Israel. *Middle Upper Palaeol. Archaeol.* 165:e260.

Stiner, M. C. (2001). Thirty years on the "Broad Spectrum Revolution" and paleolithic demography. *Proc. Nat. Acad. Sci.* 98, 6993–6996. doi: 10.1073/pnas.121176198

Stiner, M. C., and Munro, N. D. (2002). Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. *J. Archaeol. Method Theory* 9, 181–214. doi: 10.1023/A:1016530308865

Stiner, M. C., Munro, N. D., and Surovell, T. A. (2000). The tortoise and the hare: small-game use, the broad-spectrum revolution, and Paleolithic demography. *Curr. Anthropol.* 41, 39–79. doi: 10.1086/300102

Stringer, C. B., Finlayson, J. C., Barton, R. N. E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R. C., et al. (2008). Neanderthal exploitation of marine mammals in Gibraltar. *Proc. Nat. Acad. Sci.* 105, 14319–14324. doi: 10.1073/pnas.0805474105

Tartar, E., and Costamagno, S. (2016). "L'utilisation des matières osseuses au Moustérien," in *Néandertal à la loupe* (Les Eyzies-de-Tayac, Musée national de Préhistoire).

Toussaint, M., Bonjean, D., and Pirson, S. (2014). "The Scladina I-4A juvenile Neandertal: a synthesis," in *The Scladina I-4A Juvenile Neandertal (Andenne, Belgium). Palaeoanthropology and Context,* eds. M. Toussaint, and D. Bonjean (Liège: Études et Recherches archéologiques de l'Université de Liège 134), 409–418.

Toussaint, M., Olejniczak, A. J., El Zaatari, S., Cattelain, P., Flas, D., Letourneux, C., et al. (2010). The Neandertal lower right deciduous second molar from Trou de l'Abîme at Couvin, Belgium. *J. Hum. Evol.* 58, 56–67. doi: 10.1016/j.jhevol.2009.09.006

Toussaint, M., and Pirson, S. (2006). Neandertal Studies in Belgium: 2000–2005. *Period. Biol.* 108, 373–387.

Toussaint, M., Semal, P., and Pirson, S. (2011). "Les Néandertaliens du bassin mosan belge: bilan 2006-2011," in *Le Paléolithique moyen en Belgique. Mélanges Marguerite Ulrix-Closset,* eds. M. Toussaint, K. Di Modica, and S. Pirson (Liège : Études et Recherches Archéologiques de l'Université de Liège 128 - Les Chercheurs de la Wallonie Hors-série 4), 149–196.

Toussaint, M., Verna, C., Le Cabec, A., Gómez-Robles, A., Draily, C., Richards, M. P., et al. (2017). The Late Neandertal permanent lower left third premolar from Walou Cave (Trooz, Belgium) and its context. *Am. J. Phys. Anthropol.* 164, 193–202. doi: 10.1002/ajpa.23252

Van Neer, W., and Wouters, W. (2011). "Les restes de poissons des niveaux du Paléolithique moyen et supérieur de la grotte Walou," in *La Grotte Walou à Trooz (Belgique). Fouilles de 1996 à 2004. Volume 2,* eds. C. Draily, S., Pirson, M. Toussaint (Namur, Département du Patrimoine et Institut du Patrimoine wallon), 68–82.

Vanhaeren, M., d'Errico, F., Julien, M., Mourer-Chauviré, C., and Lozouet, P. (2019). "Les objets de parure," in *Le Châtelperronien de la grotte du Renne (Arcy-sur-Cure, Yonne, France). Les fouilles d'André Leroi-Gourhan (1949-1963),* ed. M. Julien (Les Eyzies-de-Tayac: Musée National de Préhistoire), 259–285.

Villa, P., and Roebroeks, W. (2014). Neandertal demise: an archaeological analysis of the modern human superiority complex. *PLoS ONE* 9:e96424. doi: 10.1371/journal.pone.0096424

von den Driesch, A. (1976). *A Guide to the Measurement of Animal Bones From Archaeological Sites.* New York: Harvard.

Vonhof, H., Verheyden, S., Bonjean, D., Pirson, S., Weber, M., Scholz, D., et al. (2024). Improving the age constraints on the archeological record in Scladina Cave (Belgium): new speleothem U-Th ages and paleoclimatological data. *Clim. Past Discuss.* 2024, 1–30. doi: 10.5194/cp-2024-27

Wertz, K., Tomek, T., and Bocheński, Z. M. (2022). Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. *Int. J. Osteoarchaeol.* 33, 562–576. doi: 10.1002/oa.3144

Woelfle, E. (1967). *Vergleichend morphologische Untersuchungen an Einzelknochen des postcranialen Skelettes in Mitteleuropa vorkommender Enten, Halbgänse und Säger*. PhD thesis, München, Universität München.

Woolfenden, G. E. (1961). Postcranial osteology of the waterfowl. *Bull. State FL. State Museum, Biol. Sci.* 6, 1–129. doi: 10.58782/flmnh.amoc3264

Zilhão, J., Angelucci, D. E., Daniel, F., Dayet, L., Douka, K., Higham, et al. (2010). Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proc. Nat. Acad. Sci.* 107, 1023–1028. doi: 10.1073/pnas.0914088107

Zilhão, J., Angelucci, D. E., Igreja, M. A., Arnold, L. J., Badal, E., Callapez, P., et al. (2020). Last interglacial iberian neandertals as fisher-hunter-gatherers. *Science* 367:eaaz7943. doi: 10.1126/science.aaz7943

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Alternating carnivore and Neanderthal activities at Escoural Cave: insights from the taphonomic and machine learning analysis of leporid remains

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Exploring the varied subsistence strategies and cave occupation patterns of Neanderthals is key to understanding their complex behaviors and ecological adaptations. Small game consumption, in particular, is considered a relevant indicator of their behavioral complexity. Rabbit assemblages from Pleistocene cave sites provide valuable insights into Neanderthal interactions with small prey and potential competition with carnivores. Here, we present the first detailed taphonomic analysis of faunal remains from Escoural Cave (Portugal), where a European rabbit (*Oryctolagus cuniculus*) assemblage was found alongside Middle Paleolithic stone tools and some macromammal remains. This study combines traditional zooarchaeological and taphonomic analysis of the rabbit remains with multivariate statistics and machine learning methods to establish the origin of the accumulation, and the implications for Neanderthal subsistence and cave use. Results from the taphonomic analysis show no evidence of human consumption but abundant evidence of small terrestrial carnivore activity, primarily from lynxes. This could indicate a sequential occurrence of Neanderthal and carnivore activities in the cave, with Neanderthal activities likely related to something other than rabbit consumption. Our study contributes to characterizing Iberian carnivore fossil accumulations and differentiating between faunal assemblages accumulated by carnivores and those by hominins. Additionally, we show that the use of machine learning analysis provides a robust and objective method for identifying and classifying taphonomic signatures, enhancing the accuracy and reliability of our interpretations. Future work will focus on analyzing additional faunal collections from both past and new excavations at Escoural, to test whether carnivores and Neanderthals focused on different prey types and how they shared the cave space.

KEYWORDS

hominin-carnivore interactions, rabbit, zooarchaeological analysis, Middle Paleolithic, southern Portugal

1 Introduction

In recent years, our understanding of Neanderthal complex behavior has significantly increased. Studies have demonstrated diverse and context-dependent strategies, including advanced planning, social structures (e.g., Duveau et al., 2019; Skov et al., 2022), varying landscape use and mobility (e.g., Marín et al., 2019; Valde-Nowak and Cieśla, 2020; Moncel et al., 2019), and campsite organization (e.g. Gabucio et al., 2023; Vaquero, 2022; Roebroeks and Soressi, 2016). Regarding their subsistence behavior, while Neanderthals often focused on hunting ungulates (e.g. Daujeard et al., 2019; Daujeard and Moncel, 2010; Gaudzinski-Windheuser and Kindler, 2012; Livraghi et al., 2021; Marín et al., 2017, 2020; Richards et al., 2000; Smith, 2014; Yravedra and Cobo-Sánchez, 2015; Yravedra et al., 2024), they also occasionally exploited large carnivores, such as lions, bears and wolves, as suggested by evidence of hunting and butchery marks (Russo et al., 2023; Auguste, 1995; Herranz-Rodrigo et al., 2024; Buccheri et al., 2016; Hussain et al., 2022). Moreover, the hunting and consumption of small game, such as leporids, have also been documented and recognized as evidence of sophisticated foraging strategies and adaptive behaviors (Pérez Ripoll, 2001; Blasco et al., 2022). Research has shown that small game, including leporids, birds, tortoises, small terrestrial carnivores, and marine resources, also played a role in Neanderthal diet (Real, 2020; Blasco and Fernández Peris, 2012; Brown et al., 2011; Carvalho et al., 2018; Cochard et al., 2012; Gabucio et al., 2014; Gómez-Olivencia et al., 2018; Gutiérrez-Zugasti et al., 2018; Hardy et al., 2013; Nabais and Zilhão, 2019; Pelletier et al., 2019; Romandini et al., 2023; Rufà et al., 2014; Stiner et al., 1999, 2000).

Rabbits occur abundantly at archaeological sites and are present across various biotopes in the Iberian Peninsula given their high reproductive rates and rapid adaptability (Delibes and Hiraldo, 1981; Pérez Ripoll, 1992; Rodríguez-Hidalgo et al., 2020; Rufà et al., 2014). Understanding the origins of leporid accumulations has long been an important focus for taphonomists, not only because they were a part of human subsistence during the late Pleistocene and early Holocene but also due to the complexities they present, as these accumulations can result from many different processes (e.g. Pérez Ripoll, 1992; Cochard, 2004; Yravedra et al., 2019). The most significant cause of death in rabbits recovered from archaeological Middle Paleolithic contexts is predator activity (e.g. Pérez Ripoll, 1977; Rufà et al., 2014). Rabbits are prey to around 40 predators in Western Europe (Delibes and Hiraldo, 1981; Cochard, 2004), including terrestrial carnivores such as the Iberian lynx (*Lynx pardinus*) (Lloveras et al., 2008a; Rodríguez-Hidalgo et al., 2013, 2015, 2020), foxes (*Vulpes vulpes*) (Cochard, 2004; Hockett and Haws, 2002; Krajcarz and Krajcarz, 2012; Lloveras et al., 2012a,b; Sanchis Serra and Pascual Benito, 2011), wildcats (*Felis silvestris*) (Cohen and Kibii, 2015; Lloveras et al., 2016; Scheifler et al., 2020), wolves (*Canis lupus*) (Schmitt and Juell, 1994; Armstrong, 2016; Lloveras et al., 2020), as well as birds of prey, including nocturnal (e.g., Lloveras et al., 2009, 2012a,b; Sanchis, 1999; Yravedra, 2004) and diurnal raptors (e.g. Hockett, 1996; Lloveras et al., 2008b).

Rabbit bone accumulations can result from a variety of processes that are not mutually exclusive, with several agents contributing to leporid assemblages within the same deposit. According to Callou's (1997) classification, these accumulations can be categorized as intrusive (e.g., accidental deaths within the site due to rabbits entering or burrowing), exogenous (e.g., remains brought into the site by predators), or anthropic (i.e., associated with human activities such as hunting, butchering or consumption). This classification also encompasses natural causes, such as accidental deaths in natural traps or burrows, where the accumulation occurs without direct involvement from other predators (Pelletier et al., 2016; Seuru et al., 2024). Thus, rabbit bones in fossil assemblages may reflect contributions from non-human predators, humans, natural processes, or a combination of these factors (e.g. Callou, 1997; Yravedra, 2008; Yravedra and Andrés, 2013).

Identifying the specific accumulation origins is essential for understanding broader ecological interactions between Neanderthals and carnivores. These interactions can shed light on the evolutionary pressures that shaped hominin behavior and reveal critical aspects of Neanderthal diet, competition for resources, and foraging strategies, while also providing insights into Neanderthal use of shelters, risk mitigation, and responses to carnivore presence (e.g. Camarós et al., 2017; Hussain et al., 2022; Rivals et al., 2022; Romandini et al., 2023; Rosell et al., 2017; Linares-Matás and Yravedra, 2024).

Faunal accumulations are often palimpsests of multiple overlaid occupation events produced by several bone-modifying agents, which is challenging for archaeological interpretation. Additionally, complex site formation processes, particularly in cave sites, can obscure the original context and sequence of events (e.g., Rufà et al., 2014; Saladié et al., 2018; Linares-Matás and Yravedra, 2024). Despite these complexities, researchers attempt to classify the different types of dynamics or co-occurrences of hominin and carnivore activity at sites along a continuum of scenarios, which considers both the timing (temporality) and the nature (proportion and types) of the activities carried out by each agent: (a) sequential succession of hominin and carnivore occupations, (b) concurrent events of carnivore and human activity (with the presence of stone tools and fireplaces), (c) human settlement with sporadic carnivore visits, and (d) carnivore den with occasional human occupation (Picin et al., 2020; Villa et al., 2004; Linares-Matás and Yravedra, 2024; Pinto-Llona et al., 2023; Yravedra, 2006). Taphonomy has the potential to enhance the accuracy and reliability of these classifications by incorporating advanced statistical methodologies. However, current approaches often lack the robustness needed to clearly differentiate the origins of rabbit accumulations, especially at Pleistocene and early Holocene sites where evidence is often ambiguous. This highlights the need for new, more rigorous methods to better identify human involvement in complex assemblages. To address this gap, our study applies advanced statistical methods and contributes to developing a more comprehensive methodological framework for future research.

Southwestern Iberia's Middle Paleolithic sites are critical for understanding Neanderthal flexibility and resilience in response to changing environmental conditions and carnivore presence, as this region may have served as a refugium for Neanderthals. At some of these sites, which present the challenges of containing palimpsests and complex deposits, there is a need for re-excavation and re-analysis using modern analytical techniques to obtain more accurate and comprehensive data. One significant gap in current

research in the region is the lack of faunal taphonomic analysis, which is essential for understanding the interactions between Neanderthals, their environment, and other fauna. The present study is part of a broader project (FINISTERRA: ERC-2021-COG-101045506) aimed at excavating and reanalyzing several such sites.

Here we present a detailed taphonomic and zooarchaeological analysis of a sample of rabbit bones recovered from the Middle Paleolithic site of Escoural Cave to assess the role Neanderthals or other agents played in the formation of the assemblage. Although this analysis is preliminary and based on a subset of materials, it represents the first comprehensive taphonomic study conducted for Escoural cave and offers essential contextual information into the role of small prey species in Neanderthal-carnivore interactions and the use of cave spaces. Additionallly, the methods developed here will provide a foundational framework for future studies at Escoural.

1.1 Site overview

The Escoural Cave or Gruta do Escoural (38°32′55″ N, −8°8′18″E, Alentejo, Portugal) is a dolomitic cave located about 15 km from the city of Montemor-o-Novo, near the village of Santiago do Escoural (3 km) (Lattao et al., 2023). Discovered in 1963 during mining activities for extracting marble, the cave holds significant potential for investigating Neanderthal-carnivore interactions during the Middle Paleolithic. The karstic system is composed of a main gallery, which spans ∼12 ×15 m, connected with ∼17 large karstic channels of around one meter in diameter (Figure 1). The original entrance collapsed after the Middle Paleolithic occupations, although investigations are ongoing to establish the exact timing of this event.

Excavations were conducted during the 1960s and 1990s and unearthed abundant archaeological findings, including Chalcolithic occupations outside the cave, Neolithic burials, Upper Paleolithic engravings and paintings, and archaeological remains from the Upper and Middle Paleolithic. The Middle Paleolithic levels were characterized by abundant quartz industries and faunal remains. Close to 600 lithic artifacts were reported from the original excavations inside the cave (Otte and da Silva, 1996), while our work in 2021 recovered 206 additional lithics from P1. Preliminary analysis of this assemblage aligns largely with previous findings, indicating a predominantly expedient technology, alongside the presence of blanks obtained through discoidal and Levallois methods. U-Th dating of a horse tooth suggested an age of ∼48 Ka for the Middle Paleolithic levels identified inside the cave (Otte and da Silva, 1996). Current sampling and dating efforts aim to further refine the chronology.

1.2 Previous studies

Earlier research on the faunal remains recovered from the Middle and Upper Paleolithic levels at the cave indicate it was occupied by humans and other carnivores (Otte and da Silva, 1996). Although contributions would have come from both groups, carnivores were likely the primary accumulating agents. The reported identified assemblage represents 27.8% of the total, increasing to 73.4% when including rabbit remains. Despite being very fragmented, the assemblage showed good preservation. The macrofaunal collection is dominated by several species of equids and cervids but also includes a diverse taxonomic list including bovids, suids, ibex, and carnivores (see Supplementary Table S1). Smaller fauna include rabbits, birds, mollusks, gastropods, reptiles, and microfauna (see Otte and da Silva, 1996 for the exhaustive taxonomic list). Carnivore activity on macromammals was mainly attributed to hyenas, alongside digested bones and coprolites. However, a portion of the assemblage, including gastropods, frogs, lizards, bats, most carnivores, and rodents, would have been mainly accumulated by nocturnal birds of prey. Birds were likely accumulated by wildcats or lynxes, while toads and rabbits could have been collected by either carnivores or humans. Hyenas are believed to have been the primary accumulating agent, and potentially responsible for much of the assemblage, although lynxes and wolves would also have contributed by hunting various animals, including rabbits, hares, deer, and young suids (Otte and da Silva, 1996).

The authors of the study also observed that the ratio of large animal remains relative to carnivores increased from the Middle Paleolithic, suggesting changes in environmental conditions or selective hunting by carnivores. Equid remains also appear to increase in the upper levels, potentially indicating a drier and colder environment. However, in the Upper Paleolithic levels, the number of identified specimens decreases due to higher fragmentation or increased mixing and reshaping of the deposits, which suggests that these observations should be taken with caution. Additionally, their findings were based on the Number of Identified Specimens (NISP), including various ratios used in the analysis. The reliance on NISP requires careful interpretation, as estimates may not be accurate due to fragmentation of the archaeofaunal collection. Moreover, the absence of detailed taphonomic analyses or reported modification frequencies underscores the need for further studies, including both the re-examination of previously excavated materials and the analysis of new finds.

2 Materials and methods

2.1 Materials

This study focuses on materials recovered during recent excavations from the Middle Paleolithic layers of Escoural cave. The analysis of additional materials housed in Lisbon is planned but currently on hold due to museum renovations. Meanwhile, the FINISTERRA project (https://finisterra.icarehb.com/) has initiated new excavations at the site opening and excavating larger areas to understand the connection between the exterior and interior of the cave and reconstruct site formation processes. Excavations began in 2020 with the expansion of the profiles left by previous excavation areas in one of the SE chambers (Profile 1 in Gallery 17—see Figure 1B) and outside the cave (Profile 2), and included sampling for dating and micromorphological analyses, the latter of which are currently ongoing (Alzate-Casallas et al., in prep.). This study focuses on remains from Profile 1, which yielded more abundant and

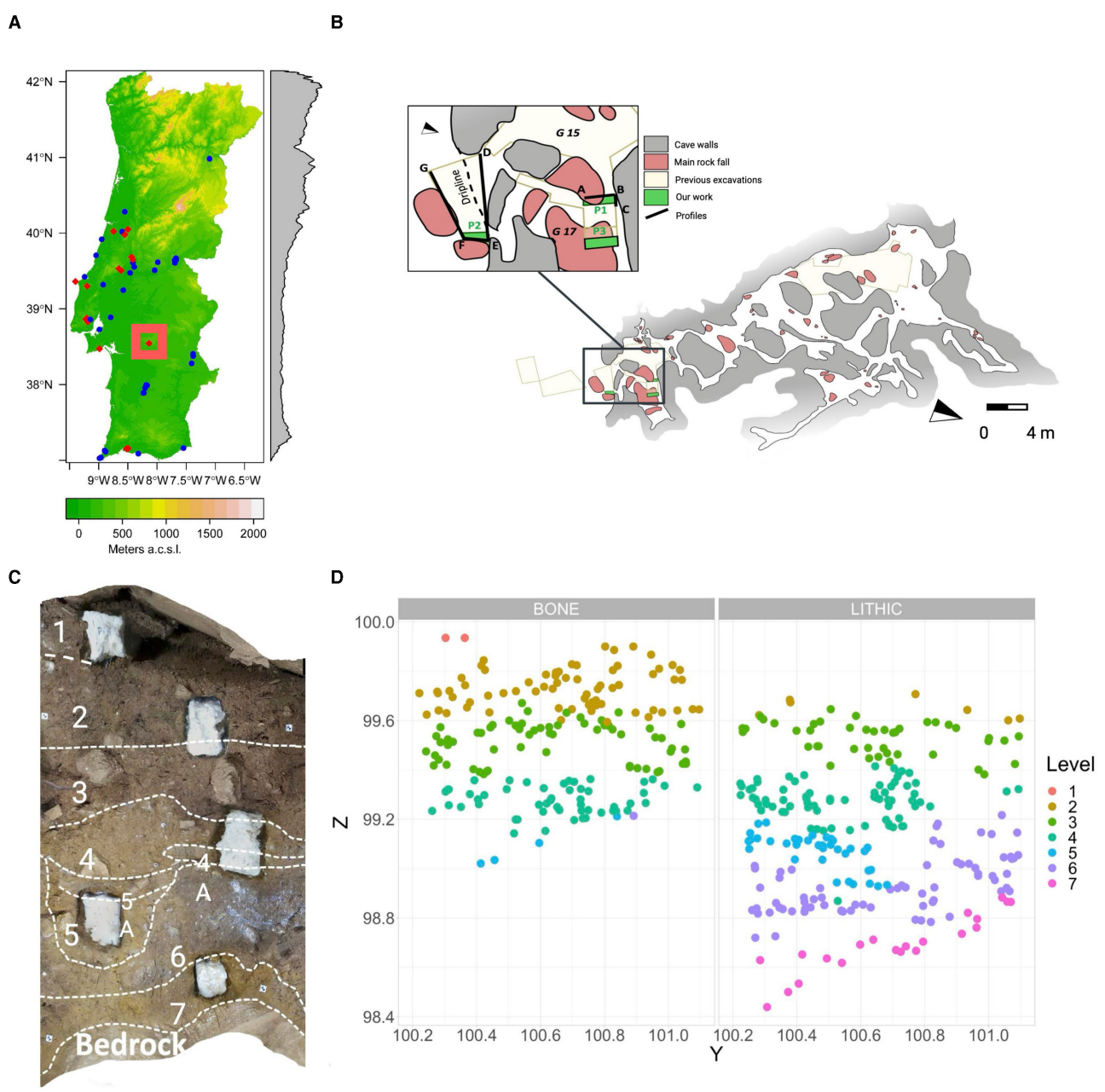

FIGURE 1
(A) Geographic location of Escoural Cave in Portugal; **(B)** cave outline and location of the test profiles excavated in 2020 inside (P1) and outside (P2); **(C)** stratigraphic section of P1 showing the defined geological levels; **(D)** spatial vertical distribution of the recovered archaeological materials in each level.

better preserved materials than Profile 2. The vertical spatial distribution of the remains in Profile 1 revealed an overlap between bones and lithics, primarily in Levels 2, 3, and 4 (Figures 1C, D). Faunal remains decreased drastically in Level 5 and were absent in Levels 6 and 7. Preliminary microstratigraphic analyses suggest potential reworking of the sediments; however, distinct depositional episodes are evident, as multiple geological levels could be identified. The deposition of these levels was not continuous but alternated with breaks during which calcite crusts formed.

Profile 1 inside Escoural Cave yielded macrofaunal remains; yet, the sample size ($N = 88$) was insufficient for a comprehensive zooarchaeological and taphonomic analysis. However, rabbit remains were abundant in Geological Levels (GL) 2, 3, and 4. This study focuses on the rabbit remains from GL 2, where the sample size was $N = 1{,}313$. In this level, macromammal remains amounted to $N = 37$, and plotted rabbit remains to $N = 27$. These 27 plotted remains, recovered due to their larger size and identifiability, are each associated with precise spatial coordinates, whereas the majority of specimens were recovered from sieve bags,

resulting in only approximate spatial locations corresponding to each 10 L bucket of excavated sediment. Each rabbit bone specimen recovered from the sieve bags was assigned a unique identification number in the lab to ensure the reproducibility of the analysis.

2.2 Methods

Zooarchaeological and taphonomic attributes of the bones were recorded using E5 data entry program (McPherron, 2022), and analyzed according to anatomical representation, breakage, bone surface modifications, and digestion. Bone breakage planes and cortical surfaces were inspected using hand lenses and a Euromex stereomicroscope (Nexius Zoom NZ 1902-P) with magnification up to 45×. Wherever possible, the resulting data were treated statistically by comparing them to other archaeological and actualistic rabbit assemblages to enhance the robustness of the analysis and help identify the accumulating agent. Assemblages were selected based on the availability of detailed taphonomic and zooarchaeological data presented in a consistent format to enable reliable comparison and analysis. We used the dataset and site selection criteria from Rodríguez-Hidalgo et al. (2020) as a baseline for our analysis, adopting their format of taphonomic variables. The variables included in our analyses are MAU% or RA% data, as well as percentages of cut marks, burned remains, digested remains, tubes/cylinders, tooth/beak marks, complete long bones, and adults. Sites with very incomplete data on these variables were excluded. Additionally, a minimum threshold of 9 MNI was established to ensure that the percentages were representative of the assemblage, and sites or actualistic studies with smaller rabbit assemblages were not included. The following sections outline the specific methodologies used.

The entirety of the R code used for the analysis, datasets, and visual representations contained in this paper can be accessed through our online research compendium at https://osf.io/zyu4p/. We used the rrtools package by Marwick et al. (2018) to create a research compendium and write a reproducible journal article. The provided files include the complete set of raw data used in the analysis, along with a custom R project (Wickham, 2015) containing the code required to generate all tables and figures. To enable maximum reuse, the code is made available under the MIT license, data under CC-0, and figures under CC-BY (additional details can be found in Marwick, 2017).

2.2.1 Taxonomic identification and age profiles

The zooarchaeological analysis involved identifying animal bones to the genus or species level where possible, and the selection of rabbit remains for detailed analysis. The taxonomic identification of leporid remains was based on comparative collections housed at ICArEHB laboratory and reference bibliography (e.g. Barone et al., 1973; Callou, 1997). Following established zooarchaeological methods (e.g. Reitz and Wing, 1999), we determined the skeletal element, the preserved portion of the bone, and bone laterality. We used the stage of epiphyseal fusion to establish the approximate age of rabbits at death (e.g. Jones, 2006; Callou, 2003; Cochard, 2004; Hockett and Bicho, 2000). Specifically, we used the distal epiphysis of the humerus, which begins to fuse at about 2 months of age, and the distal epiphysis of the tibia, which fuses at around 3 months, to identify juveniles (<3 months) (Jones, 2006). The remaining epiphyses of the long bones typically fuse between 9 and 10 months (Pelletier et al., 2019), which marks the threshold between subadults and adult individuals. The latter are characterized by the complete fusion of the proximal epiphysis of the humerus and tibiae (Pelletier et al., 2019).

2.2.2 Anatomical representation

We calculated the Number of Identified Specimens (NISP) (Lyman, 1994), the Minimum Number of Elements (MNE) (Bunn, 1982; Marean et al., 2001), the Minimum Number of Individuals (MNI) (White, 1953; Lyman, 2008), as well as the Minimum Number of Animal Units (%MAU) (Binford, 1978). The MNE was estimated by counting the number of times the most represented portion of a certain element was present. This estimation involved including the consideration of diaphyses as well as epiphyses (Marean et al., 2001). Long bone shafts were identified when possible to a specific element using anatomical landmarks like muscle insertions or foramina, as well as diaphyseal cross-section and medullary cavity shape and size (Yravedra and Domínguez-Rodrigo, 2009). MNI was determined by considering the most abundant anatomical element, bone laterality and animal age. MAUs were calculated from the MNE values, as established by Binford (1978, 1981, 1984), by dividing the MNEs of each skeletal part by the number of times that such element occurs in the animal's skeleton. Each resulting MAU was subsequently transformed into %MAU by standardizing each MAU with reference to the largest original MAU, also as described originally by Binford (1978, 1981). Following the established methodology for the study of leporid assemblages, we calculated the relative abundance (%RA) (Dodson and Wexlar, 1979; Andrews, 1990). In addition, the proportions of skeletal elements were evaluated using the indices outlined in Table 1 and described and applied in studies such as Andrews (1990), Lloveras et al. (2008a) or Rodríguez-Hidalgo et al. (2020).

Moreover, to evaluate whether biases in skeletal representation were consequence of bone density-mediated attrition or influenced by other post-depositional or biostratinomic processes affecting the preservation of specific skeletal parts, we calculated Spearman's correlation coefficient (Pavao and Stahl, 1999). This coefficient determines if there is a significant correlation between the bone density values of rabbit bones and the relative abundance of each skeletal element.

2.2.3 Principal component analysis (PCA) and machine learning (ML) analysis of skeletal part abundances

Subsequently, we performed a PCA analysis using skeletal part abundance data (%RA values) following the approach in Rodríguez-Hidalgo et al. (2020) to visualize the distribution of a set of assemblages and sites generated by different predators by reducing the dimensionality of the dataset and to identify potential patterns and clusters among the samples. We chose relative abundance data for the statistical analysis, because it

TABLE 1 Indices used to evaluate the proportions of leporid skeletal elements.

Index	Description
PCRT/CR	Total numbers of postcrania compared with total numbers of crania (mandibles, maxillae, and teeth)
PCRAP/CR	Appendicular elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals, and phalanges) compared with crania specimens
PCRLB/CR	Humerus, radius, ulna, femur and tibia specimens compared with mandibles and teeth
HU + FE/CR + MD	Humerus and femur specimens compared with mandibles and maxillae
TA/MD	Tibiae compared with mandibles
TAE/MDE	Tibia elements compared with mandible elements
AUT/ZE	Autopodium (metapodials, carpals, tarsals and phalanges) compared with zygopodium and stylopodium (radius, ulna, tibia, humerus, femur and patella)
Z/E	Zygopodium (tibia, radius, and ulna) compared with stylopodium (femur and humerus)
AN/PO	Humerus, radius, ulna, and metacarpus compared with femur, tibia and metatarsus
HU/FE	Humerus compared to femur specimens
RDU/TA	Radius and ulna compared to tibia specimens
MCP/MTT	Metacarpal compared to metatarsal specimens

TABLE 2 Skeletal part frequencies of rabbit remains expressed in number of identified specimens (NISP), %NISP, minimum number of elements (MNE), %MNE, relative abundance (RA), %RA, and minimum animal units (MAU), %MAU.

Element	NISP	%NISP	MNE	%MNE	%RA	%MAU
Cranium	40	3.36	21	5.39	55.26	72.41
Mandible	21	1.77	15	1.94	39.47	51.72
Incisor	31	2.52	31	4.00	27.19	35.63
Upper molar	65	5.47	65	8.39	28.51	37.36
Lower molar	24	2.02	24	3.1	12.63	16.55
Tooth	6	0.50	6	0.77	1.13	1.48
Vertebra	25	2.10	19	2.45	2.17	2.85
Rib	12	1.01	9	1.16	1.97	2.59
Sternum	–	–	–	–	–	–
Scapula	8	0.67	5	0.65	13.16	17.24
Humerus	41	3.45	12	1.55	31.58	41.38
Radius	35	2.94	11	1.42	28.95	37.93
Ulna	25	2.10	14	1.81	36.84	48.28
Femur	122	10.26	17	2.19	44.74	58.62
Patella	–	–	–	–	–	–
Tibia	148	12.45	22	2.84	57.89	75.86
Innominate	38	3.20	22	2.84	57.89	75.86
Metacarpus	53	4.46	50	6.45	26.32	34.48
Metatarsus	139	11.70	101	13.03	66.45	87.07
Calcaneum	38	3.20	29	3.74	76.32	100
Astragalus	19	1.60	19	2.45	50	65.52
Carpal/tarsal	23	1.93	23	2.97	9.31	12.2
Phalange	265	22.29	260	33.55	26.32	34.48
Sesamoid	–	–	–	–	–	–
Total	1,189	100	775	100		

provides standardized and comparable values, unlike the indices of skeletal part representation calculated from NISP and MNE, and thus ensures more reliable outcomes. Assemblages were included in the reference dataset only if their minimum number of individuals (MNI) was higher than 9. The reference dataset included assemblages generated by terrestrial predators (lynx, wildcat, fox, and coyote), diurnal predators (eagles and vultures), nocturnal predators (owls), and humans (Neanderthals and modern humans), as well as a combination of non-ingested and scat or pellet remains (see Supplementary Table S2 for complete dataset and references). We combined species into broader groups, as individual classifications would often comprise only one or two samples per group. This results in a dataset with increased variability, but enabled the implementation of this analysis and subsequent ML models. The PCA was performed using the factoextra library in R (Kassambara and Mundt, 2020). The dataset was preprocessed to handle missing values using the "missForest" library (Stekhoven and Buehlmann, 2012) and normalized.

Next, we explored the use of machine learning (ML) techniques to identify the agent of accumulation of rabbits at Escoural based on skeletal representation data. Machine learning models generally perform better with larger datasets, because small sample sizes can lead to overfitting, where the model learns noise and specific details of the training data rather than general trends. However, there are several techniques that can help mitigate this effect, especially feature selection, cross-validation, and hyperparameter tuning (Vabalas et al., 2019). To ensure robust models and minimize the risk of overfitting, we used a combination of these techniques. We first used Random Forest to select the 10 most important features of the dataset. Next, using a correlation matrix, we identified and removed the highest correlated features (>0.7) to reduce multicollinearity. Then, we split the data into training (70%) and test (30%) sets using stratified sampling. Stratified sampling is similar to k-fold, but ensures that each fold has approximately the same percentages of samples of each target class as the entire dataset, which can help in maintaining the balance of class distributions (Kuhn and Johnson, 2013). Subsequently we bootstrapped the training set with 100 iterations, involving repeatedly resampling the training data with replacement, coupled with internal cross-validation (Kuhn and Johnson, 2013). We trained three different ML models, Random Forest (RF), Support Vector Machine (SVM), and Gradient Boosting Machine (GBM), with hyperparameter tuning and cross-validation to ensure that they generalized well to unknown data. We calculated precision, recall, F1-score and other performance metrics across multiple

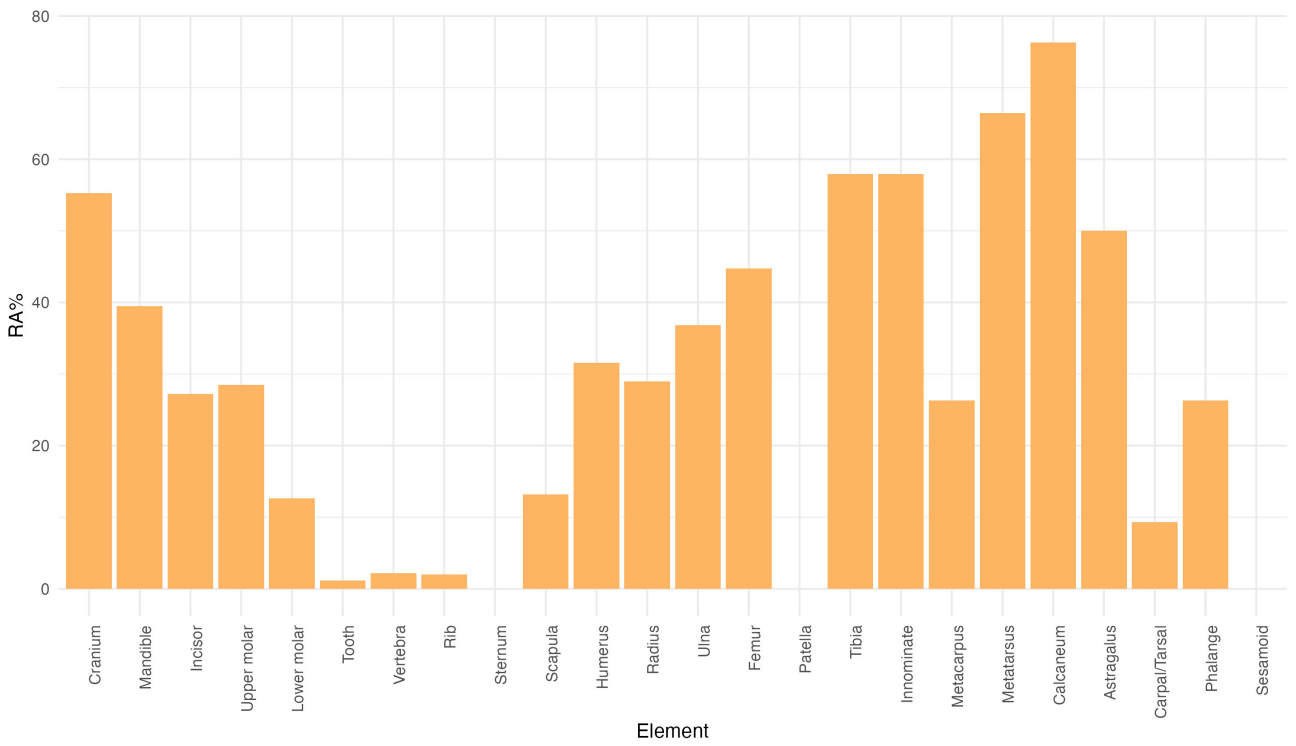

FIGURE 2
Barplot showing the relative abundance (%RA) of rabbit skeletal elements.

resamples, and compared the outcomes of the three models. We used the "caret" (Kuhn, 2008) "e1071" (Meyer et al., 2023), and "randomForest" (Liaw and Wiener, 2002) libraries in R.

2.2.4 Breakage

All identified bone specimens were classified into the breakage categories defined and described by Lloveras et al. (2008b). Breakage categories vary depending on bone element, and percentages are also recorded for complete elements and isolated and *in-situ* teeth. Long bones and metapodial breakage categories include complete, proximal epiphysis (PE), proximal epiphysis and shaft (PES), shaft (S), shaft and distal epiphysis (SDE), and distal epiphysis (DE) portions. Scapulae, innominates, mandibles, crania, and ribs are classified into four to six breakage patterns, whereas patellae, carpals, tarsals, and teeth were only classified as complete or fragmented. Phalanges are recorded as complete, proximal, distal or fragmented, vertebrae are divided into complete, vertebral body, vertebral epiphysis or spinous processes. In the case of immature individuals, the long bone shafts preserving unfused epiphyses were considered complete elements (Rodríguez-Hidalgo et al., 2020).

Additionally, we documented the type of fracture (green, dry, modern or indeterminate) (Villa and Mahieu, 1991), shaft circumference (Bunn, 1982) and length, along with fracture outlines (Bunn, 1983; Villa and Mahieu, 1991). We also recorded bone cylinders, or "tubes," which are shafts of long bones that preserve the complete circumference and have broken ends resulting from consumption. Following the criteria established by Rodríguez-Hidalgo et al. (2020), we considered only the humerus, tibia, and femur as potential "tubes" due to their significant marrow content, and distinguished them from "fake tubes," long bone cylinders with sign of dry breakage (jagged or right-angle-smooth ends; see also Gabucio et al., 2024). We also identified notches according to the classifications proposed by Pickering and Egeland (2006). Helical and V-shaped fractures, typically indicative of carnivore breakage, were also recorded (Villa and Mahieu, 1991; Sanchis, 1999).

TABLE 3 Rabbit skeletal parts relative proportions.

Indices	Percent	Interpretation
PCRT/CR	598.40	Much more post-cranial
PCRAP/CR	578.61	Much more post-cranial
PCRLB/CR	804.26	Much more limbs than cranial
HU + FE/CR + MD	277.05	Much more upper limbs than skull
TA/MD	709.52	More tibiae than mandible
TAE/MDE	146.67	More tibiae than mandible (MNE)
AUT/ZE	160.32	More autopodium than zygopodium and stylopodium
Z/E	123.67	More zygopodium than stylopodium
AN/PO	37.56	More posterior
HU/FE	33.61	More femur
RDU/TA	40.27	More tibia
MCP/MTT	38.13	More metatarsal

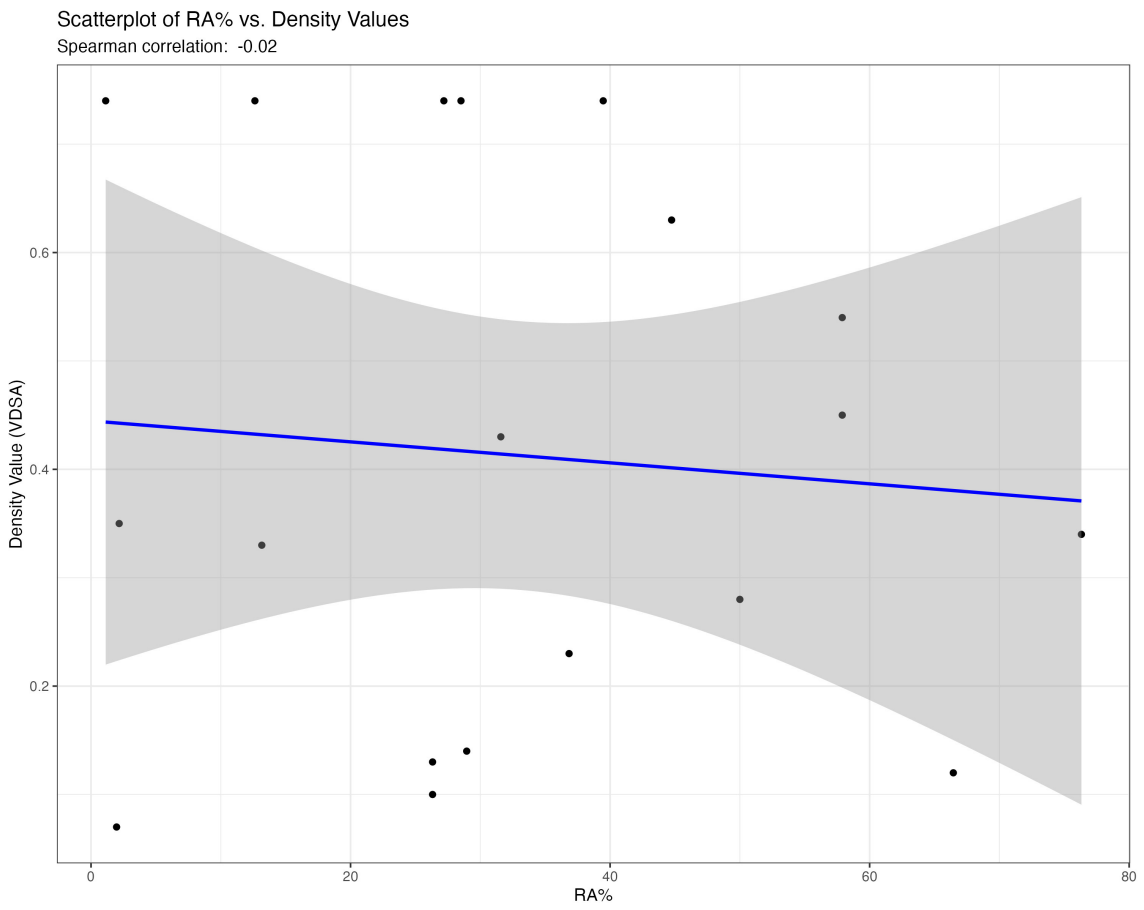

FIGURE 3
Scatterplot illustrating the relationship between %RA and bone density values. The linear regression line shows no evident trend, supporting the lack of significant correlation.

2.2.5 Bone surface modifications and digestion

We recorded the presence, number, location and distribution (isolated, dispersed or grouped) of pits, punctures, gnawing, digestion, helical fractures, and crenulated edges (Andrés et al., 2012; Binford, 1981; Capaldo and Blumenschine, 1994; Haynes, 1980; Lloveras et al., 2014; Sanchis et al., 2011). We also recorded measurements of the pits, punctures and scores using a microscope camera. We considered the possibility that these modifications were caused by hominins, although the criteria for differentiating them from marks made by other carnivores remain ambiguous (Fernandez-Jalvo and Andrews, 2016; Landt, 2007; Saladié et al., 2024). We compared the widths of pits and punctures on the cortical surfaces of long bone shafts with samples of marks made by small carnivores, based on studies by Andrés et al. (2012), Massigoge et al. (2014), Rodríguez-Hidalgo et al. (2013, 2015), and Saladié et al. (2024). In the comparative dataset, the animals consumed were primarily small, except for the human-made marks from Andrés et al. (2012). We included two samples of tooth marks made by lynxes, two by foxes, three by humans, one by hyena cubs, and one by wildcats (see Supplementary Table S5). We also carefully examined bones for cut marks (Pérez Ripoll, 1992; Binford, 1981; Blumenschine et al., 1996; Fernández Jalvo et al., 1999; Fisher, 1995) and several postdepositional modifications, including the presence of weathering, root etching, chemical corrosion, marks produced by bacteria colonies, manganese oxide staining, polishing, rounding, trampling, and microabrasion (Fernandez-Jalvo and Andrews, 2016). We also considered potential damage caused by fire, following stages described by Fernandez-Jalvo and Andrews (2016). Conspicuous marks were photographed using a microscope camera [Model: MicrosCopiaDigital XM Full HD Camera ALPHA B Series, resolution: 1080p (Full HD)].

2.2.6 Hierarchical Clustering on Principal Components (HCPC) and K-means cluster analysis on taphonomic data

We conducted a Hierarchical Clustering on Principal Components (HCPC) analysis on a combination of breakage and bone surface modification data, following a similar approach in Rodríguez-Hidalgo et al. (2020) and using the dataset shared by these authors, which includes reference assemblages generated by lynx, fox, eagles, owls, and humans (see Supplementary Table S3). Before performing the HCPC analysis, we handled missing data through imputation using the "missForest" package (Stekhoven and Buehlmann, 2012). The HCPC analysis was conducted using

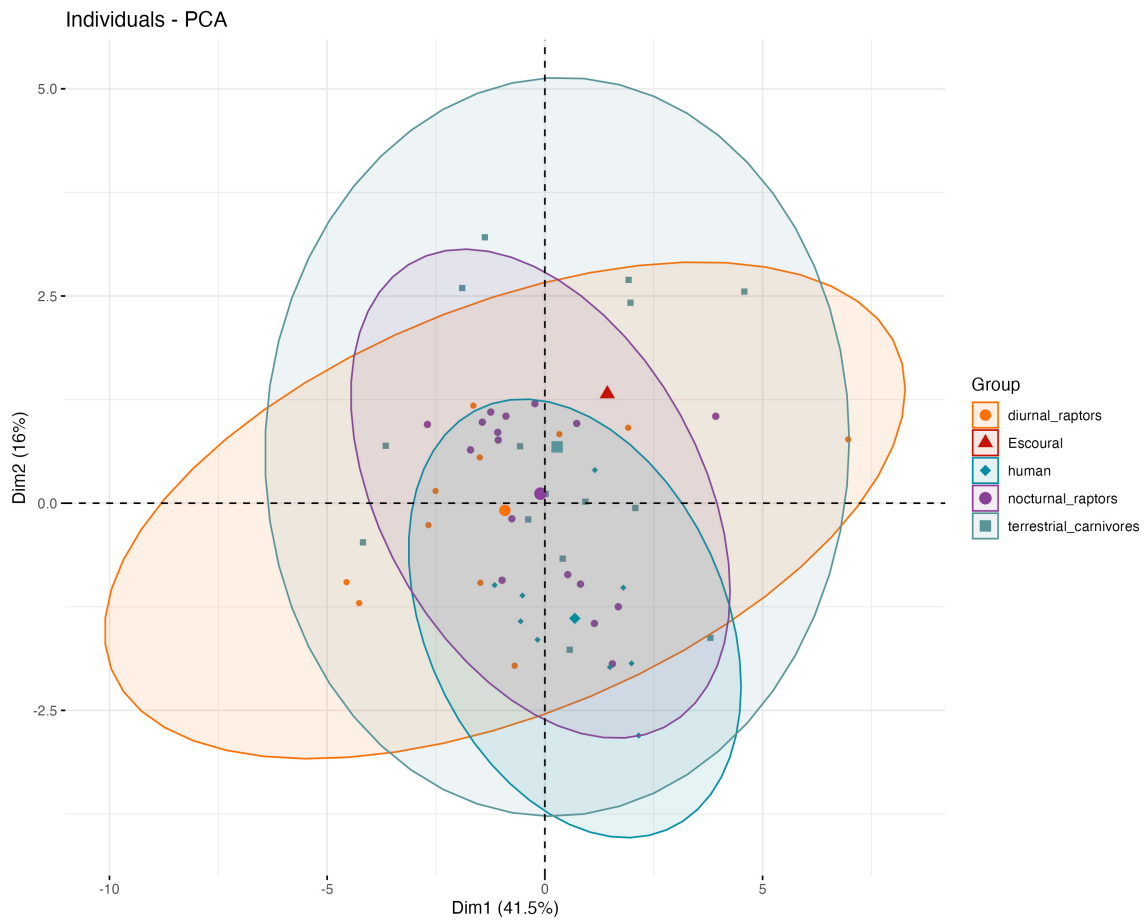

FIGURE 4
PCA biplot showing the distribution of samples across the two principal components, with samples colored according to their respective groups. Confidence ellipses illustrate the variability within groups. See similar plot with the labels of the assemblages in Supplementary Figure S1.

the "FactoMineR" package in R (Le et al., 2008), which performs PCA on the data, followed by hierarchical clustering on the principal components. We evaluated the results by calculating the silhouette scores and using the gap statistic method. Following this, we implemented the K-means clustering algorithm with six clusters. For this, we used the "cluster" (Maechler et al., 2023) and "factoextra" (Kassambara and Mundt, 2020) packages in R.

3 Results

3.1 Anatomical representation

A total of 1,189 European rabbit (*Oryctolagus cuniculus*) specimens (NISP) were identified to a specific skeletal element. Based on left calcanei, a total of 19 individuals (MNI) was estimated. Based on unfused distal tibiae and distal humeri, we estimated a minimum of three infantile individuals (younger than 2 or 3 months) and a minimum of six juveniles. Adult rabbit individuals therefore comprise 52.6% of the total MNI.

The total MNE is 775. Phalanges and metatarsals are the highest represented elements based on MNE, followed by isolated upper molars and metacarpals. Scapulae and ribs appear in much lower numbers (Table 2). The relative abundance (%RA) values show a predominance of calcanei and metatarsals (more than 60% of the RA), followed by tibiae, innominates, and cranial elements (up to 60% of the RA). The lowest represented elements in relative terms are axial remains like ribs and vertebrae (<5% of the RA; Figure 2).

The indices for the relative proportions of skeletal elements indicate a significant overrepresentation of postcranial elements compared to cranial elements (Table 3). This overrepresentation remains evident even when using indices that give considerable weight to the mineral density of skeletal elements, such as the TA/MD index. However, it is less pronounced when considering the MNEs (146.67; Table 3). Among limb bones, posterior (hind limb) elements are better represented than anterior (front limb) bones across the autopodium, zygopodium and stylopodium regions, and this relationship is consistent from proximal to distal elements (Table 3). The Spearman correlation coefficient of −0.02 (Figure 3) suggests a very weak negative correlation between relative abundance and bone density values. The *p*-value (0.93) indicates the correlation is not statistically significant. This implies that there is no

meaningful relationship between skeletal representation and bone density, which suggests that density-mediated attrition does not appear to have biased the preservation of the assemblage.

3.2 Principal component analysis (PCA) and machine learning (ML) analysis of skeletal part abundances

The PCA analysis revealed a plot with considerable overlap between all predator groups. The variance explained by the principal components was relatively low, accounting for only 41.9% and 16% of the variance, respectively (Figure 4). This indicates high variability within the dataset. The PCA analysis also revealed a large distribution of samples across the principal component axes. While some samples cluster closely according to their respective groups (e.g. several non-ingested lynx samples at the top of the factor map and several owl assemblages underneath), indicating similarity in their anatomical representation characteristics, others are dispersed and located far from their group centers. This wide distribution suggests substantial variability within and between groups. A significant contributing factor to this high variability is the inclusion of both ingested (e.g., predator scats and pellets) and non-ingested samples in the dataset. These two types of assemblages often exhibit opposing characteristics, as the elements missing from the non-ingested samples are typically those that are digested, and vice versa. The groups from the diurnal raptors, nocturnal raptors, and terrestrial carnivores overlap significantly, making it impossible to distinguish these groups based solely on PCA. While the human sample forms a somewhat distinct cluster, it almost completely overlaps with the other groups. These results complicate a straightforward classification of the Escoural assemblage, which is positioned near the human cluster but also inside the raptors and terrestrial carnivores clusters. This could possibly be suggesting a complex taphonomic history involving multiple accumulating agents, however, it is impossible to determine whether the position of the sample indicates such complexity or simply reflects the ambiguity of the groups' distributions. The observed variability in the PCA results is to be expected given the diverse nature of the dataset and the fact that predators generally exhibit variable behaviors. It is also possible that the PCA is insufficient to discern clear patterns of difference between groups, and machine learning techniques might be better suited to uncover patterns.

Following the results of feature selection and variable correlation analysis, we excluded the skeletal abundance values for cranium, humerus, and metacarpals (see Supplementary Figure S2

TABLE 4 Selected hyperparameters and performance metrics for random forest (RF), support vector machine (SVM), and gradient boosting machine (GBM) models, including accuracy, 95% confidence intervals (CI), and Kappa values.

Model	Hyper parameters		Accuracy	95% CI	Kappa
RF	mtry	1	0.6429	0.3514–0.8724	0.5139
	splitrule	gini			
	min.node.size	1			
SVM	Sigma	0.01	0.5	0.2304–0.7696	0.295
	C	100			
GBM	n.trees	300	0.79	0.492–0.934	0.7063
	interaction.depth	3			
	Shrinkage	0.1			
	n.minobsinnode	5			

TABLE 5 Sensitivity (recall), specificity, positive predictive value, negative predictive value, balanced accuracy, precision, and F1-score for each predator group across the random forest (RF), support vector machine (SVM), and gradient boosting machine (GBM) models.

Model	Predator group	Sensitivity (recall)	Specificity	Positive predictive value	Negative predictive value	Balanced accuracy	Precision	F1-score
RF	Terrestrial carnivores	0.2500	1.0000	1.0000	0.7692	0.6250	0.25	0.25
	Humans	1.0000	0.9167	0.6667	1.0000	0.9583	0.67	0.80
	Nocturnal raptors	0.8000	0.7778	0.6667	0.8750	0.7889	0.80	0.80
	Diurnal raptors	0.6667	0.8182	0.5000	0.9000	0.7424	0.50	0.50
SVM	Terrestrial carnivores	0.5000	0.8000	0.5000	0.8000	0.6500	0.40	0.40
	Humans	0.5000	1.0000	1.0000	0.9231	0.7500	1.00	0.67
	Nocturnal raptors	0.6000	0.6667	0.5000	0.7500	0.6333	0.60	0.60
	Diurnal raptors	0.3333	0.8181	0.3333	0.8181	0.5757	0.33	0.33
GBM	Terrestrial carnivores	0.7500	1.0000	1.0000	0.9091	0.8750	0.75	0.75
	Humans	1.0000	1.0000	1.0000	1.0000	1.0000	1.00	1.00
	Nocturnal raptors	0.8000	0.8889	0.8000	0.8889	0.8444	1.00	0.89
	Diurnal raptors	0.6667	0.8182	0.5000	0.9000	0.7424	0.67	0.57

TABLE 6 Representation of different breakage categories.

Breakage categories								
	C		PE		PES		S	
	N	%	*N*	%	*N*	%	*N*	%
Humerus	0	/	6	14.63	0	/	27	65.85
Radius	0	/	1	2.86	9	25.71	17	48.57
Ulna	0	/	8	32	4	16	12	48
Femur	0	/	10	8.20	5	4.10	98	80.33
Tibia	0	/	12	8.11	2	1.35	114	76.4
Metacarpal	37	69.81	0	/	13	24.53	0	/
Metatarsal	30	21.58	1	0.72	67	48.20	9	6.47
	67		38		100		277	

	SDE		DE		Total
	N	%	N	%	
Humerus	4	9.76	4	9.76	41
Radius	7	20	1	2.86	35
Ulna	0	/	0	/	25
Femur	4	3.28	5	4.10	122
Tibia	14	9.46	7	4.73	149
Metacarpal	3	5.66	0	/	53
Metatarsal	32	23.02	0	/	139
	64		17		

Mandible	*N*	%	Cranium	*N*	%	Innominate	*N*	%
C	0	/	C	0	/	C	0	/
IP	0	/	IB	2	5	A	2	5.26
MBI	15	71.43	IBM	0	/	AIS	9	23.68
MB	4	19.05	M	27	67.5	AISIL	5	13.16
MBB	2	9.52	ZA	1	2.5	AIL	12	31.58
CP	0	/	NC	10	25	IS	7	18.42
	21	100		40	100	IL	3	7.90
							38	100

Scapula	*N*	%	Ribs	*N*	%
C	0	/	C	2	16.67
GC	4	50	PE	1	8.33
GCN	1	12.5	PES	0	/
NF	3	37.5	S	9	75
F	0	/	SDE	0	/
	8	100		12	100

Patella	*N*	%	Car/Tar	*N*	%
C	0	/	C	23	100
F	0	/	F	0	/
	0	100		23	100

(Continued)

TABLE 6 (Continued)

Cal	*N*	%	Ast	*N*	%
C	20	52.63	C	18	94.74
F	18	47.37	F	1	5.26
	38	100		19	100

Vertebrae	*N*	%	Phalanges	*N*	%
C	1	4	C	219	82.64
VB	24	96	P	26	9.81
	25	100	D	20	7.55
				265	100

Teeth	*"in situ"*					
	Incisors		Upper molars		Lower molars	
	N	%	*N*	%	*N*	%
C	1	100	7	100	14	100
F	0	/	0	/	0	/

Isolated					
Incisors		Upper molars		Lower molars	
N	%	*N*	%	*N*	%
0	/	5	33.73	10	41.67
31	100	60	66.27	14	58.33
		65	100	24	100

and Supplementary Table S4). Tables 4, 5 summarize the results of the ML models. The RF model showed moderate performance and balanced outcomes in precision and recall across most groups. However, it struggled with identifying terrestrial carnivores. Compared to RF, the SVM underperformed, showing lower accuracy and kappa values, and was not good in distinguishing between classes, especially nocturnal and diurnal raptors. The best results were obtained using GBM. This model showed better performance in identifying humans and terrestrial carnivores and yielded higher accuracy, kappa, precision, recall and F1-scores across the different predator groups (Tables 4, 5).

The classification results of the GBM indicated terrestrial carnivores as the primary accumulating agents of the Escoural sample with a probability of 0.99. In contrast, the RF model classified Escoural as a human-made accumulation, while the SVM model also grouped Escoural with terrestrial carnivores. The high confidence of the GBM model in classifying the Escoural sample, despite the variability of the dataset, raises concerns about overfitting. However, given the comprehensive cross-validation and the model's consistent performance (see Supplementary Figure S3), the prediction appears reliable. However, it is important to interpret these results within the broader context of taphonomic and archaeological evidence. Escoural could have been influenced by multiple agents, in this case, several terrestrial carnivores and humans, and this classification should be viewed as identifying the predominant agent rather than excluding other possible contributors.

3.3 Breakage

Approximately 26.8% of the rabbit specimens are complete. Table 6 details the preservation status of the different bone portions. Smaller bones, such as phalanges, metapodials, and carpals/tarsals, are typically found intact. In contrast, longer bones, including limb bones, girdles, and cranial elements, were predominantly recovered in a broken state. The size of the rabbit remains ranges from 3.98 to 60.36 mm, with an average length of 14.23 mm, and over 85% of the specimens exceeding 10 mm in length (Figure 5). Upper and intermediate limb bones were highly fragmented, with shafts being the most represented bone portion. Specifically, shafts accounted for 48% of radii-ulnae specimens, 66% of humeri, 76% of tibiae, and 80% of femora. Conversely, lower limb bones were often found complete, with 70% of metacarpals and 22% of metatarsals recovered intact. With the exception of the ulnae, which preserved the proximal end significantly more than the distal end, the remaining upper and intermediate long bones showed somewhat varied preservation rates between their proximal and distal ends. For instance, the humeri preserved 14% of their proximal ends compared to 18% of their distal ends, with similar variations observed in other long bones. The radii and femora exhibited more preservation of the proximal ends, while the tibia had greater distal preservation (Table 6). Additionally, metapodials preserved their proximal ends around 36% of the time and their distal ends 14%. Cranial portions were primarily represented by M and NC fragments, while mandibles were mostly represented by MBI portions. No complete crania or mandibles were recovered.

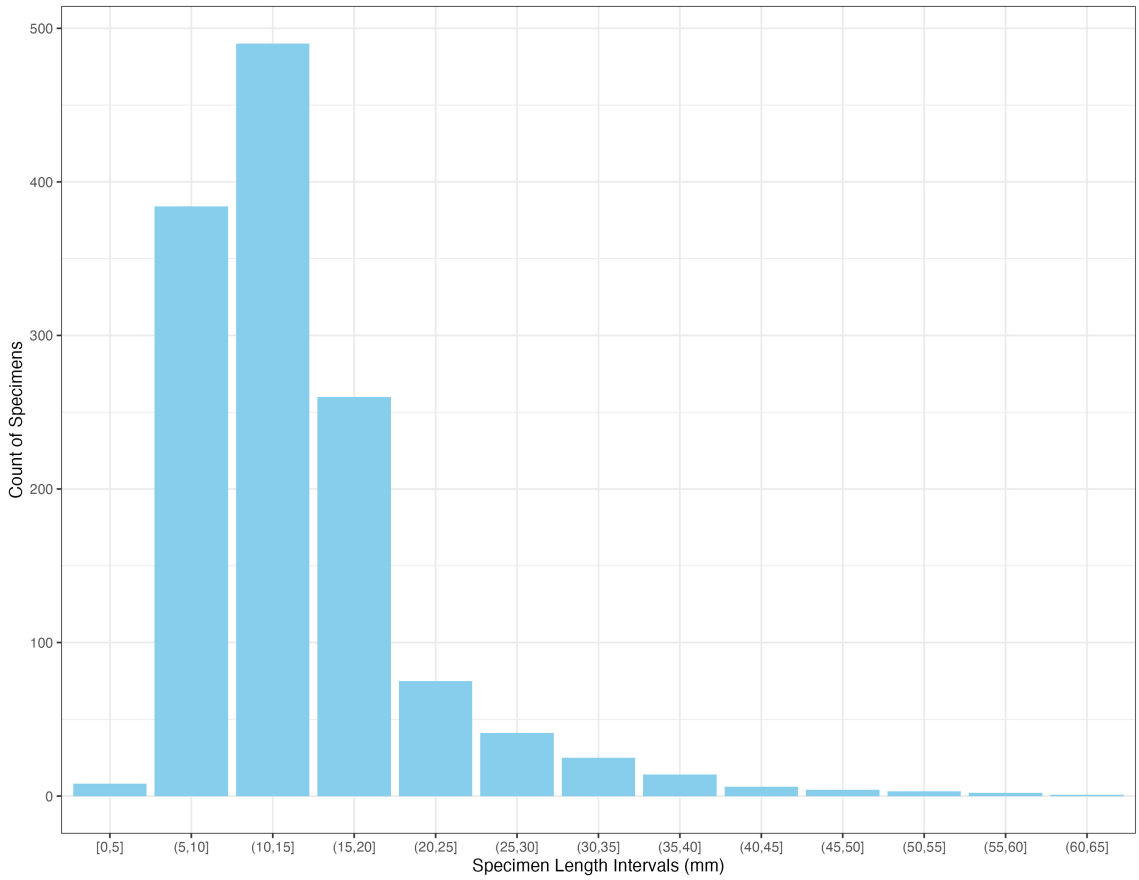

FIGURE 5
Specimen length distribution of the recovered rabbit remains.

Innominates were mainly represented by fragments retaining the acetabulum (AIL, AIS, AISIL), scapulae retained the GC portion, and ribs were primarily found as shaft fragments (S). Phalanges, carpals, tarsals, and isolated teeth were mostly complete (Table 6).

Green fractures were recorded on 34% of the rabbit assemblage, while dry fractures were identified on ∼6% of the specimens. Additionally, 34% of the specimens exhibited indeterminate breakage patterns, and another 6% had recent fractures. Table 7 summarizes the frequencies of green breakages on the different portions of marrow-rich long bones (humerus, femur and tibia) and the number of green broken shaft cylinders or "tubes." In total, around 70% of the marrow-rich long bone sample presented green breakages. Cylinders occurred most often on tibiae. Fifteen marrow-rich long limb bones (one humerus, five femora, and nine tibiae) retained the epiphysis and part of the shaft presenting a helical or V-shaped fracture, which has been described as a morphotype of carnivore breakage (Rodríguez-Hidalgo et al., 2020) (Figure 6). While shaft fragments were more abundant, epiphyses were still fairly represented across all long bones. This pattern suggests that felid activity may have played a more significant role in the assemblage compared to canids, as felids tend to leave more epiphyses unconsumed. Only 9% of the marrow-rich long bone specimens presented clear dry breakages, which suggests limited postdepositional damage and an overall high integrity of the rabbit assemblage. A total of 22 notches were recorded on marrow-rich long bones. Most notches were "complete or type A" (60%), although there were some micro-notches (type E) (36%) and overlapping notches (type C).

TABLE 7 Counts and frequencies (parentheses) of green breakage across the different marrow rich long bone portions and tube counts.

	Humerus	Femur	Tibia
PE*	3/3 (100)	5/7 (71)	1/3 (33)
PES*	0/0 (0)	5/5 (100)	1/2 (50)
S	20/27 (74)	78/98 (80)	89/114 (78)
SDE*	4/4 (100)	3/4 (75)	10/13 (77)
DE*	1/4 (25)	1/2 (50)	2/2 (100)
Total	28/41 (62)	92/122 (75)	103/149 (70)
Tubes	5	5	9

*Not counting unfused epiphyses.

3.4 Bone surface modifications and digestion

Approximately 75% of the bone cortical surfaces exhibited good or moderate preservation, indicating an overall high preservation

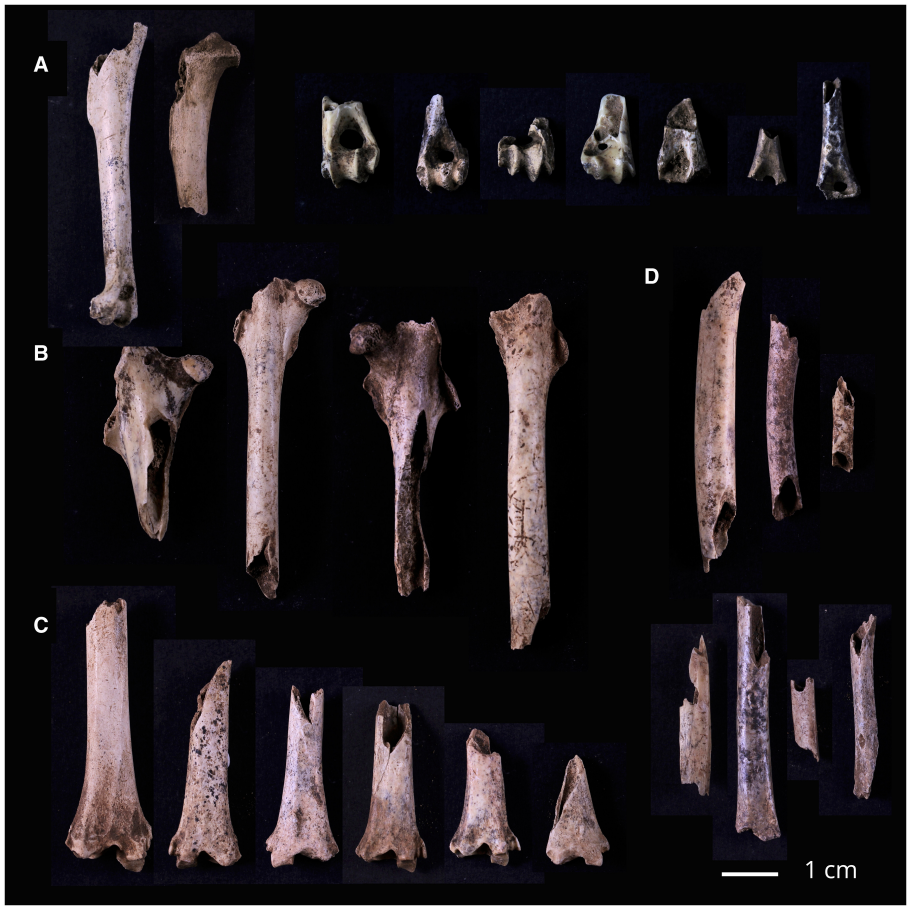

FIGURE 6
Examples of typically preserved marrow-rich long bone breakage portions and tubes in the Escoural rabbit sample. **(A)** examples of humeri specimens, represented mostly by distal epiphysis plus a small portion of the shaft, **(B)** femora specimens generally represented by proximal epiphysis plus shaft, **(C)** tibiae specimens preserving distal epiphysis plus shaft, **(D)** examples of tubes or cylindrical femora and tibia shafts.

state of the assemblage. Fissures resulting from changes in humidity and concretions, typical modifications associated with karstic environments, were present in 2% of the assemblage. Weathering on the rabbit bones was minimal, with 98% of the bones classified as stage 0, indicating no visible weathering, and the remaining 2% at stage 1, which is characterized by slight splitting of bone parallel to fiber structure (Andrews, 1990). These weathering stages suggest that the remains were exposed for 0–2 years (stage 0) or 1–5 years (stage 1) in a wet temperate climate (Andrews, 1990). This further supports the overall high preservation and limited exposure of the assemblage. Traces of trampling and microabrasion were observed also on ∼2% of the remains. Biochemical marks were present on 8% of the specimens, while root etching occurred on 23%. Manganese staining affected 60% of the bones, with 35% of these showing generalized or complete coverage. Rounding was observed in 16% of the bone sample, with 15% classified as R1 (rounding affects the anatomical edges and fractures at the microscopic level) and only 1% as R2 (rounding affects certain areas of the bone and can be observed at the macroscopic level). Polished surfaces or edges were found on <5% of the specimens. Signs of burning were present on only two bone fragments, characterized by a black, homogeneous coloration on the bone surface. Rodent gnawing was observed on 11 rabbit bone specimens.

Carnivore damage in the form of tooth marks was observed on 96 specimens, accounting for 8% of the NISP of the rabbit bone assemblage. Digestive damage affected 9% of the sample. Specific types of damage include pits on 55 specimens (4.6%), punctures on 27 specimens (2.3%), scoring on 35 specimens (2.9%), and crenulated edges on 85 specimens (7.2%). Tooth marks appeared mainly on long bones and innominates. Metatarsals and tibiae are the most frequently tooth-marked elements (18.8 and 17.7% respectively), followed by femora (13.5%) and innominates (11.5%). Table 8 shows the counts and percentages of tooth-marked and digested specimens across elements. Hind limbs (femora, tibiae, metatarsals, and innominates) exhibit a significantly higher amount of carnivore damage in absolute terms. However, in relative terms, ulnae and innominates stand out as the elements with the highest percentages of tooth marks. Innominates also show significantly higher percentages of punctures and scores compared to other elements (Figure 7). Figure 8 provides examples of damage inflicted by carnivores on the rabbit bone sample. All three types of tooth marks (pits,

TABLE 8 Counts and percentages per NISP of tooth-marked and digested bone specimens per element.

Element	TM	TM %	Pits	Pits %	Punctures	Punctures %	Scores	Scores %	Digested	Digested %
Cranium	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Mandible	3	14.29	0	0.00	3	14.29	0	0.00	1	4.76
Tooth	0	0.00	0	0.00	0	0.00	0	0.00	1	0.79
Vertebra	2	8.00	1	4.00	1	4.00	0	0.00	1	4.00
Rib	1	8.33	0	0.00	0	0.00	1	8.33	0	0.00
Scapula	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Humerus	6	14.63	4	9.76	2	4.88	2	4.88	5	12.20
Radius	4	11.43	3	8.57	2	5.71	1	2.86	2	5.71
Ulna	7	28.00	3	12.00	2	8.00	1	4.00	5	20.00
Femur	13	10.66	10	8.20	3	2.46	3	2.46	10	8.20
Tibia	17	11.49	11	7.43	3	2.03	10	6.76	7	4.73
Innominate	11	28.95	5	13.16	4	10.53	7	18.42	3	7.89
Metacarpus	1	1.89	1	1.89	0	0.00	0	0.00	5	9.43
Metatarsus	18	12.95	13	9.35	1	0.72	7	5.04	10	7.19
Metapodial indet	2	2.90	0	0.00	2	2.90	0	0.00	3	4.35
Long bone indet	2	3.92	1	1.96	0	0.00	1	1.96	0	0.00
Tarsal	3	3.75	0	0.00	2	2.50	0	0.00	33	41.25
Phalange	6	2.26	3	1.13	2	0.75	2	0.75	22	8.30
Total	96		55		27		35		108	

The column TM refers to the total tooth-marked specimens. Some specimens had multiple tooth marks.

punctures, and scores) occur in relatively similar percentages across long bones.

The comparison between tooth mark sizes from Escoural and those documented for various terrestrial carnivores and humans indicates that the marks fall within the size ranges associated with foxes, wildcats, and humans (Figure 9). Indeed, mean tooth mark size is relatively small and several v-shaped scores, typical of cubs, were identified. The upper range of the 95% confidence interval for the Escoural sample reaches the range of one of the lynx samples. This analysis indicates that rabbits were likely consumed by small carnivores, although the overlap makes it unclear whether multiple predators were involved. Lynx and especially lynx cubs should not be completely ruled out as contributors, and humans could have been involved as well. Despite these observations, the variability within groups, as well as the overlap between carnivore types, makes it challenging to draw definitive conclusions about the specific predator involved. This analysis alone is insufficient to clearly identify the accumulating agent.

Regarding digestion, among all elements, tarsals exhibited the highest amount of digestion (41%). This was followed by ulnae at 20%, humeri at 12%, and phalanges at 8% (Table 8). Approximately 66% of the digested remains were classified as light, around 27% as moderate and 7% as heavy. Extreme digestive damage was not documented. Anthropogenic marks in the form of cut marks were not observed. Only two burned remains (a metatarsal and an indeterminate long bone shaft) were observed.

3.5 Hierarchical Clustering on Principal Components (HCPC) and K-means cluster analysis on taphonomic data

The HCPC analysis reveals several clusters based on the selected taphonomic variables that more or less align with the known predator groups. The discrepancies could be due to high variability and overlap in taphonomic modification patterns within and between the predator groups, or to limitations in the dataset and the resolution of the method used. The first two principal components explain 63.6% of the variance. Clusters 1, 2, and 3 include assemblages where humans were involved (Figure 10; see also Supplementary Figure S4). Cluster 4 contains assemblages of mixed origins, including one with human modifications as well as others associated with fox and lynx activity. Assemblages with direct anthropogenic evidence are clearly separated along the first dimension from the remaining clusters, which include only carnivore-made assemblages. Cluster 5 contains a mixture of carnivore-made assemblages. The Escoural assemblage clustered with an assemblage made by fox and one made by wildcat (Álvarez et al., 2012), and lies very close to Navalmaíllo Rockshelter, an assemblage interpreted as generated by lynxes (Arriaza et al., 2017). It also falls near to other assemblages made by lynxes and foxes, further supporting the interpretation that the assemblage may have mostly originated from terrestrial carnivore activity (Figure 10). The average silhouette width showed that clusters had varying quality (see Supplementary Figure S5a). Whereas clusters

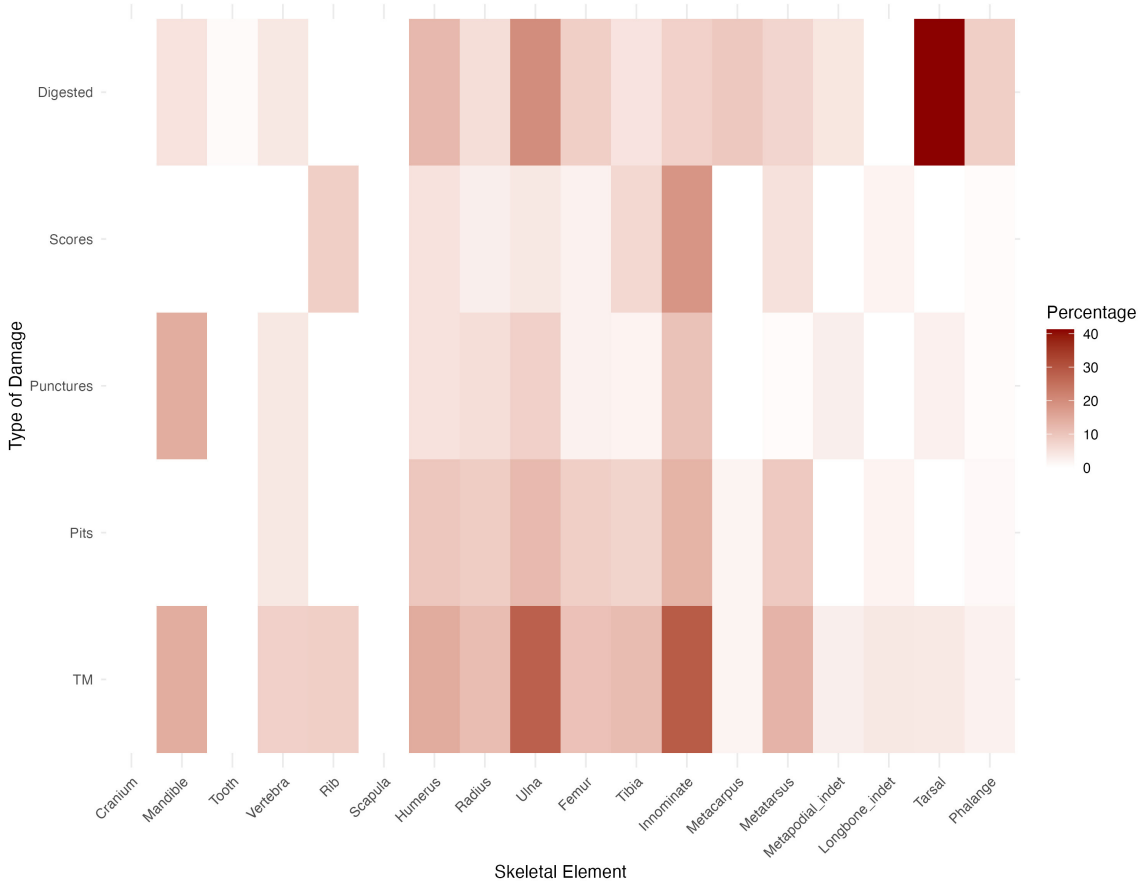

FIGURE 7
Heatmap of types of carnivore damage across skeletal elements. TM refers to the sum of the remains with any kind of tooth mark modification (pits, punctures and scores).

2, 3, and 7 seemed to be well-defined, clusters 1, 4, 5, and 6 had some misclassified samples and moderate quality (as shown in Supplementary Figure S5a and Supplementary Table S6a).

The K-means clustering analysis with six clusters yielded a slightly higher average silhouette width of 0.37, suggesting the analysis is more reliable (Supplementary Figure S5b and Supplementary Table S6b). In this case, the clusters showed similar alignment with the known groups. For example, cluster 1 seemed to be mostly related with non-ingested assemblages, cluster 3 with ingested samples, and clusters 5 and 6 contained only assemblages with human input (Figure 11). In fact, the coordinates of the centroids for each cluster, which describe the main characteristics of each cluster, show that an important feature in describing cluster 3 are indeed digested remains, and clusters 2, 3, and 4 are characterized by the amount of adult individuals (Table 9). Interestingly, Escoural showed taphonomic similarities to Cova del Gegant IIIa, which has been interpreted as an assemblage made primarily by lynxes (Rodríguez-Hidalgo, 2022), and Navalmaíllo, which has a similar interpretation (Arriaza et al., 2017). This cluster also contains an eagle nest assemblage and an Layer III at Estebanvela, which has a higher proportion of evidence for non-human accumulation agents, such as carnivores and raptors than Estebanvela I and II (Yravedra et al., 2019). This groups seems to be defined best by the proportion of adult individuals and tubes or cylinders (Table 9). Clusters 1 and 2 lie close and are also mainly characterized by the amount of adults and complete long bones, respectively. Cut marks, burned remains and tooth marks do not appear to be very important in this classification.

4 Discussion

Faunal studies have revealed that Neanderthals displayed complex and flexible subsistence strategies and variability in site use patterns, and that rabbit hunting and consumption were sometimes part of them (Cochard et al., 2012; Carvalho et al., 2018; Pérez et al., 2017; Rufà et al., 2014; Pelletier et al., 2019). At Escoural Cave, clear evidence for human consumption of rabbits in the form of cut marks is absent. Only two burned specimens were recorded, suggesting that cremation occurred most likely post-depositionally, given the small number of remains (Pérez et al., 2017; Rodríguez-Hidalgo et al., 2020; Téllez et al., 2022). This indicates that Neanderthals may have focused on other food sources or different subsistence strategies during their occupation of the site.

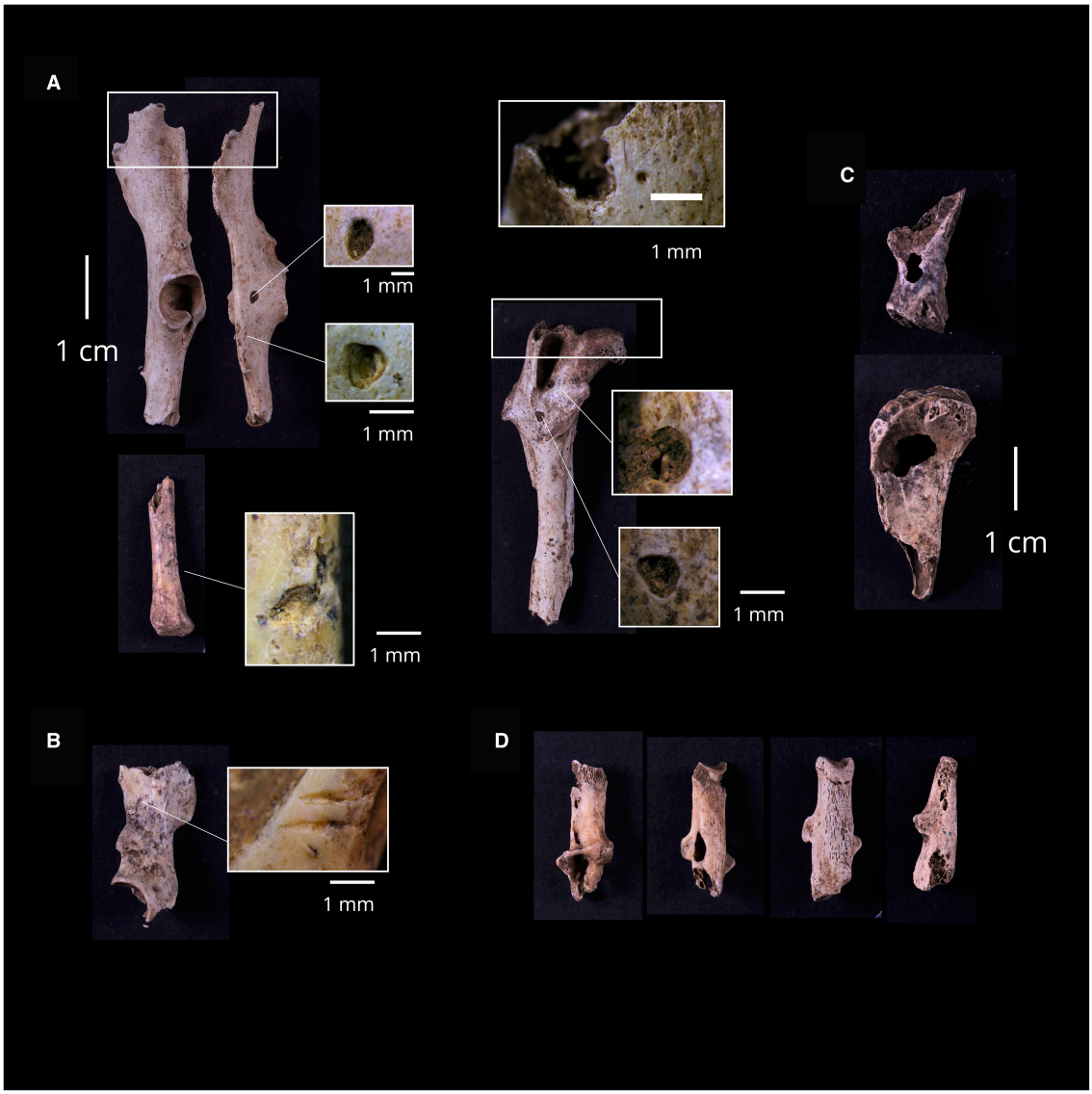

FIGURE 8
Examples of tooth marked and digested specimens. **(A)** Specimens showing pits and crenulated edges, **(B)** pelvis fragment with carnivore scores, **(C)** examples of punctured specimens, **(D)** several digested calcanei.

The results suggest that small and medium-sized terrestrial carnivores, primarily lynxes, and possibly also red foxes and wildcats, played the main role in the accumulation and modification of the remains. These three carnivores are represented in the faunal assemblage from Escoural, analyzed in previous studies (Otte and da Silva, 1996), and Iberian lynx and a smaller carnivore have been documented in the remaining assemblage recovered in 2020 from Profile 1. Substantial carnivore activity is reflected in the frequencies of carnivore damage and digested elements. The anatomical representation showed a predominance of hind limb elements like tibiae and metatarsals. Phalanges and tarsals were also highly represented. This pattern is consistent with accumulations by Iberian lynxes and by red foxes, which show a high prevalence of distal limb elements and often the preservation of complete autopodial bones (Rodríguez-Hidalgo et al., 2013, 2015, 2020; Rodríguez-Hidalgo, 2022). Similarly, wildcat accumulations show a high representation of cranial elements, metatarsals, and femora (Lloveras et al., 2016). In contrast, diurnal and nocturnal raptors exhibit a different pattern, with a higher proportion of proximal upper limbs (humerus, femur) (Rodríguez-Hidalgo et al., 2013).

The high confidence of the GBM model in classifying the Escoural sample as predominantly created by terrestrial carnivores supports this interpretation. However, pinpointing the exact predator species remains challenging. Mortality profiles could potentially help in this differentiation, as foxes and wildcats generally prey on juvenile rabbits due to their smaller size and relative vulnerability, which results in age profiles skewed toward younger individuals. Lynxes, in turn, as well as larger predators in general, including humans, tend to prey on prime adults

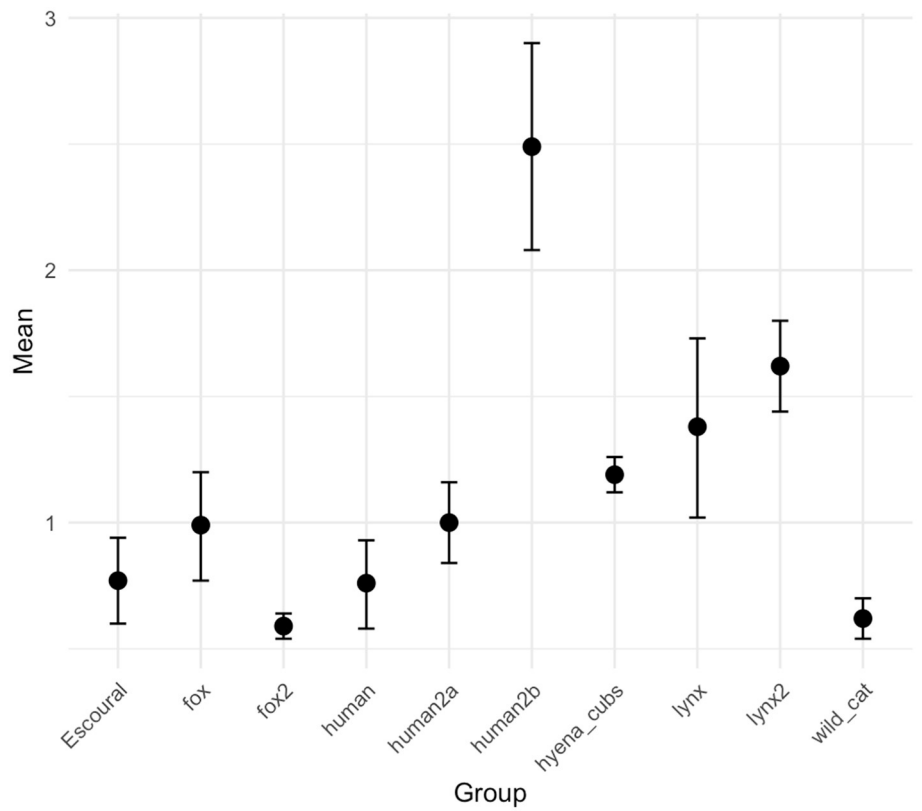

FIGURE 9
Mean values and 95% confidence intervals of tooth pit and puncture widths on cortical surfaces of long bone shafts on bone assemblages modified by fox, humans, hyena cubs, lynxes and wildcats. Comparative samples from Andrés et al. (2012), Massigoge et al. (2014), Rodríguez-Hidalgo et al. (2013, 2015), and Saladié et al. (2024). The values can be found in Supplementary Table 4.

(Pelletier et al., 2019). The Escoural sample is dominated by adults, which would suggest lynx as the primary accumulators. Additionally, the presence of infant rabbits in the assemblage could indicate individuals that likely died within their burrows, as infant rabbits typically remain in the burrow until they reach the juvenile stage.

Regarding breakage patterns, high rates of green fractures and minimal dry fractures suggested limited postdepositional damage and high assemblage integrity, and typical carnivore breakage patterns, including helical fractures, were predominant. The analyzed sample also showed extensive breakage of long bones, which has been typically observed in lynx-made rabbit assemblages. However, red foxes and wildcats and humans can also cause significant breakage, often associated with gnawing and scavenging behaviors. Notably, foxes tend to leave a higher number of tooth marks on skeletal elements compared to lynxes (Rodríguez-Hidalgo et al., 2013). This characteristic aligns with the findings from Escoural, which exhibits a relatively high frequency of tooth marks compared to other assemblages attributed to lynxes, such as Cova del Gegant IIIa and Navalmaíllo (Rodríguez-Hidalgo et al., 2020; Arriaza et al., 2017). The comparison of tooth mark sizes indicates that the damage observed in the Escoural assemblage could be consistent with various agents, including small carnivores and potentially humans, but the overlap and variability in tooth mark sizes prevent a definitive identification of the contributors. Moreover, there is no additional evidence of anthropogenic modification on the bones to support human involvement conclusively.

However, equifinality in rabbit assemblages complicates the identification of human activities. Studies have shown that even when cut marks and burning damage, which are exclusively attributed to humans, are considered, detecting human involvement as predators of rabbit assemblages remains challenging. Most experiments aimed at describing the human taphonomic signature on rabbit remains have focused on exclusive products of human activity, including butchering processes and cooking, which leave cut marks and burned remains (Lloveras et al., 2009; Sanchis et al., 2011). However, these modifications are variable and sometimes even absent in archaeological assemblages (Hockett and Bicho, 2000; Hockett and Haws, 2002; Ripoll, 2004). Given the fact that rabbits can be processed without the use of tools, additional taphonomic features can be caused by human activity, namely tooth marks, shafts with notches on fractured edges or cylinders resulting from marrow extraction (Saladié et al., 2024; Hockett and Haws, 2002; Cochard et al., 2012). The relatively low proportion of cylinders observed at Escoural aligns with patterns typically associated with lynx activity, while humans generally produce a much more extensive pattern of cylinders along with the disappearance of epiphyses. Additionally, the presence of tooth marks on metapodials and phalanges, which are not commonly found in human accumulations as these elements are usually not consumed and often remain articulated,

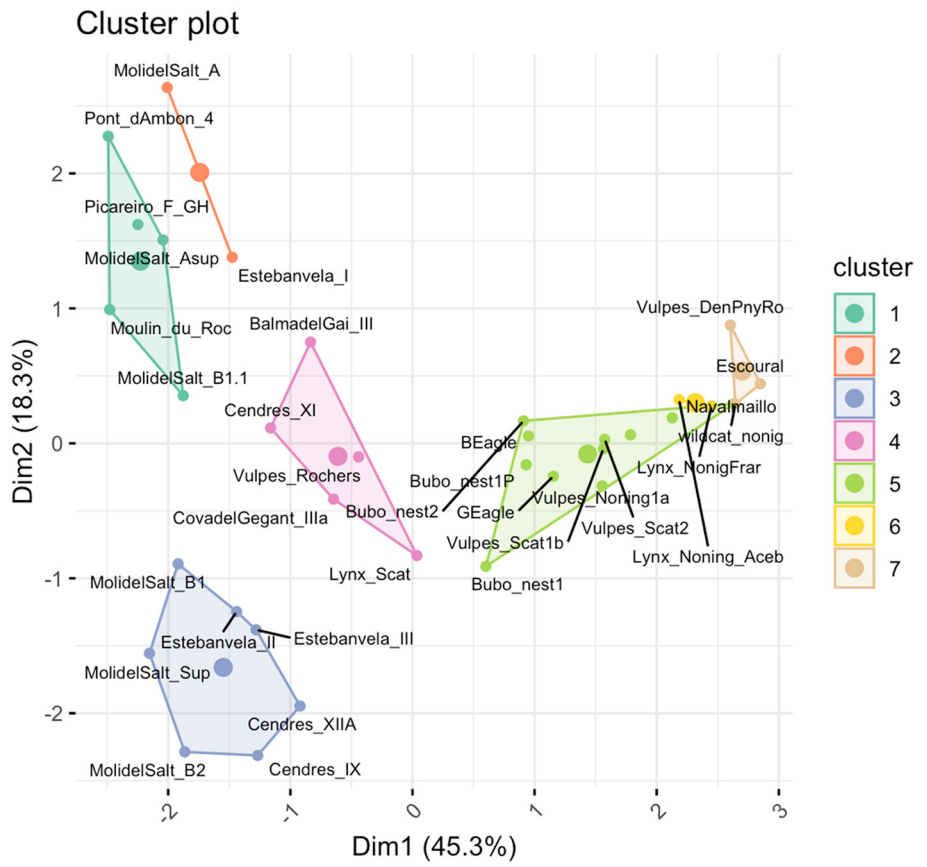

FIGURE 10
HCPC cluster plot of taphonomic data.

further supports the likelihood of carnivore activity at the site (Yravedra et al., 2019). In the case of Escoural, no metapodials were found with articulated phalanges, which may provide additional evidence favoring carnivore involvement over human agency. Yet, some taphonomic evidence at Escoural suggest that Neanderthal activity could potentially be underrepresented or masked, like the predominance of adult individuals, extensive breakage or some tooth mark sizes. These and other typical characteristics of Neanderthal consumption of rabbit, which include a relatively balanced representation of cranial and postcranial remains and a significant presence of metapodials, scapulae and humeri, have been observed in several rabbit accumulations with Neanderthal input, including Bolomor Cave (Blasco and Fernández Peris, 2012), Arbreda Cave (Lloveras et al., 2010), Les Canalettes (Cochard et al., 2012), Columbeira Cave (Carvalho et al., 2018), El Salt (Pérez et al., 2017), or Teixoneres (Rufà et al., 2014). As Saladié et al. (2024) have pointed out, misinterpreting human marks could be as problematic as overestimating carnivore involvement in the formation of assemblages. Given the lack of clear evidence, we cannot argue that humans contributed to the Escoural assemblage, but we also cannot entirely exclude the possibility of some human involvement until more data and comprehensive analyses are available.

Taphonomic attributes left by the same predator species exhibit significant variability. The same type of predator, including humans, can create bone accumulations with particular characteristics depending on how the site is used, e.g. as a consumption area, defecation and abandonment zone, breeding den, transitional area, or prey acquisition zone (Cochard, 2004). At the same time, very similar modification patterns can be found on scats, pellets or non-ingested remains in nests and dens of different predators. This means that this variability must be considered when accurately characterizing archaeological assemblages. On the one hand, expanding frames of reference is crucial to address the challenge of identifying human activity in rabbit assemblages beyond cut marks and burning, as well as to distinguish between other non-human predators. On the other hand, several authors have pointed out that only a comprehensive approach combining multiple variables can aid in identifying the agent(s) responsible for rabbit archaeological assemblages (Lloveras et al., 2012a,b; Rodríguez-Hidalgo et al., 2020). Thus, taphonomic studies have introduced the use of multivariate analyses that consider multiple criteria, such as anatomical representation, breakage patterns, and the frequency and type of surface modifications to classify sites among a set of archaeological and reference assemblages to help reduce the effects of equifinality (e.g. Arriaza et al., 2017; Rodríguez-Hidalgo et al., 2020). However, since assemblages can have a complex history involving multiple accumulating agents and processes, studies have to consider that finding a single perfect

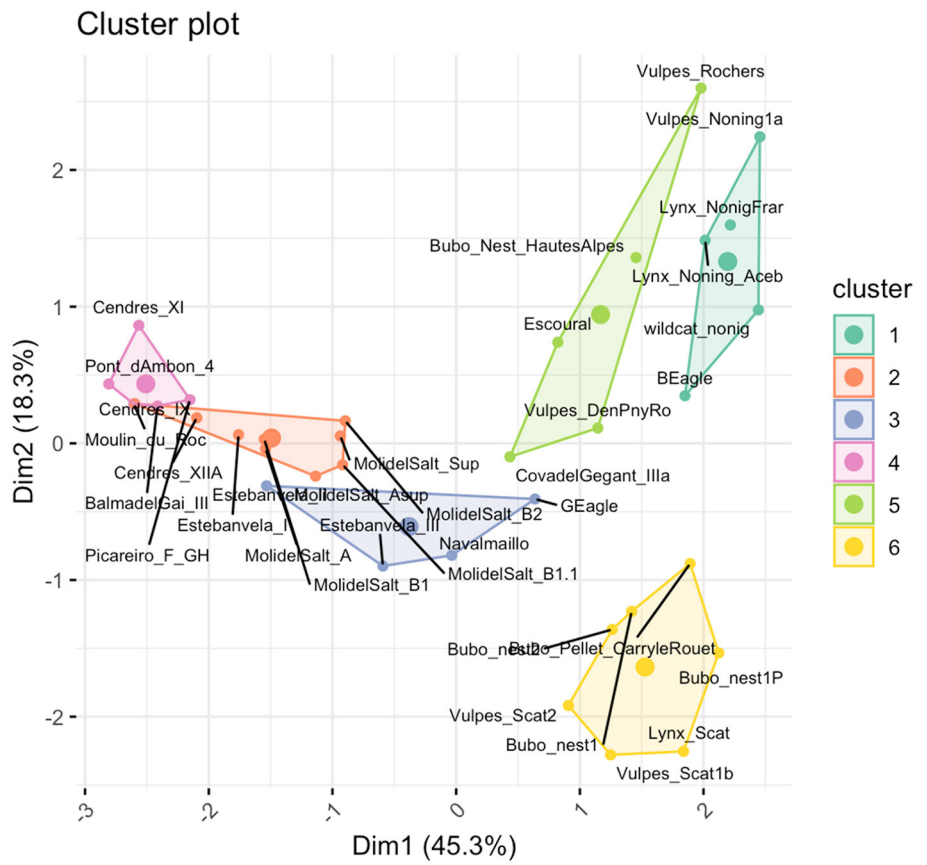

FIGURE 11
Factor map of the K means clustering analysis of taphonomic data.

prediction may not accurately reflect the true nature of the assemblage. For instance, the Escoural sample is composed of both ingested and non-ingested remains and very likely has contributions from various predators. While these analyses can provide valuable insights, they must be interpreted in the context of the potential for multiple agents and processes influencing the assemblage.

Similarly, the application of machine learning models presents its own set of challenges. Although they can handle high-dimensional data and complex interactions between variables more effectively and provide a probabilistic framework that accounts for the possibility of multiple accumulating agents, the inherent variability in predator behavior, the limitations of current reference frameworks and comparative collections, and the fact that datasets are generally small, can impact the accuracy and reliability of the predictions. Thus, while machine learning offers powerful tools for taphonomic analysis, its results should be integrated with traditional taphonomic evidence and expert interpretation to form a holistic understanding of the assemblage formation. Nevertheless, the use of ML models, can reduce the subjectivity of manual classification, as well as provide a more standardized approach in identifying taphonomic agents. Even on small datasets, models can establish a framework that can be applied to larger datasets in the future. As more data becomes available, the models can be retrained and improved so that their predictive power is increased.

This study provides an example of how multiple analytical methods (PCA, HCPC, ML) can contribute to interpreting complex rabbit assemblages by complementing traditional taphonomic analysis. Additionally, it expands the reference frameworks for carnivore fossil accumulations, which can be useful for future studies.

Our findings also offer insights into Neanderthal behavioral complexity. The absence of evidence for rabbit consumption by Neanderthals at Escoural suggests a context-dependent variability in their subsistence strategies, supporting the idea that Neanderthals were highly adaptable, selecting alternative food resources or exploiting different ecological niches according to specific environmental conditions. Moreover, the lack of anthropic consumption indicates that human occupations were likely of short duration, allowing carnivores to occupy the site during periods of human absence. This suggests potential behavioral influences between Neanderthals and carnivores, affecting the duration of occupations, settlement choices, mobility patterns, and other aspects of subsistence strategies (Picin et al., 2020; Daujeard et al., 2012; Linares-Matás and Yravedra, 2024; Pinto-Llona et al., 2023). Future research will include the analysis of additional faunal remains from both previous and recent excavations and will explore whether humans focused on other prey types at Escoural. Ongoing dating and microstratigraphic analyses will also help refine the site's occupation history.

TABLE 9 Centroid values for each cluster obtained from k-means clustering, showing the mean values of each taphonomic feature within each cluster.

Cluster	CM	BU	DI	TB	CLL	T	AD
1	0	0	7.44	3.28	68.3	0.1	29.246
2	3.877	25.640	1.607	1.3	2.382	8.018	82.911
3	1.275	10.172	31.475	1	8.847	6.891	82.4
4	9.7	12.74	0.394	0.84	1.99	26.210	95.16
5	0.006	0.28	7.96	8.74	20.252	3.786	51.806
6	0	0	84.114	2.286	10.043	0.471	44.486

The features include CM (%Cut marks), BU (%Burning), DI (%Digestion), TB (%Tooth/Beaks marks), CLL (%Complete Long bones), T (%Tubes), and AD (%Adult individuals).

5 Conclusions

The rabbit assemblage from Escoural Cave resulted from the activity and accumulation of a mixture of terrestrial carnivores, among which the Iberian lynx stands out. The classification of the Escoural sample as predominantly influenced by terrestrial carnivores is supported by consistent taphonomic evidence across all the analyses included here, with the lynx identified as the primary agent. However, the variability and overlap observed in the PCA and HCPC analyses between different small and medium-sized terrestrial carnivore species, indicate that multiple agents may have contributed to the assemblage. The results also highlight the challenges of distinguishing between different accumulation agents in highly variable datasets, but underscore the potential of advanced statistical and ML techniques to enhance taphonomic analyses.

Complexity in subsistence behavior includes the ability to adapt to different environmental and ecological conditions. At Escoural, even though Neanderthals were using the cave or its surroundings, they were not consuming the rabbits accumulated there. This shows that Neanderthal subsistence behavior was variable and dependent on the context. While Neanderthals are known to have consumed small game in other contexts, the absence of rabbit consumption in this assemblage suggests they may have had alternative food sources available during their occupation of the cave.

Future studies will further explore whether the cave could have functioned mainly as a carnivore den, and have been occupied by Neanderthals only intermittently. The cave has yielded a very diverse faunal spectrum, which includes multiple carnivore species, suggesting varied interactions between different species and a dynamic use of the site over time. Thus, Escoural holds significant importance in the southern Portugal Mousterian context. Research on Middle Paleolithic occupation in central Portugal has provided significant insights into Neanderthal behavior and adaptations. Key sites such as Figueira Brava, Gruta da Oliviera, Gruta da Companheira, Foz do Enxarrique, and Almonda Cave have revealed a complex picture of Neanderthal life, yielding evidence of diverse subsistence strategies, including the hunting of large game and the exploitation of aquatic resources. Despite these advances, more comprehensive studies and excavations using modern analytical techniques are still needed. Continued research at Escoural will soon contribute to a deeper understanding of Neanderthal behavior and the interplay between human and carnivore activities.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Author contributions

LC-S: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. AR: Formal analysis, Methodology, Writing – review & editing. JC: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2024.1473266/full#supplementary-material

References

Álvarez, M. C., Kaufmann, C. A., Massigoge, A., Gutiérrez, M. A., Rafuse, D. J., Scheifler, N. A., et al. (2012). Bone modification and destruction patterns of leporid carcasses by Geoffroy's cat (*Leopardus geoffroyi*): an experimental study. *Quat. Int.* 278, 71–80. doi: 10.1016/j.quaint.2011.11.029

Andrés, M., Gidna, A. O., Yravedra, J., and Domínguez-Rodrigo, M. (2012). A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeol. Anthropol. Sci.* 4, 209–219. doi: 10.1007/s12520-012-0093-4

Andrews, P. (1990). *Owls, Caves and Fossils*. London: Natural History Museum Publications.

Armstrong, A. (2016). Eagles, owls, and coyotes (oh my!): taphonomic analysis of rabbits and guinea pigs fed to captive raptors and coyotes. *J. Archaeol. Sci. Rep.* 5, 135–155 doi: 10.1016/j.jasrep.2015.10.039

Arriaza, M. D. C., Huguet, R., Laplana, C., Pérez-González, A., Márquez, B., Arsuaga, J. L., et al. (2017). Lagomorph predation represented in a middle Palaeolithic level of the Navalmaíllo Rock Shelter site (Pinilla del Valle, Spain), as inferred via a new use of classical taphonomic criteria. *Quatern. Int.* 436, 294–306. doi: 10.1016/j.quaint.2015.03.040

Auguste, P. (1995). Chasse et charognage au Paléolithique moyen: l'apport du gisement de BiacheSaint-Vaast (Pas-de-Calais). *Bull. Soc. Prehist. Fr.* 92, 155–168. doi: 10.3406/bspf.1995.10003

Barone, R., Paavaux, C., Blin, P. C., and Cuq, P. (1973). *Atlas of Paris: Rabbit Anatomy*. Issy les Moulineaux Cedex: Masson and Co. Editeurs.

Binford, L. R. (1978). *Nunamiut Ethnoarchaeology*. Clinton Corners, NY: Eliot Werner Publications/Percheron Press.

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths*. Cambridge, MA: Academic Press.

Binford, L. R. (1984). Butchering, sharing, and the archaeological record. *J. Anthropol. Archaeol.* 3, 235–257. doi: 10.1016/0278-4165(84)90003-5

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals* (Academic Press), 123–143. doi: 10.1016/B978-0-12-821428-2.00010-X

Blasco, R., and Fernández Peris, J. (2012). A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quat. Int.* 252, 16–31. doi: 10.1016/j.quaint.2011.03.019

Blumenschine, R. J., Marean, C. W., and Capaldo, S. D. (1996). Blind test of interanalyst correspondence and accuracy in the identification of cut marks. Percussion marks and carnivore tooth marks on bone surface. *J. Archaeol. Sci.* 23, 493–505. doi: 10.1006/jasc.1996.0047

Brown, K., Fa, D. A., Finlayson, G., and Finlayson, C. (2011). "Small game and marine resource exploitation by Neanderthals: the evidence from Gibraltar," in *Trekking the Shore: Changing Coastlines and the Antiquity of Coastal Settlement*, ed. N. F. Bicho, J. A. Haws, and L. G. Davis (Cham: Springer), 247–272. doi: 10.1007/978-1-4419-8219-3_10

Buccheri, F., Bertè, D. F., Berruti, G. L. F., Cáceres, I., and Volpe, L. y Arzarello, M. (2016). Taphonomic analysis on fossil remains from the Ciota Ciara Cave (Piedmont, Italy) and new evidence of cave bear and wolf exploitation with simple quartz flakes by Neanderthal. *Riv. Ital. Paleontol. Stratigr.* 122, 41–54. doi: 10.13130/2039-4942/7674

Bunn, H. T. (1982). *Meat-eating and human evolution: Studies in the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa* (Ph.D. Dissertation). Berkeley, CA: University of California, Berkeley.

Bunn, H. T. (1983). Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari Desert, Botsuwana, and from a spotted hyena den near Nairobi, Kenya. *Anim. Archaeol.* 163, 141–148.

Callou, C. (1997). "Diagnose différntielle des principaux éléments squelettiques du lapin (Genre Oryctolagus) et du Lèvres (Genre Lepus) en Europe Occidentale," in *Fiches d'ostéologie animale pour l'archéologie. Series B: Mammifères. Centre de recherches Archéologiques du CNRS*, eds. N. Desse-Berset, and J. Desse (Valbonne-Sophia Antipolis), 8–21.

Callou, C. (2003). De la garenne au clapier: Étude archéozoologique du Lapin en Europe occidentale. *Mus. Natl. Hist. Nat.* 189:356.

Camarós, E., Cueto, M., Rosell, J., Díez, J. C., Blasco, R., Duhig, C., et al. (2017). Hunted or scavenged Neanderthals? Taphonomic approach to hominin fossils with carnivore damage. *Int. J. Osteoarchaeol.* 27, 606–620. doi: 10.1002/oa.2584

Capaldo, S. D., and Blumenschine, R. J. (1994). A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* 59, 724–748. doi: 10.2307/282345

Carvalho, M., Pereira, T., and Manso, C. (2018). Rabbit exploitation in the middle Paleolithic at Gruta Nova da Columbeira, Portugal. *J. Archaeol. Sci. Rep.* 21, 821–832. doi: 10.1016/j.jasrep.2018.09.003

Cochard, D. (2004). Etude taphonomique des léporidés d'une tanière de renard actuelle: apport d'un référentiel à la reconnaissance des accumulations anthropiques. *Rev. Paléobiol.* 23, 659—673.

Cochard, D., Brugal, J.-P., Morin, E., and Meignen, L. (2012). Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. *Quat. Int.* 264, 32–51. doi: 10.1016/j.quaint.2012.02.014

Cohen, B. F., and Kibii, J. M. (2015). Experimental study of bone modification by captive caracal (*Caracal caracal*); a model for fossil assemblage analysis. *J. Archaeol. Sci.* 62, 92–104. doi: 10.1016/j.jas.2015.07.008

Daujeard, C., Fernandes, P., Guadelli, J. L., Moncel, M. H., Santagata, C., Raynal, J. P., et al. (2012). Neanderthal subsistence strategies in Southeastern France between the plains of the Rhone Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). *Quat. Int.* 252, 32–47. doi: 10.1016/j.quaint.2011.01.047

Daujeard, C., and Moncel, M.-H. (2010). On neanderthal subsistence strategies and land use: a regional focus on the Rhone Valley area in southeastern France. *J. Anthropol. Archaeol.* 29, 368–391. doi: 10.1016/j.jaa.2010.05.002

Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., et al. (2019). Neanderthal selective hunting of reindeer? The case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011. doi: 10.1007/s12520-017-0580-8

Delibes, M., and Hiraldo, F. (1981). "The rabbit as prey in the Iberian Mediterranean ecosystem," in *Proceedings of the world lagomorph conference*, *Vol. 1979* (Guelph: University of Guelph), 614–622.

Dodson, P., and Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology* 5, 275–284. doi: 10.1017/S0094837300006564

Duveau, J., Berillon, G., Verna, C., Laisné, G., and Cliquet, D. (2019). The composition of a Neandertal social group revealed by the hominin footprints at Le Rozel (Normandy, France). *Proc. Nat. Acad. Sci.* 116, 19409–19414. doi: 10.1073/pnas.1901789116

Fernández Jalvo, Y., Andrews, P., and Denys, S. C. (1999). Cut marks on small mammals at Olduvay Gorge Bed I. *J. Hum. Evol.* 36, 587–589. doi: 10.1006/jhev.1999.0292

Fernandez-Jalvo, Y., and Andrews, P. (2016). *Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification*. Cham: Springer. doi: 10.1007/978-94-017-7432-1

Fisher, D. C. (1995). Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory* 2, 7–68. doi: 10.1007/BF02228434

Gabucio, M. J., Bargalló, A., Saladié, P., Romagnoli, F., Chacón, M. G., Vallverdú, J., et al. (2023). Using GIS and geostatistical techniques to identify Neanderthal Campsites at archaeolevel Ob at Abric Romaní. *Archaeol. Anthropol. Sci.* 15:24. doi: 10.1007/s12520-023-01715-6

Gabucio, M. J., Cáceres, I., Rodríguez-Hidalgo, A., Rosell, J., and Saladié, P. (2014). A wildcat (*Felis silvestris*) butchered by Neanderthals in Level O of the Abric Romaní site (Capellades, Barcelona, Spain). *Quat. Int.* 326–327, 307–318. doi: 10.1016/j.quaint.2013.10.051

Gabucio, M. J., Sanz, M., and Daura, J. (2024). Lynxes and foxes among hyenas, bears and humans. Unit 3 of the Cova del coll Verdaguer Upper Pleistocene site (Barcelona, Iberian Peninsula). *Quat. Sci. Rev.* 333:108671. doi: 10.1016/j.quascirev.2024.108671

Gaudzinski-Windheuser, S., and Kindler, L. (2012). Research perspectives for the study of Neandertal subsistence strategies based on the analysis of archaeozoological assemblages. *Quat. Int.* 247, 59–68. doi: 10.1016/j.quaint.2010.11.029

Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garaizar, J., et al. (2018). First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* 8:10551. doi: 10.1038/s41598-018-28377-y

Gutiérrez-Zugasti, I., Rios-Garaizar, J., Marín-Arroyo, A. B., Rasines del Río, P., Maroto, J., Jones, J. R., et al. (2018). A chrono-cultural reassessment of the levels VI–XIV from El Cuco rock-shelter: a new sequence for the Late Middle Paleolithic in the Cantabrian region (northern Iberia). *Quat. Int.* 474, 44–55. doi: 10.1016/j.quaint.2017.06.059

Hardy, B. L., Moncel, M.-H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., et al. (2013). Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). *Quat. Sci. Rev.* 82, 23–40. doi: 10.1016/j.quascirev.2013.09.028

Haynes, G. (1980). Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. *Paleobiology* 6, 341–351. doi: 10.1017/S0094837300006849

Herranz-Rodrigo, D., Estaca-Gómez, V., Torres, T., de Baena, J., and Yravedra J. (2024). El aprovechamiento de *Ursus spelaeus* en el Paleolítico Medio. Novedades desde la cueva de El Esquilléu (Cillórigo de Liébana, Cantabria). *ZEPHYRVS. XCII*, 161–173.

Hockett, B., and Haws, J. (2002). Taphonomic and methodological perspectives of leporid hunting during the upper Paleolithic of the Western Mediterranean basin. *J. Archaeol. Method Theory*. 9, 269–302. doi: 10.1023/A:1019503030246

Hockett, B. S. (1996). Corroded, thinned and polished bones created by golden eagles (*Aquila chrysaetos*): taphonomic implications for archaeological interpretations. *J. Archaeol. Sci.* 23, 587–591. doi: 10.1006/jasc.1996.0055

Hockett, B. S., and Bicho, N. F. (2000). The rabbits of picareiro cave: small mammal hunting during the late upper palaeolithic in the Portuguese estremadura. *J. Archaeol. Sci.* 27, 715–723. doi: 10.1006/jasc.1999.0496

Hussain, S. T., Weiss, M., and Nielsen, T. K. (2022). Being-with other predators: cultural negotiations of Neanderthal-carnivore relationships in Late Pleistocene Europe. *J. Anthropol. Archaeol.* 66:101409. doi: 10.1016/j.jaa.2022.101409

Jones, E. L. (2006). Prey choice, mass collecting, and the wild European rabbit (*Oryctolagus cuniculus*). *J. Anthropol. Archaeol.* 25, 275–289. doi: 10.1016/j.jaa.2005.11.002

Kassambara, A., and Mundt, F. (2020). *_factoextra: Extract and Visualize the Results of Multivariate Data Analyses_. R package version 1.0.7.* Available at: https://CRAN.R-project.org/package=factoextra (accessed July, 2024).

Krajcarz, M., and Krajcarz, M. T. (2012). The Red Fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. *Int. J. Osteoarchaeol.* 24, 459–475. doi: 10.1002/oa.2233

Kuhn, M. (2008). Building predictive models in R using the caret package. *J. Stat. Softw.* 28, 1–26. doi: 10.18637/jss.v028.i05

Kuhn, M., and Johnson, K. (2013). *Applied Predictive Modeling, Vol. 26*. New York, NY: Springer, 13. doi: 10.1007/978-1-4614-6849-3

Landt, M. J. (2007). Tooth marks and human consumption: ethnoarchaeological mastication research among foragers of the Central African Republic. *J. Archaeol. Sci.* 34, 1629–1640. doi: 10.1016/j.jas.2006.12.001

Lattao, V., Hipólito, C. G., Hugo, G. S. G., Maria, H., Elena, M., Pierluigi, R., et al. (2023). *Cave sediments stable isotopic analysis to attempt an environmental reconstruction: the case of Cadaval and Escoural (Portugal) and Postes (Spain) caves XI*. Coimbra: Congresso Nacional de Geologia.

Le, S., Josse, J., and Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25, 1–18. doi: 10.18637/jss.v025.i01

Liaw, A., and Wiener, M. (2002). Classification and regression by random forest. *R News* 2, 18–22.

Linares-Matás, G. J., and Yravedra, J. (2024). Competing forces: Subsistence strategies and human-carnivore interactions during the middle to Upper Palaeolithic transition in Northern Iberia. *Quat. Sci. Rev.* 334:108703. doi: 10.1016/j.quascirev.2024.108703

Livraghi, A., Fanfarillo, G., Colle, M. D., Romandini, M., and Peresani, M. (2021). Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: a study on De Nadale cave, Italy. *Quat. Int.* 586, 24–41. doi: 10.1016/j.quaint.2019.11.024

Lloveras, L., Moreno García, M., and Soler i Masferrer, N. (2010). The application of actualistic studies to assess the taphonomic origin of Musterian rabbit accumulations from Arbreda Cave (North-East Iberia). *Archaeofauna Int. J. Archaeozool.* 19, 99–119.

Lloveras, L., Moreno-Garcia, M., and Nadal, J. (2008a). Taphonomic study of leporid remains accumulated by the Spanish Imperial Eagle (*Aquila adalberti*). *Geobios* 41, 91–100. doi: 10.1016/j.geobios.2006.11.009

Lloveras, L., Moreno-García, M., and Nadal, J. (2008b). Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats. *J. Archaeol. Sci.* 35, 1–13. doi: 10.1016/j.jas.2007.02.005

Lloveras, L., Moreno-García, M., and Nadal, J. (2009). The eagle owl (*Bubo bubo*) as a leporid remains accumulator: taphonomic analysis of modern rabbit remains recovered from nests of this predator. *Int. J. Osteoarchaeol.* 19, 573–592. doi: 10.1002/oa.995

Lloveras, L., Moreno-García, M., and Nadal, J. (2012a). Assessing the variability in taphonomic studies of modern leporid remains from Eagle Owl (*Bubo bubo*) nest assemblages: the importance of age of prey. *J. Archaeol. Sci.* 39, 3754–3764. doi: 10.1016/j.jas.2012.06.033

Lloveras, L., Moreno-García, M., and Nadal, J. (2012b). Feeding the foxes: an experimental study to assess their taphonomic signature on leporid remains. *Int. J. Osteoarchaeol.* 22, 577–590. doi: 10.1002/oa.1280

Lloveras, L., Moreno-García, M., Nadal, J., and Thomas, R. (2014). Blind test evaluation of accuracy in the identification and quantification of digestion corrosion damage on leporid bones. *Quat. Int.* 330, 150–155. doi: 10.1016/j.quaint.2013.07.033

Lloveras, L., Nadal, J., and Fullola, J. M. (2020). Distinguishing the taphonomic signature of wolves from humans and other predators on small prey assemblages. *Sci. Rep.* 10:8030. doi: 10.1038/s41598-020-64716-8

Lloveras, L., Thomas, R., Cosso, A., Pinyol, C., and Nadal, J. (2016). When wildcats feed on rabbits: an experimental study to understand the taphonomic signature of European wildcats (*Felis silvestris silvestris*). *Archaeol. Anthropol. Sci.* 10, 449–464. doi: 10.1007/s12520-016-0364-6

Lyman, R. L. (1994). Relative abundance of skeletal specimens and taphonomic analysis of vertebrate remains. *Palaios* 9, 288–298. doi: 10.2307/3515203

Lyman, R. L. (2008). *Quantitative Paleozoology*. Cambridge, MA: Cambridge University Press. doi: 10.1017/CBO9780511813863

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. (2023). *cluster: Cluster Analysis Basics and Extensions*. R package version 2.1.6.

Marean, C. W., Abe, Y., Nilssen, P. J., and Stone, E. C. (2001). Estimating the minimum number of skeletal elements (MNE) in zooarchaeology: a review and a new image-analysis GIS approach. *Am. Antiq.* 66, 333–348. doi: 10.2307/2694612

Marín, J., Daujeard, C., Saladié, P., Rodríguez-Hidalgo, A., Vettese, D., Rivals, F., et al. (2020). Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). *Quat. Sci. Rev.* 243:106472. doi: 10.1016/j.quascirev.2020.106472

Marín, J., Rodríguez-Hidalgo, A., Vallverdú, J., de Soler, B. G., Rivals, F., Rabuñal, J. R., et al. (2019). Neanderthal logistic mobility during MIS3: zooarchaeological perspective of Abric Romaní level P (Spain). *Quat. Sci. Rev.* 225:106033. doi: 10.1016/j.quascirev.2019.106033

Marín, J., Saladié, P., Rodríguez-Hidalgo, A., and Carbonell, E. (2017). Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence. *PLoS ONE* 12:e0186970. doi: 10.1371/journal.pone.0186970

Marwick, B. (2017). Computational reproducibility in archaeological research: basic principles and a case study of their implementation. *J. Archaeol. Method Theory*, 24, 424–450. doi: 10.1007/s10816-015-9272-9

Marwick, B., Boettiger, C., and Mullen, L. (2018). Packaging data analytical work reproducibly using R (and friends). *Am. Stat.* 72, 80–88. doi: 10.1080/00031305.2017.1375986

Massigoge, A., Gutierrez, M. A., Alvarez, M. C., Kaufmann, C. A., Rafuse, D. J., Gonzalez, M. E., et al. (2014). Estudio comparativo de las marcas de dientes producidas por dos pequeños carnívoros sudamericanos. *Rev. Chil. Antropol.* doi: 10.5354/0719-1472.2014.36264

McPherron, S. P. (2022). *E5 [Computer software]*. Available at: https://github.com/surf3s/E5 (accessed November, 2023).

Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., and Leisch, F. (2023). *_e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien_*. R package version 1.7-14. Available at: https://CRAN.R-project.org/package=e1071 (accessed July, 2024).

Moncel, M. H., Fernandes, P., Willmes, M., James, H., and Grün, R. (2019). Rocks, teeth, and tools: new insights into early Neanderthal mobility strategies in South-Eastern France from lithic reconstructions and strontium isotope analysis. *PLoS ONE* 14:e0214925. doi: 10.1371/journal.pone.0214925

Nabais, M., and Zilhão, J. (2019). The consumption of tortoise among last interglacial Iberian Neanderthals. *Quat. Sci. Rev.* 217, 225–246. doi: 10.1016/j.quascirev.2019.03.024

Otte, M., and da Silva, A. C. (Eds.). (1996). *Recherches préhistoriques à la grotte d'Escoural, Portugal*. Liège: Service de Préhistoire, Université de Liège.

Pavao, B., and Stahl, P. (1999). Structural density assays of leporid skeletal elements with implications for taphonomic, actualistic and archaeological research. *J. Archaeol. Sci.* 26, 53–66. doi: 10.1006/jasc.1998.0299

Pelletier, M., Brugal, J.-P., Cochard, D., Lenoble, A., Mallye, J.-B., Royer, A., et al. (2016). Identifying fossil rabbit warrens: insights from a taphonomical analysis of a modern warren. *J. Archaeol. Sci. Rep.* 10, 331–344. doi: 10.1016/j.jasrep.2016.10.016

Pelletier, M., Desclaux, E., Brugal, J.-P., and Texier, P.-J. (2019). The exploitation of rabbits for food and pelts by last interglacial Neandertals. *Quat. Sci. Rev.* 2019:105972. doi: 10.1016/j.quascirev.2019.105972

Pérez Ripoll, M. (1977). *Los mamíferos del yacimiento musteriense de Cova Negra (Játiva, Valencia), Serie Trabajos Varios S.I.P. 23*. Valencia: Diputación de Valencia.

Pérez Ripoll, M. (1992). *Marcas de Carnívoros, fracturas incipientes y mordeduras de carnívoros en huesos prehistóricos del Mediterráneo español*. Alicante: Instituto de Cultura, Juan Gil-Albert (Colección Patrimonio).

Pérez Ripoll, M. (2001). "Les marques antròpiques en ossos de conill," in *De Neandertals a Cromanyons: l'inici del Poblament Humà a les Terres Valencianes*, ed. V. Villaverde (València: Universitat de València), 119–124.

Pérez, L., Sanchis, A., Hernández, C. M., Galván, B., Sala, R., Mallol, C., et al. (2017). Hearths and bones: an experimental study to explore temporality in archaeological contexts based on taphonomical changes in burnt bones. *J. Archaeol. Sci. Rep.* 11, 287–309. doi: 10.1016/j.jasrep.2016.11.036

Picin, A., Blasco, R., Arilla, M., Rivals, F., Chacón, M. G., Gómez de Soler, B., et al. (2020). "Short-term Neanderthal occupations and carnivores in the Northeast of Iberian Peninsula," in *Short-term Occupations in Paleolithic Archaeology: Definition and Interpretation*, eds. J. Cascalheira, and A. Picin (Cham: Springer), 183–213. doi: 10.1007/978-3-030-27403-0_8

Pickering, T. R., and Egeland, C. P. (2006). Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33, 459–469. doi: 10.1016/j.jas.2005.09.001

Pinto-Llona, A. C., Estaca, V., Grandal-d'Anglade, A., Romero, A. J., and Yravedra, J. (2023). Alternation between humans and carnivores in the occupations of the Mousterian site of Sopeña rock-shelter (Asturias, Spain). *Quat. Sci. Rev.* 108468. doi: 10.1016/j.quascirev.2023.108468

Real, C. (2020). Rabbit: more than the Magdalenian main dish in the Iberian Mediterranean region. new data from Cova de les Cendres (Alicante, Spain). *J. Archaeol. Sci. Rep.* 32:102388. doi: 10.1016/j.jasrep.2020.102388

Reitz, E. J., and Wing, E. S. (1999). *Zooarchaeology*. Cambridge University Press.

Richards, M., Pettitt, P., Trinkaus, E., Smith, F., Paunović, M., Karavanić, I., et al. (2000). Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *Proc. Natl. Acad. Sci. USA*. 97, 7663–7666. doi: 10.1073/pnas.120178997

Ripoll, M. P. (2004). "La consommation humaine des lapins pendant le Paléolithique dans la région de Valencia (Espagne) et l'étude des niveaux gravétiens de La Cova de les Cendres (Alicante)," in *Actes des XXIV rencontres internationales d'Archéologie et d'Histoire d'Antibes* (Antibes: Editions APDCA), 191–206.

Rivals, F., Bocherens, H., Camarós, E., and Rosell, J. (2022). "Diet and ecological interactions in the Middle and Late Pleistocene," in *Updating Neanderthals* (Academic Press), 39–54.

Rodríguez-Hidalgo, A. (2022). Comments on 'Hyaenids, felids and canids as bone accumulators: Does the natural history of extant species support zooarchaeological inferences?', by Palomares et al. [Quat. Sci. Rev. 284 (2022) 107459]. *Quatern. Sci. Rev.* 295:107632. doi: 10.1016/j.quascirev.2022.107632

Rodríguez-Hidalgo, A., Lloveras, L., Moreno-García, M., Saladié, P., Canals, A., Nadal, J., et al. (2013). Feeding behaviour and taphonomic characterization of non-ingested rabbit remains produced by the Iberian lynx (*Lynx pardinus*). *J. Archaeol. Sci.* 40, 3031–3045. doi: 10.1016/j.jas.2013.03.006

Rodríguez-Hidalgo, A., Saladié, P., Marín, J., and Canals, A. (2015). Expansion of the referential framework for the rabbit fossil accumulations generated by Iberian lynx. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 418, 1–11. doi: 10.1016/j.palaeo.2014.11.010

Rodríguez-Hidalgo, A., Sanz, M., Daura, J., and Sánchez-Marco, A. (2020). Taphonomic criteria for identifying Iberian lynx dens in quaternary deposits. *Sci. Rep.* 10:7225. doi: 10.1038/s41598-020-63908-6

Roebroeks, W., and Soressi, M. (2016). Neandertals revised. *Proc. Nat. Acad. Sci.* 113, 6372–6379. doi: 10.1073/pnas.1521269113

Romandini, M., Silvestrini, S., Real, C., Lugli, F., Tassoni, L., Carrera, L., et al. (2023). Late Neanderthal "menu" from northern to southern Italy: freshwater and terrestrial animal resources. *Quat. Sci. Rev*. 2023:108233. doi: 10.1016/j.quascirev.2023.108233

Rosell, J., Blasco, R., Rivals, F., Chacón, M. G., Arilla, M., Camarós, E., et al. (2017). A resilient landscape at Teixoneres Cave (MIS 3; Moià, Barcelona, Spain): the Neanderthals as disrupting agent. *Quatern. Int.* 435, 195–210. doi: 10.1016/j.quaint.2015.11.077

Rufà, A., Blasco, R., Rivals, F., and Rosell, J. (2014). Leporids as a potential resource for predators (hominins, mammalian carnivores, raptors): an example of mixed contribution from level III of Teixoneres Cave (MIS 3, Barcelona, Spain). *Comptes Rendus Palevol*. 13, 665–680. doi: 10.1016/j.crpv.2014.06.001

Russo, G., Milks, A., Leder, D., Koddenberg, T., Starkovich, B. M., Duval, M., et al. y Terberger, T. (2023). First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals. *Sci. Rep.* 13:16405. doi: 10.1038/s41598-023-42764-0

Saladié, P., Rodríguez-Hidalgo, A., Marín, J., i Poch, J. V., and Carbonell, E. (2018). The top of the Gran Dolina (Atapuerca, Spain) sequence: a zooarchaeological and occupational perspective. *Quatern. Sci. Rev.* 195, 48–71. doi: 10.1016/j.quascirev.2018.07.010

Saladié, P., Rosas, A., García-Tabernero, A., Fidalgo, D., Fero Meñe, M., Ebana Ebana, C., et al. (2024). An actualistic taphonomic model of human tooth marks on bone remains: a sample recovered in villages of continental Equatorial Guinea. *J. Archaeol. Sci. Rep.* 55:104514. doi: 10.1016/j.jasrep.2024.104514

Sanchis Serra, A., and Pascual Benito, J. L. (2011). Análisis de las acumulaciones óseas de una guarida de pequeños mamíferos carnívoros (Sitjar Baix, Onda, Castellón): implicaciones arqueológicas. *Archaeofauna* 20, 47–71. doi: 10.15366/archaeofauna2011.20.003

Sanchis, A. (1999). *Análisis tafonómico de los restos de Oryctolagus cuniculus a partir de la alimentación de Bubo bubo y Vulpes vulpes y su comparación con materiales antrópicos* (Degree Thesis). València: Universitat de València, 260.

Sanchis, A., Morales Pérez, J., and PérEZ-riPoll, M. (2011). "Creación de un referente experimental para el estudio de las alteraciones causadas por dientes humanos sobre huesos de conejo," in *Actas Del Segundo Congreso Internacional de Arqueología Experimental*, *Ronda, Málaga*, eds. A. Morgado, J. Baena, and D. García (Granada: Universidad de Granada), 343–349.

Scheifler, N. A., Álvarez, M. C., Rafuse, D. J., Kaufmann, C. A., Massigoge, A., González, M. E., et al. (2020). Taphonomic signature of Geoffroy's cat (*Leopardus geoffroyi*) on small sized preys: a comparative study of ingested and non-ingested leporid bones. *J. Archaeol. Sci. Rep.* 31:102340. doi: 10.1016/j.jasrep.2020.102340

Schmitt, D. N., and Juell, K. E. (1994). Toward the identification of coyote scatological faunal accumulations in archaeological contexts. *J. Archaeol. Sci.* 21, 249–262. doi: 10.1006/jasc.1994.1025

Seuru, S., Burke, A., and Perez, L. (2024). Evidence of an age and/or gender-based division of labor during the Last Glacial Maximum in Iberia through rabbit hunting. *J. Archaeol. Sci. Rep.* 56:104560. doi: 10.1016/j.jasrep.2024.104560

Skov, L., Peyrégne, S., Popli, D., Iasi, L. N. M., Devièse, T., Slon, V., et al. (2022). Genetic insights into the social organization of Neanderthals. *Nature* 610, 519–525. doi: 10.1038/s41586-022-05283-y

Smith, G. M. (2014). Neanderthal megafaunal exploitation in Western Europe and its dietary implications: a contextual reassessment of La Cotte de St Brelade (Jersey). *J. Hum. Evol.* 10:007. doi: 10.1016/j.jhevol.2014.10.007

Stekhoven, D. J., and Buehlmann, P. (2012). MissForest - non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28, 112–118. doi: 10.1093/bioinformatics/btr597

Stiner, M. C., Munro, N. D., and Surovell, T. A. (2000). The tortoise and hare. Small-game use, the broad-spectrum revolution, and paleolithic demography. *Curr. Anthropol.* 41, 39–73. doi: 10.1086/300102

Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E., and Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal explotation. *Science* 283, 190–193. doi: 10.1126/science.283.5399.190

Téllez, E., Saladié, P., Pineda, A., Marín, J., Vallverdú, J., Chacón, M. G., et al. (2022). Incidental burning on bones by Neanderthals: the role of fire in the Qa level of Abric Romaní rock-shelter (Spain). *Archaeol. Anthropol. Sci.* 14:119. doi: 10.1007/s12520-022-01577-4

Vabalas, A., Gowen, E., Poliakoff, E., and Casson, A. J. (2019). Machine learning algorithm validation with a limited sample size. *PLoS ONE* 14:e0224365. doi: 10.1371/journal.pone.0224365

Valde-Nowak, P., and Cieśla, M. (2020). "Models of raw material exploitation as an indicator of middle paleolithic mobility: case studies from uplands of Northern Central Europe," in *Short-term occupations in Paleolithic archaeology: Definition and Interpretation*, eds. J. Cascalheira, and A. Picin (Cham: Springer), 105–120. doi: 10.1007/978-3-030-27403-0_5

Vaquero, M. (2022). "The organisation of living spaces in Neanderthal campsites," in *Updating Neanderthals* (New York, NY: Academic Press), 207–225. doi: 10.1016/B978-0-12-821428-2.00001-9

Villa, P., Castel, J. C., Beauval, C., Bourdillat, V., and Goldberg, P. (2004). Human and carnivore sites in the European Middle and Upper Paleolithic: similarities and differences in bone modification and fragmentation. *Rev. Paléobiol.* 23, 705–730.

Villa, P., and Mahieu, E. (1991). Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48. doi: 10.1016/0047-2484(91)90034-S

White, T. E. (1953). A method of calculating the dietary percentage of various food animals utilized by aboriginal peoples. *Am. Antiq.* 18, 396–398. doi: 10.2307/277116

Wickham, H. (2015). *R Packages: Organize, Test, Document, and Share Your Code.* Sebastopol, CA: O'ReillyMedia. Inc.

Yravedra, J. (2004). "Implications taphonomiques des modifications osseuses faites par les vrais Hiboux (*Bubo bubo*) sur les lapins," in *Pettits animaux et sociétés. Du complement alimentaire aux ressources utilitaires XXIV. Reencontres Internationales d'Archeologie et d'histoire d'Antibes, eds.* J. P. Brugal and J. Desse (Antibes: APDCA), 321–323. I.S.B.N. 2-904110-38-0

Yravedra, J. (2006). Acumulaciones biológicas en yacimientos arqueológicos: amalda VII y esquilleu III-IV. *Trabajos Prehist.* 63, 55–78.

Yravedra, J. (2008). Los lagomorfos como recurso alimenticio en Cueva de Ambrosio (Almería, España). *Zephirus* 61, 63–80.

Yravedra, J., and Andrés, M. (2013). "Estrategias de subsistencia entre los grupos magdalenienses de La Peña de Estebanvela (Ayllón, Segovia)," in *Ocupaciones Magdaleniense en el Interior de la Península Ibérica*, ed. C. Cacho (Ayllón: La Peña de Estebanvela), 213–244. ISBN: 978-84-616-5992-0.

Yravedra, J., and Cobo-Sánchez, L. (2015). Neanderthal exploitation of ibex and chamois in southwestern Europe. *J. Hum. Evol.* 78, 12–32. doi: 10.1016/j.jhevol.2014.10.002

Yravedra, J., and Domínguez-Rodrigo, M. (2009). The shaft-based methodological approach to the quantification of long limb bones and its relevance to understanding hominid subsistence in the Pleistocene: application to four Palaeolithic sites. *J. Quat. Sci.* 24, 85–96. doi: 10.1002/jqs.1164

Yravedra, J., Estaca-Gómez, V., Grandal-d'Anglade, A., and Pinto-Llona, A. C. (2024). Neanderthal subsistence strategies: new evidence from the Mousterian Level XV of the Sopeña rock shelter (Asturias, northern Spain). *Archaeol. Anthropol. Sci.* 16:6. doi: 10.1007/s12520-023-01914-1

Yravedra, J., Herranz, D., Sesé, C., López-Cisneros, P., Linares-Matás, G. J., Pernas-Hernández, M., et al. (2019). Lagomorph exploitation during the upper Palaeolithic in the Northern Iberian Peninsula. new evidence from Coímbre Cave (Asturias, Spain). *Quat. Int.* 506, 59–68. doi: 10.1016/j.quaint.2018.06.016

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Hunters of the "Mediterranean Triad": persistent and intensive exploitation of faunal resources during the Late Middle Pleistocene at Cueva del Ángel (Lucena, Spain)

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This study focuses on the Neanderthal subsistence strategies at Cueva del Ángel, a site in southern Spain with a stratigraphic sequence from the Late Middle Pleistocene. Using zooarchaeological and taphonomic methodologies, we conducted a diachronic analysis of over 3,500 faunal remains to explore the exploitation patterns of medium- and large-sized ungulates. Results reveal a systematic and intensive exploitation of large mammals, particularly horses, red deer, and large bovids, with an emphasis on high-energy resources, such as meat and marrow. The anatomical representation and fragmentation patterns suggest selective hunting strategies and an intensive use of animal resources. Complementary resources, such as small game, were also exploited, potentially reflecting adaptive responses to increase predictability and minimize risks. The results align with other Eurasian sites from this period, emphasizing the persistence of large-game hunting as a core subsistence strategy, supplemented by diversified resources to mitigate risk. These findings underscore a consistent and flexible approach to resource management over time, highlighting the adaptability of Neanderthal subsistence strategies in Mediterranean ecosystems.

KEYWORDS

big game, faunal exploitation, subsistence strategies, persistent behavior, Middle Pleistocene, southern Spain

1 Introduction

In Western Eurasia, archaeological sites with substantial stratigraphic depth during the Middle Pleistocene are scarce, especially in the first half. However, the number of such sites increases in the second half around MIS 12-11, providing wider perspectives and revealing a distinct change in subsistence strategies (Chazan, 2009; Villa and Lenoir, 2009). These changes are likely related to climate and paleoenvironment (Blain et al., 2021), the emergence of fire technology (Rolland, 2000; Gowlett, 2006; Karkanas et al., 2007; Roebroeks and Villa, 2011; Shimelmitz et al., 2014; Rosell and Blasco, 2019), the appearance of post-Acheulean technocomplexes (Moncel et al., 2015, 2021; Kuhn et al., 2021), a transition from the exploitation of megafauna to large-medium-sized animals (Gaudzinski-Windheuser and Niven, 2009; Gaudzinski-Windheuser and Kindler, 2012a,b; Lee-Thorp et al., 2015; White et al., 2016; Kuhn and Stiner, 2019) and to broad-spectrum diets (Stiner, 2004b; Blasco, 2008; Blasco and Peris, 2009; Nabais and Zilhão, 2019; Nabais et al., 2023a).

Our current understanding of Neanderthal hunting and exploitation strategies is that they were based on the exploitation of large ungulates through selective and/or opportunistic behavior, depending on the context and species (Rendu, 2022). In the Mediterranean region, this was complemented by a more diverse diet that included rabbits, tortoises, birds, and shellfish for various purposes—dietary, aesthetic, and symbolic—that reflect flexible behavior in different environments and regions (Zilhão et al., 2020; Blasco et al., 2022; Moigne et al., 2023). One of the key aspects that has been proposed is the 'mono-specific' exploitation of large-medium-sized adult animals, particularly during the temperate isotopic stages MIS 9 and 7 (Gaudzinski, 2006; Gaudzinski-Windheuser and Kindler, 2012a), supported by the high energy returns they provided, which in turn required a high degree of flexibility in the tactics employed (Gaudzinski-Windheuser and Niven, 2009). In addition to this selective behavior, zooarchaeological and taphonomic analyses point toward intensive and systematic exploitation strategies (Yravedra-Sainz de los Terreros et al., 2016; Vettese et al., 2017; Marín et al., 2020; Linares-Matás and Yravedra, 2024). In this regard, significant advancements have been made in recent decades regarding the understanding of exploitation strategies for Faunal resources during the Middle Paleolithic. Some studies illustrate the massive communal hunting of bison (Rodríguez-Hidalgo et al., 2016), the exploitation of large bovids (Jaubert et al., 1990; van Kolfschoten et al., 2015, 2018; Rivière et al., 2023) and horses (Diedrich, 2010; Hutson et al., 2020; Pope et al., 2020; Uzunidis, 2020), as well as the predominance of deer or reindeer (Daujeard et al., 2019; Valensi et al., 2022; Rendu et al., 2023; Ruebens et al., 2023; Silvestrini et al., 2024) and the exploitation of medium-sized ungulates (Yravedra and Cobo-Sánchez, 2015). The abundance of these taxa in their various combinations, both in open-air sites and caves, underscores their significance in diet and derived products, while also acknowledging the complementary and diverse introduction of small animals (Hardy and Moncel, 2011; Blasco et al., 2016; Negro et al., 2016; Lebreton et al., 2017; Morin et al., 2019; Nabais and Zilhão, 2019; Crater Gershtein et al., 2022; Nabais et al., 2023b,a). However, diachronic analyses of complete sequences (Stiner et al., 2011; Niven, 2013; García-Medrano et al., 2017; Starkovich, 2017; Roditi and Starkovich, 2022; Berlioz et al., 2023) which would allow us to better understand the evolution of these strategies, remain scarce.

The Cueva del Ángel site in southern Spain features a robust and rich stratigraphic sequence from the Late Middle Pleistocene, offering opportunities for diachronic analyses of the subsistence strategies and lifestyles of its inhabitants. Previous studies highlight the site's long and intensive occupation as a habitat (Botella Ortega et al., 2006; Barroso Ruíz et al., 2011), evidence of fire use (Monge et al., 2016, 2020), the presence of bone retouchers (Moigne et al., 2016) and the extensive and sustained exploitation of animal resources (Solano García, 2024). The emergence of broad-spectrum diets during the Middle Pleistocene somewhat overshadowed the dominance of large mammals as the primary sources of food and resource exploitation. We now know that hunting strategies were well established (Gaudzinski-Windheuser et al., 2018) and that a significant portion of the diet was based on meat resources (Jaouen et al., 2019; Wißing et al., 2019), though the supplementary importance of other sources should not be overlooked (Hardy et al., 2022). Cueva del Ángel is no exception to the trends and innovations that began in MIS 11, which enrich and complicate our understanding of human behavior. In this context, it is necessary to explore the role that ungulates played over time and to search for possible long-term patterns that could help us infer continuities or discontinuities in subsistence strategies. This study aims to explore these patterns through the zooarchaeological analysis of ungulate species, their anatomical representation, and the degree of exploitation they underwent, within a broad temporal framework of analysis.

2 The site of Cueva del Ángel

The Cueva del Ángel is located at 605 m above sea level on the southern slope of a paleogeographical highland (Sierra de Aras; Figure 1B), flanked by two small fluvial valleys to the north and south, which flow into the Genil River. This range forms part of the western foothills of the Subbética mountain range in the province of Córdoba, 5 km south of the town of Lucena (Figure 1A). The karst complex, developed along a fault in Lower and Middle Jurassic limestones and dolomites, consists of three well-defined areas: (1) an open-air exterior platform where Middle Pleistocene deposits are found, which connects to (2) the inner entrance of the cave, leading to (3) a large, lower sinkhole. Currently, the Paleolithic site is located in the open-air section (area 1) due to the collapse of the cave's walls and roof at an unknown point in the past (Figure 1C). The site covers an area of ~100 m², with at least 5 m of sedimentary fill in the excavated area (Barroso Ruíz et al., 2011).

The site underwent two initial excavation campaigns in 1995 and 1996 to assess its potential, followed by numerous additional campaigns within broader multidisciplinary research projects between 2002 and 2018. During the early archaeological cleaning efforts, a trench and a 2-m diameter mining shaft (Figure 1D) were discovered, likely dating to the late 18th century (Botella Ortega et al., 2006). The existence of the shaft allowed for the rapid recovery of a stratigraphic sequence from the site's archaeological fill. The initial goal was to remove large limestone and breccia blocks from the shaft while simultaneously excavating its southern profile (trench K) to obtain the most complete stratigraphy possible. In subsequent campaigns, the possible base of the fill was reached, and the excavation area was expanded to adjacent grids (J7 and trench 8; Figure 2A).

2.1 Stratigraphy and geochronology

Between the mining trench and the excavation of the shaft (cross-section J/K), 17 stratigraphic units (I–XVII) have been documented with a thickness of more than 4 m, varying in thickness, color, and texture (Figure 2B). The average thickness is 18 cm ($\sigma = 9.3$) and ranges between 2 and 50 cm, with the lower levels having the greatest thickness. They exhibit frequent erosive contacts and a sub-horizontal or northeastward dipping arrangement (levels VII–XV), with a bulging morphology that suggests post-depositional collapse processes. The colors (Figure 2C) range from various shades of brown, gray, pink, and reddish hues, with a dominant texture of silts and sands

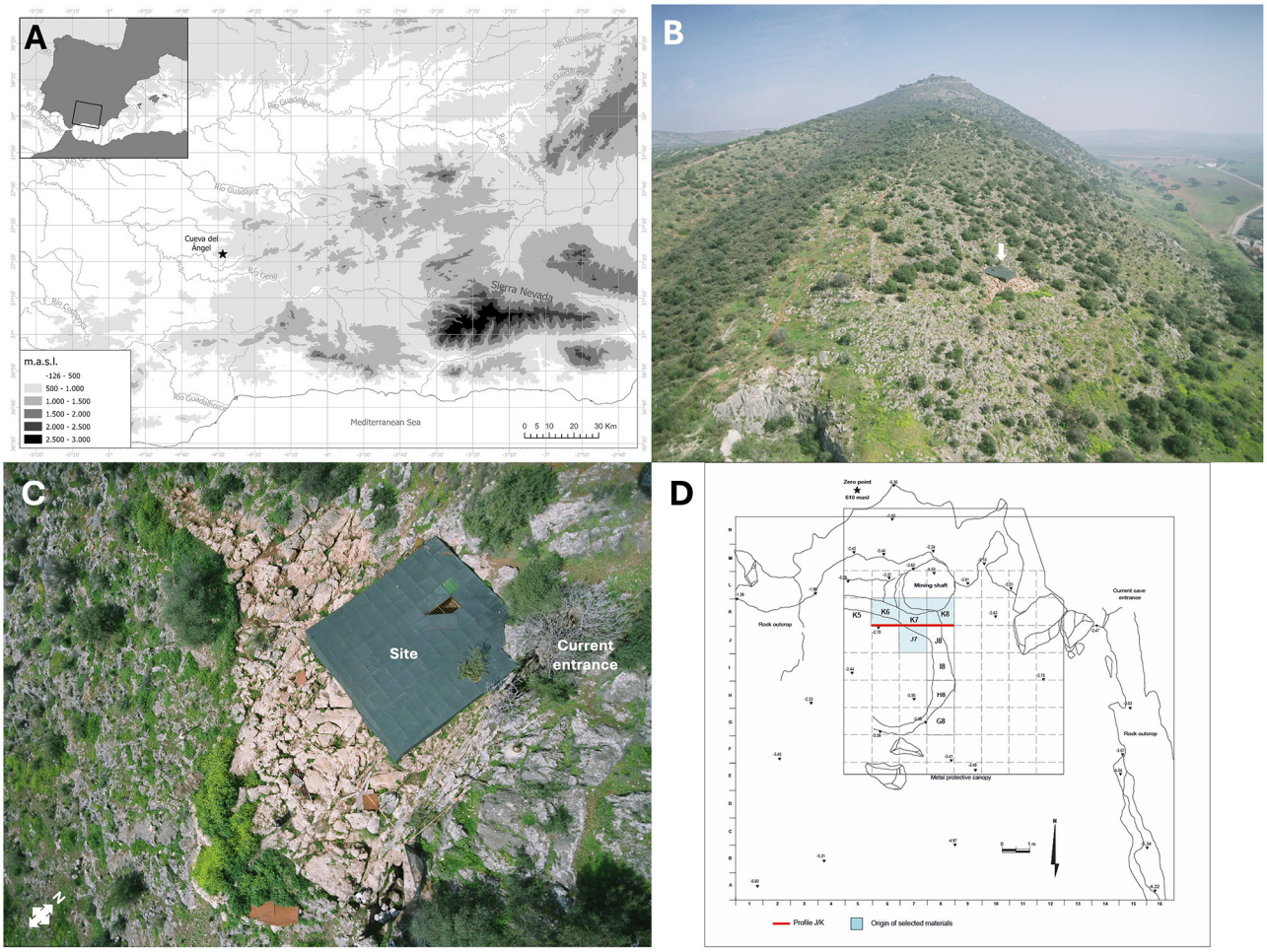

FIGURE 1
(A) Location map of the site. **(B)** Aerial view of the Sierra de Aras from the west, showing the location of the site. **(C)** Aerial view of the site. **(D)** Planimetry of the site area with indication of the selected grids and the corresponding stratigraphic profile (Photographs by D. Botella).

and a notable granular structure. The consistency is highly heterogeneous, varying from soft to hard depending on the extent of secondary calcite precipitation affecting each level. Porosity is generally absent or minimal (when present, it is always vacuolar in type), and the contacts between the layers are mostly sharp (Barroso Ruíz et al., 2011). So far, no hiatus has been detected in the stratigraphy.

Based on sedimentological, geomorphological, and geochemical analyses (Barroso Ruíz et al., 2011), it has been determined that this area (profile J/K) of the site was heavily exposed to anthropogenic fire activity. The stratigraphic units have been grouped into three major structural complexes (Monge et al., 2014): I (I–VII), II (VIII–XII), and III (XIII–XVII), with evidence suggesting a possible increase in thermo-alteration intensity from complex III to I, as indicated by the increase in organic carbon from complex III to I (Barroso Ruíz et al., 2011). In contrast, moving southward from this area, in trench 8, evidence of fire activity appears to be significantly lower (Monge et al., 2020). These data support the hypothesis of the existence of a recurrently used fireplace at the same location for thousands of years (Barroso Ruíz et al., 2011; Solano García, 2024). The presence of lithic industry remains and burned bone in all levels (Barroso Ruíz et al., 2011), along with low carnivore activity (Solano García, 2024) and the absence of guano (Monge et al., 2016), indicates a recurrent use of the site by human groups.

The chronology of the site was initially estimated to be over 130,000 years based on $^{230}Th/^{234}U$ dating of a sample from the upper part of the archaeological fill (Botella Ortega et al., 2006). The analysis of lithic industry and faunal spectrum suggested a broad chronological range from MIS 11 to MIS 5 (Barroso Ruíz et al., 2011; Moigne et al., 2016). Shortly afterward, a new series of ESR/U-series dates were published (Falguères et al., 2019) which, despite some limitations inherent to the method, identified ages ranging from MIS 9 to MIS 7, suggesting continuous human occupation between 320–180 ka. Recently, the discovery of a human tooth was reported (Bermúdez et al., 2023) which was dated using amino acid racemization and yielded a date of 104,300 years. However, the tooth came from a loose block from surface cleaning, possibly originating from previously eroded upper layers. Nevertheless, this date allows us to estimate an upper limit for the original fill, providing a timeframe from MIS-9/10 to MIS-5d, though the

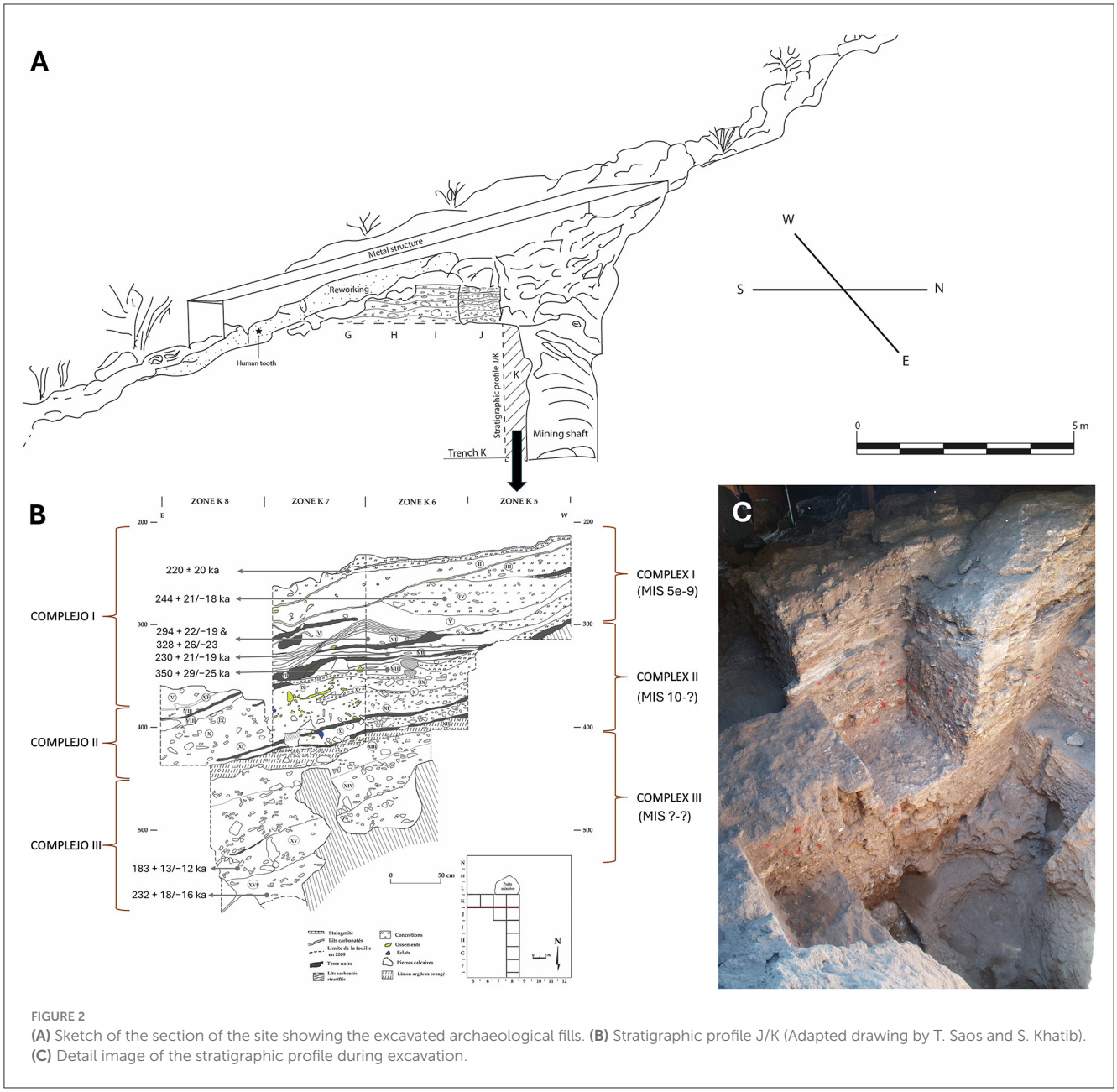

FIGURE 2
(A) Sketch of the section of the site showing the excavated archaeological fills. **(B)** Stratigraphic profile J/K (Adapted drawing by T. Saos and S. Khatib). **(C)** Detail image of the stratigraphic profile during excavation.

chronology of the lower part of the stratigraphic sequence remains uncertain (Figure 2B).

3 Materials and methods

Tackling large stratigraphic sequences in cave settings presents a challenge, primarily due to the presence of palimpsests (Bailey, 2007; Bailey and Galanidou, 2009) and the sheer volume of information. However, the goal of this study is not to dissect the palimpsests for high-resolution detail, but rather to obtain a diachronic overview of the long-term exploitation of ungulates. Despite this, the volume of data from the zooarchaeological and taphonomic analyses is substantial due to the number of stratigraphic units and species involved. Therefore, an exhaustive synthesis has been carried out by level and taxon to characterize and group the main ungulate species based on their skeletal recurrence and carcass treatment. This approach allows for the exploration of potential patterns of selection, standardization, or systematization in the exploitation processes.

3.1 Sample and materials background

In this study, remains from grids J7, K6, K7, and K8, which make up the J/K stratigraphic profile (Figure 1D), were used. We analyzed 3,700 remains, of which 2,000 are indeterminate fragments smaller than 2 cm that cannot even be classified as long bone or non-long bone (Pickering et al., 2003). These small fragments fall outside the scope of the zooarchaeological analysis

of this study but were used to assess the overall fragmentation of the assemblage (Solano García, 2024). Stratigraphic units IV–XVII were selected from the entire sequence, while levels I to III were not considered due to the low number of remains, as these levels could not have been systematically excavated in this area. The analysis focuses on the exploitation of ungulates throughout the stratigraphic sequence. The presence of carnivores is attested by a low proportion of remains from *Ursus arctos*, *Lynx pardinus*, *Canis lupus*, and *Felis silvestris* across the entire sequence (Barroso Ruíz et al., 2011; Solano García, 2024) (Supplementary Table S1), which will be referred to as a general carnivore group (Table 1). Small fauna, such as birds, lagomorphs, tortoises, amphibians, rodents, etc. (Barroso Ruíz et al., 2011), were also excluded from the analysis, as they fall outside the objectives of this study (see Solano García, 2024 for more details). The sample used consists of 3,514 remains, including 1,394 identified herbivore remains (NISP), 145 carnivore remains, 1,569 remains classified by size category, and 406 indeterminate remains.

The preservation state of the fossil remains is generally good, as they exhibit a high degree of mineralization. Between 65 and 80% of the remains, depending on the level, show no cortical modifications, and when they do, they appear as small dissolution pits. There are no evident signs of weathering (Behrensmeyer, 1978) throughout the sequence, although longitudinal and transverse fissures (25%) filled with precipitated calcite are common, sometimes contributing to the compaction of the fossil due to the weight of the sediments. Most of the fissures appear to be a direct result of fire action (Cain, 2005; Stiner, 2005; Théry-Parisot et al., 2010) and their subsequent development through fossil-diagenetic karstification processes. The most frequent alterations are calcite concretions and the presence of manganese oxide distributed as small dendritic patterns on the cortical surface. In contrast, biochemical modifications are scarcely described. Moisture and carbonated waters have been the main agents of alteration, aside from the anthropogenic effects of fire (Solano García, 2024).

The accumulation is anthropogenic in origin, as evidenced by the large volume of lithic tools, retouchers (Moigne et al., 2016), and anthropogenic activities related to butchery and food cooking (Barroso Ruíz et al., 2011). Carnivore remains are scarce throughout the assemblage (3.9%), and their impact is minimal (0.8%), except in unit XIII (1%), where there is a slight increase but with low activity (0.5%). Additionally, the skeletal representation and the dominant adult mortality profile (Stiner, 1994; Steele, 2004), along with the abundance of cut marks, intentional fracturing, and extensive use of fire, also suggest an anthropogenic accumulation. Access to carcasses was likely primary for large ungulates (Bos, Bison, Equus, and Cervus) and secondary for larger animals like elephants or rhinoceroses and probably *Sus* (Solano García, 2024).

It is important to note that the excavation area of each grid, except for J7, does not reach a full square meter in surface area. The excavation of this zone corresponds to the edge of the mining shaft dug along the K band (Figure 1D). Consequently, depending on the width of the sides and the depth, the excavated surface area will vary. On the other hand, grid J7, which covers the entire surface, began to be excavated in 1995 from level V at level XIII. Therefore, the material density is biased and uneven across different levels and may influence the frequencies of the number of identified remains. Nevertheless, the sample presented allows for the first diachronic zooarchaeological approach to nearly the entire stratigraphic sequence that we have so far.

3.2 Faunal analysis procedures

Taxonomic and anatomical identifications were carried out using the osteological collection of the Center for Prehistoric Research of Tautavel (CERPT) and specialized reference literature (Heintz, 1970; Pales et al., 1971; Schmid, 1972; Hillson, 2005; Barone, 2010). At the taxonomic level, some remains could be identified as *Bos primigenius* and *Bos bison* (Brugal, 1984; Gee, 1993), but for the purposes of this study, they have been unified under *Bos/Bison* (BB). When taxonomic identification was not possible, size-based criteria (adapted from Bunn, 1981; Bunn et al., 1986)Bunn, 1981; Bunn et al., 1986): were used to categorize animal mass: (1) small, 5–100 kg (e.g., *Capra*, *Dama*, *Canis*, *Lynx*); (2) medium, 100–250 kg (e.g., *Sus scrofa*, *Cervus elaphus*, *Equus hydruntinus*); (3) medium-large, 250–500 kg (e.g., *Equus ferus*, *Ursidae*); (4) large, 500–800 kg (e.g., *Bos primigenius*, *Bison priscus*); (5) very large, >800 kg (e.g., *Stephanorhinus*, *Palaeoloxodon*). To simplify the analysis, unidentified herbivore remains were grouped into two sets: large herbivores (LH: categories 3, 4, 5), mainly composed of categories 3 and 4; and small herbivores (SH: categories 1, 2). Anatomically unidentified remains were classified into one of the following categories: long bone, flat bone, and articular bone (Saladié et al., 2011).

The determination of age at death, when possible, is based on the fusion of epiphyses and dental eruption/replacement patterns and wear (Mariezkurrena, 1983; Wegrzyn and Serwatka, 1984; Stiner, 1990, 1998; Forsten and Moigne, 1998; Guadelli, 1998; Hillson, 2005; Barone, 2010) and has been classified into infant, juvenile, adult, and senile categories.

Abundance measures for all ungulates were recorded following the number of identified specimens (NISP), the minimum number of elements (MNE), the minimum number of individuals (MNI), and the minimum animal unit (MAU). The skeletal survival index per individual (SI) was calculated using the following formula: MAU × 100/MNI (Binford, 1981; Grayson, 1984; Klein and Cruz Uribe, 1984; Lyman, 1994a, 2008). To synthesize the information for each ungulate by stratigraphic units, the MAU for each taxon was calculated based on the total MNE (excluding teeth) and the complete skeleton, along with its corresponding SI. The %ΣMAU represents the proportion of MAU for each taxon within each stratigraphic unit as a summary value, and not Binford (1981) index, which has been replaced by the SI equivalent. However, it has been verified that the results are equivalent. The carnivore/herbivore percentage ratio (Klein and Cruz Uribe, 1984) has also been included. Additionally, the total MAU for each stratigraphic unit was calculated by summing all the complete skeletons present for each taxon.

For the analysis of the anatomical representation of the stratigraphic sequence, given the large number of skeletal elements and with the aim of identifying general exploitation patterns and synthesizing the results, the elements have been grouped into six main categories: skull, axial, long bones, girdles (scapula

TABLE 1 Composition of the faunal assemblage of J/K stratigraphic profile and index.

Level	Taxa	NISP (Und.)	%NISP	NISP LB	MNE	%MNE	MNE LB	MAU	%ΣMAU	%SI	MNI (I/J/A/S)	C/H* 100
IV		**27 (15)**		**13 (5)**	**26**		**11**	**0.03**	**0.21**	**0.50**	**7**	**4.76**
	BB	5	18.52	3	5	19.23	3	0.04	19.98	4.24	0/0/1/0	
	Cervus	8	29.63	2	8	30.77	2	0.07	31.96	3.39	1/0/1/0	
	Dama	2	7.41		2	7.69		0.02	7.99	1.69	0/0/1/0	
	Sus	2	7.41		2	7.69		0.01	3.83	0.81	0/0/1/0	
	Equus	9	33.33	8	8	30.77	6	0.07	32.89	6.98	0/0/1/0	
	Stephanorhinus	1	3.70		1	3.85		0.01	3.34	0.71	0/0/1/0	
	Large herbivore	5		1								
	Small herbívore	10		4								
	Undet.	0		0								
	Carnivore	2										
V		**4 (166)**		**3 (63)**	**4**		**3**	**0.01**	**0.21**	**0.20**	**4**	**3.49**
	BB	1	25.00		1	25.00		0.01	25.81	0.85	0/0/1/0	
	Cervus	1	25.00	1	1	25.00	1	0.01	25.81	0.85	0/0/1/0	
	Sus	1	25.00	1	1	25.00	1	0.01	24.76	0.81	0/0/1/0	
	Equus	1	25.00	1	1	25.00	1	0.01	23.61	0.78	0/0/1/0	
	Large herbivore	20		12								
	Small herbívore	62		40								
	Undet.	84		11								
	Carnivore	3										
VI		**22 (16)**		**11 (14)**	**21**		**11**	**0.03**	**0.17**	**0.31**	**8**	**17.14**
	BB	8	36.36	3	7	33.33	3	0.06	34.95	2.97	0/0/1/0	
	Cervus	2	9.09	2	2	9.52	2	0.02	9.99	0.85	1/0/1/0	
	Dama	1	4.55	1	1	4.76	1	0.01	4.99	0.85	0/0/1/0	
	Sus	1	4.55		1	4.76		0.01	4.79	0.81	0/0/1/0	
	Equus	9	40.91	4	9	42.86	4	0.07	41.10	3.49	1/0/1/0	
	Stephanorhinus	1	4.55	1	1	4.76	1	0.01	4.18	0.71	0/0/1/0	
	Large herbivore	10		8								
	Small herbívore	3		3								
	Undet.	3		3								
	Carnivore	6										
VII		**89 (64)**		**32 (34)**	**57**		**13**	**0.07**	**0.44**	**0.88**	**8**	**2.08**
	BB	27	30.34	5	10	17.54	3	0.08	19.10	4.24	0/0/2/0	
	Cervus	25	28.09	9	21	36.84	3	0.18	40.11	17.80	0/0/1/0	
	Sus	1	1.12		1	1.75		0.01	1.83	0.81	0/0/1/0	
	Equus	28	31.46	14	19	33.33	5	0.13	29.70	6.59	1/0/1/0	
	Stephanorhinus	6	6.74	4	5	8.77	2	0.04	7.99	3.55	0/0/1/0	
	Palaeoloxodon	2	2.25		1	1.75		0.01	1.27	0.56	0/0/1/0	
	Large herbivore	29		16								
	Small herbívore	26		15								
	Undet.	9		3								
	Carnivore	3										

(Continued)

TABLE 1 (Continued)

Level	Taxa	NISP (Und.)	%NISP	NISP LB	MNE	%MNE	MNE LB	MAU	%ΣMAU	%SI	MNI (I/J/A/S)	C/H* 100
VIII		**51 (29)**		**20 (21)**	**36**		**17**	**0.05**	**0.24**	**0.46**	**10**	**1.30**
	BB	16	31.37	1	7	19.44	1	0.05	19.22	5.08	0/0/1/0	
	Cervus	9	17.65	4	7	19.44	3	0.06	22.42	5.93	0/0/1/0	
	Dama	1	1.96	1	1	2.78	1	0.01	3.20	0.85	0/0/1/0	
	Sus	1	1.96		1	2.78		0	0.00	0	0/0/1/0	
	Equus	21	41.18	12	17	47.22	10	0.13	49.80	3.29	1/0/2/1	
	Stephanorhinus	3	5.88	2	3	8.33	2	0.01	5.36	0.71	1/0/1/0	
	Large herbivore	22		17								
	Small herbívore	4		2								
	Undet.	3		2								
	Carnivore	1										
IX		**275 (373)**		**133 (238)**	**135**		**48**	**0.18**	**0.88**	**1.64**	**11**	**2.41**
	BB	67	24.36	27	31	22.96	10	0.19	21.25	6.21	0/1/2/0	
	Cervus	50	18.18	32	22	16.30	8	0.18	20.29	17.80	0/0/1/0	
	Dama	9	3.27	5	6	4.44	2	0.05	5.80	5.08	0/0/1/0	
	Sus	9	3.27		8	5.93		0.03	3.71	3.25	0/0/1/0	
	Equus	128	46.55	65	59	43.70	24	0.38	43.30	9.50	1/1/2/0	
	Stephanorhinus	12	4.36	4	9	6.67	4	0.05	5.66	4.96	0/0/1/0	
	Large herbivore	204		144								
	Small herbívore	101		62								
	Undet.	68		32								
	Carnivore	14										
X		**185 (205)**		**81 (120)**	**107**		**39**	**0.14**	**0.71**	**0.83**	**20**	**2.58**
	BB	26	14.05	14	21	19.63	9	0.14	20.10	4.80	1/1/3/0	
	Cervus	36	19.46	16	23	21.50	11	0.19	27.20	6.21	1/1/2/1	
	Dama	6	3.24	3	6	5.61	3	0.04	5.91	4.24	0/0/1/0	
	Sus	14	7.57		8	7.48		0.06	7.94	1.90	1/0/2/0	
	Equus	102	55.14	48	48	44.86	16	0.27	37.86	5.43	1/1/2/1	
	Stephanorhinus	1	0.54		1	0.93		0.01	0.99	0.71	0/0/1/0	
	Large herbivore	108		76								
	Small herbívore	56		29								
	Undet.	41		15								
	Carnivore	9										
XI		**166 (231)**		**88 (130)**	**98**		**38**	**0.13**	**0.62**	**1.09**	**12**	**7.24**
	BB	24	14.46	10	16	16.33	5	0.10	16.54	3.39	0/1/2/0	
	Cervus	39	23.49	27	17	17.35	8	0.12	19.29	11.86	0/0/1/0	
	Dama	9	5.42	5	6	6.12	4	0.05	8.27	5.08	0/0/1/0	
	Sus	13	7.83	7	11	11.22	5	0.07	11.90	3.66	1/0/1/0	
	Equus	74	44.58	39	44	44.90	16	0.26	42.86	6.59	1/1/2/0	
	Stephanorhinus	7	4.22		4	4.08		0.01	1.15	0.71	0/0/1/0	
	Large herbivore	130		74								

(Continued)

TABLE 1 (Continued)

Level	Taxa	NISP (Und.)	%NISP	NISP LB	MNE	%MNE	MNE LB	MAU	%ΣMAU	%SI	MNI (I/J/A/S)	C/H* 100
	Small herbívore	77		49								
	Undet.	24		7								
	Carnivore	27										
XII		**76 (127)**		**31 (61)**	**53**		**18**	**0.06**	**0.33**	**0.64**	**9**	**5.52**
	BB	8	10.53	2	7	13.21	1	0.03	10.40	3.39	0/0/1/0
	Cervus	19	25.00	11	12	22.64	6	0.10	31.19	5.08	1/0/1/0
	Dama	1	1.32		1	1.89		0.01	2.60	0.85	0/0/1/0
	Sus	8	10.53		6	11.32		0.02	4.99	1.63	0/0/1/0
	Equus	33	43.42	16	21	39.62	9	0.13	40.41	6.59	1/0/1/0
	Stephanorhinus	6	7.89	2	5	9.43	2	0.03	8.70	2.84	0/0/1/0
	Palaeoloxodon	1	1.32		1	1.89		0.01	1.72	0.56	0/0/1/0
	Large herbivore	53		28								
	Small herbívore	52		27								
	Undet.	22		6								
	Carnivore	10										
XIII		**114 (277)**		**53 (162)**	**78**		**28**	**0.10**	**0.52**	**0.95**	**11**	**11.34**
	BB	35	30.70	13	25	32.05	7	0.16	31.21	5.37	1/0/2/0
	Cervus	23	20.18	12	15	19.23	6	0.11	21.35	5.51	1/0/1/0
	Dama	9	7.89	5	8	10.26	3	0.06	11.50	5.93	0/0/1/0
	Sus	5	4.39	1	4	5.13	1	0.02	3.15	1.63	0/0/1/0
	Equus	39	34.21	21	23	29.49	10	0.16	30.05	5.17	1/0/2/0
	Stephanorhinus	3	2.63	1	3	3.85	1	0.01	2.75	1.42	0/0/1/0
	Large herbivore	128		78								
	Small herbívore	102		69								
	Undet.	47		15								
	Carnivore	39										
XIV		**46 (100)**		**29 (72)**	**37**		**18**	**0.06**	**0.24**	**0.84**	**7**	**2.99**
	BB	13	28.26	7	10	27.03	5	0.06	24.54	2.97	0/0/2/0
	Cervus	7	15.22	5	7	18.92	4	0.06	24.54	5.93	0/0/1/0
	Sus	4	8.70		4	10.81		0.01	3.36	0.81	0/0/1/0
	Equus	20	43.48	14	14	37.84	8	0.10	41.69	5.04	0/0/2/0
	Stephanorhinus	2	4.35	3	2	5.41	1	0.01	5.87	1.42	0/0/1/0
	Large herbivore	33		23								
	Small herbívore	55		45								
	Undet.	12		4								
	Carnivore	4										
XV		**241 (279)**		**108 (178)**	**157**		**48**	**0.21**	**0.78**	**1.50**	**14**	**4.80**
	BB	47	19.50	25	26	16.56	9	0.17	21.60	8.47	0/0/2/0
	Cervus	36	14.94	20	23	14.65	10	0.19	23.76	9.32	1/0/1/0
	Dama	6	2.49	3	6	3.82	3	0.04	5.40	4.24	0/0/1/0
	Sus	6	2.49		6	3.82		0.03	4.14	1.08	1/1/1/0

(Continued)

TABLE 1 (Continued)

Level	Taxa	NISP (Und.)	%NISP	NISP LB	MNE	%MNE	MNE LB	MAU	%ΣMAU	%SI	MNI (I/J/A/S)	C/H* 100
	Equus	142	58.92	58	92	58.60	24	0.33	41.49	6.51	1/1/3/0	
	Stephanorhinus	4	1.66	2	4	2.55	2	0.03	3.61	2.84	0/0/1/0	
	Large herbivore	133		104								
	Small herbívore	84		52								
	Undet.	62		22								
	Carnivore	22										
XVI		**77 (72)**		**37 (56)**	**56**		**24**	**0.07**	**0.32**	**0.83**	**9**	**1.64**
	BB	1	1.30	1	1	1.79	1	0.01	2.64	0.85	0/0/1/0	
	Cervus	15	19.48	11	11	19.64	7	0.08	23.79	3.81	0/0/2/0	
	Dama	6	7.79	2	5	8.93	1	0.04	13.22	4.24	0/0/1/0	
	Sus	1	1.30		1	1.79		0.01	2.54	0.81	0/0/1/0	
	Equus	53	68.83	22	37	66.07	14	0.18	55.61	5.94	1/0/2/0	
	Stephanorhinus	1	1.30	1	1	1.79	1	0.01	2.21	0.71	0/0/1/0	
	Large herbivore	34		30								
	Small herbívore	11		6								
	Undet.	27		20								
	Carnivore	2										
XVII		**22 (21)**		**13 (11)**	**18**		**10**	**0.02**	**0.13**	**0.33**	**7**	**7.69**
	Capra	1	4.76		1	5.56		0.01	6.47	0.85	0/0/1/0	
	Cervus	13	61.90	10	10	55.56	7	0.08	64.72	8.47	0/0/1/0	
	Dama	2	9.52		2	11.11		0.01	6.47	0.85	0/0/1/0	
	Sus	3	14.29	1	3	16.67	1	0.01	6.21	0.41	1/0/1/0	
	Equus	2	9.52	1	2	11.11	1	0.02	11.84	1.55	0/0/1/0	
	Palaeoloxodon	1	4.76	1	1	5.56	1	0.01	4.29	0.56	0/0/1/0	
	Large herbivore	13		9								
	Small herbívore	4		1								
	Undet.	4		1								
	Carnivore	3										
Total	**8 ungulates**	**1,394 (1,975)**		**652 (1,165)**	**883**		**326**	**0.08**		**0.06**	**137**	**4.89**
	4 carnivores*	**100 (45)**										

NISP, number of identified specimens; MNI, minimum number of individuals; MNE, minimum number of elements; LB, long bones; MAU, minimal animal unit; %ΣMAU, percentage of MAU sum; %SI, percentage of survivorship index; C/H, carnivore/herbivore; I, infant; J, juvenile; A, adult; S, senile.
*Carnivores: view Supplementary Table S1.

+ coxal), articular bones, and phalanges. However, individual elements will also be used for analysis, and they will be referenced when necessary.

To analyze the fragmentation of the ungulate assemblage by stratigraphic unit, the MNE/NISP ratio was used, applied also to long bones. The intensity of fragmentation was calculated by counting incomplete elements (fragments/NISP × 100) and comparing it with the overall set of fragmented and complete remains. The degree of fragmentation was also measured based on the integrity of the remains and the circumference size of long bones (Villa and Mahieu, 1991). These data were complemented by a descriptive statistical analysis of the length of the remains and a count of all small indeterminate splinters not assigned to size categories.

Additionally, to verify the intensity of fracturing, all fragmented and complete long bones were counted by stratigraphic unit, taking into account the diaphysis and epiphysis ratios (Todd and Rapson, 1988; Lyman, 1994b, 2008). The count of fractured phalanges was also used as an indicator of intensified marrow exploitation (Starkovich, 2017) along with the count of mandibles. The longitudinal opening of these types of elements is a clear distinctive sign of marrow extraction.

Anthropogenic activity has been synthesized based on the count of cut marks (Binford, 1981; Blumenschine et al., 1996; Domínguez-Rodrigo et al., 2009), percussion marks (Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Pickering and Egeland, 2006; De Juana and Domínguez-Rodrigo, 2011), fresh bone fractures (Villa and Mahieu, 1991) and burned bones (Shipman et al., 1984; Stiner et al., 1995). Additionally, the number of carnivore tooth marks (Bunn, 1981; Fisher, 1995; Blumenschine et al., 1996) has been counted as contrasting information, highlighting carnivores as modifying agents in the assemblage.

The observation of surface bone modifications was carried out using a 10× handheld magnifying lens and a Dinolite device. The graphical analysis of the anatomical representation of each taxon by stratigraphic unit was performed using ArcGIS® software by Esri (ESRI Inc, 2023), where the MAU normalized by NISP was utilized (Orton, 2010). All statistical analysis and graphical output were conducted using the R programming language (R Core Team, 2024).

4 Results

4.1. Taxonomic and anatomical distribution

This study analyzed 1,394 remains (39.67%) identified as belonging to ungulates. As complementary information, we also present the count of unidentified material (56.2%), classified into the categories of Large Herbivores and Small Herbivores (44.65%), as well as the number of carnivore remains (4.13%) and indeterminate remains (11.55%) for each stratigraphic unit (3,514 NR; Table 1).

The number of remains is quite disproportionate throughout the entire sequence, as is the NISP (CV = 124.2 and 86.2, respectively), with a marked bias in the upper layers (IV–VI) and layer XVII, while a higher number is observed in the central layers. This bias is attributed to the smaller volume excavated in these levels, although level V may also show a potential research bias with a lower identification rate of around 0.2%, compared to the 3.1% average for the total NR. Despite the marked discrepancies in NISP throughout the sequence, we have confirmed that the use of MAU and SI as analytical variables does not affect the results and is correlatable with the material density per unit of analysis.

A total of nine ungulate taxa have been identified throughout the sequence: *Bos primigenius*, *Bison priscus*, *Cervus elaphus*, *Dama dama*, *Sus scrofa*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Palaeoloxodon antiquus*, and *Capra* sp. (Barroso Ruíz et al., 2011). The first six taxa, counting *B. priscus* and *B. primigenius* as a single group (BB), are present in almost the entire sequence, with the exception of *Dama*, which is absent in levels V, VII, and XIV; *Stephanorhinus* in levels V and XVII; and BB in level XVII. On the other hand, *Palaeoloxodon* is only found in levels VII, XII, and XVII, and *Capra* in level XVII. The absence of *Dama* and *Stephanorhinus* in level V may be due to the possible excavation or research biases mentioned earlier.

Carnivores are present in all levels of the analyzed sequence (Table 1, Supplementary Table S1), although there is considerable variability in the number of remains, ranging from just one in level VIII to 39 remains in level XIII. Unit VI has the highest carnivore-herbivore ratio (17.14%), followed by unit XIII (11.34%), within an overall carnivore-herbivore ratio of 4.89%. Among the carnivores, lynx remains are the most abundant (46.1%), followed by bear (39.2%), wolf (11.8%), and wildcat (2.9%). Bears have the widest distribution across the entire J/K stratigraphic sequence, except in levels V to VIII, followed by lynx, present in eight levels, wolves in six, and wildcats in three. However, according to Barroso Ruíz et al. (2011), brown bears are the most represented in NR across the entire site.

The predominant taxon among herbivores throughout the stratigraphic sequence (Figure 3), based on representation indices (NISP, $\bar{x} = 47.2$, $\sigma = 46.8$; MNE, $\bar{x} = 28.1$, $\sigma = 25.5$; MAU, $\bar{x} = 0.16$, $\sigma = 0.11$), is the horse, followed by BB (NISP, $\bar{x} = 19.8$, $\sigma = 19.5$; MNE, $\bar{x} = 12.85$, $\sigma = 9.95$; MAU, $\bar{x} = 0.08$, $\sigma = 0.06$) and red deer, with very similar values (NISP, $\bar{x} = 20.2$, $\sigma = 15.2$; MNE, $\bar{x} = 12.8$, $\sigma = 7.55$; MAU, $\bar{x} = 0.10$, $\sigma = 0.06$), although the red deer's MAU is slightly higher or comparable. The rest of the taxa, with lower representativity in terms of the number of remains and elements, are represented by wild boar, fallow deer, rhinoceros, elephant, and ibex. The number of individuals also confirms this taxonomic hierarchy, with horse (39), BB (26), red deer (24), wild boar (20), but more rhinoceros individuals (13) than fallow deer (11), and lastly, elephant (3) and ibex (1).

The total MNI (Minimum Number of Individuals) is 137 for the ungulate species (Table 1). The vast majority correspond to adult individuals (74.45%), compared to 16.8% juveniles, 6.6% subadults, and 2.2% elderly. The central levels, between VIII and XV, have the highest proportion of individuals, with a peak in level X, which contains 20 individuals, including two of the three elderly ones. Levels IX and XV have the highest proportion of elements relative to those expected (MNE/MNI; 12.3 and 11.2, respectively), followed by VII (8.2), XI, and XIII (7.1). The taxon with the greatest anatomical representation in this case is *Equus* (10.1), followed by *Cervus* (7.5) and BB (6.4), on one hand, and *Dama* (4), *Stephanorhinus* (3), and *Sus* (2.9), on the other. The species with the largest number of juveniles are *Equus* and *Cervus* (25% and 25.6%, respectively), followed by wild boar (20%), BB, and rhinoceros (7.7%). Subadults are present in BB (11.5%), *Equus* (10.3%), *Sus* (5%), and *Cervus* (4.2%), while elderly individuals are found in *Equus* (5.1%) and *Cervus* (4.2%). The remainder belong to adults, with proportions above 60%. In the case of fallow deer, all individuals are adults.

It is clear that the means of the main ungulate taxa show variability (Figure 3). After comparing the assumptions of normality and homogeneity of variances (S-W and Levene tests) for the indices of the six main ungulates (NISP: $D = 0.26$, df = 80, $p < 0.001$; MNE: $D = 0.24$, df = 80, $p < 0.001$; MAU: $D = 0.207$, df = 80, $p < 0.001$), a K–W test, effect size (η^2; Wolverton et al., 2016), and *post-hoc* tests were conducted. The results indicate statistically significant differences between the means of the six taxa (NISP: $H = 29.35$, df = 5, $p < 0.001$, $\eta^2 = 0.338$; MNE: $H = 31.29$, df = 5, $p < 0.001$, $\eta^2 = 0.365$; MAU: $H = 38.48$, df = 5, $p < 0.001$, $\eta^2 = 0.465$; SI: $H = 35.795$, df = 5, $p < 0.001$, $\eta^2 = 0.428$). These results suggest the differences are reliable. *Post-hoc* comparisons (Wilcox & Conover-Iman test using Holm's method) identified a greater

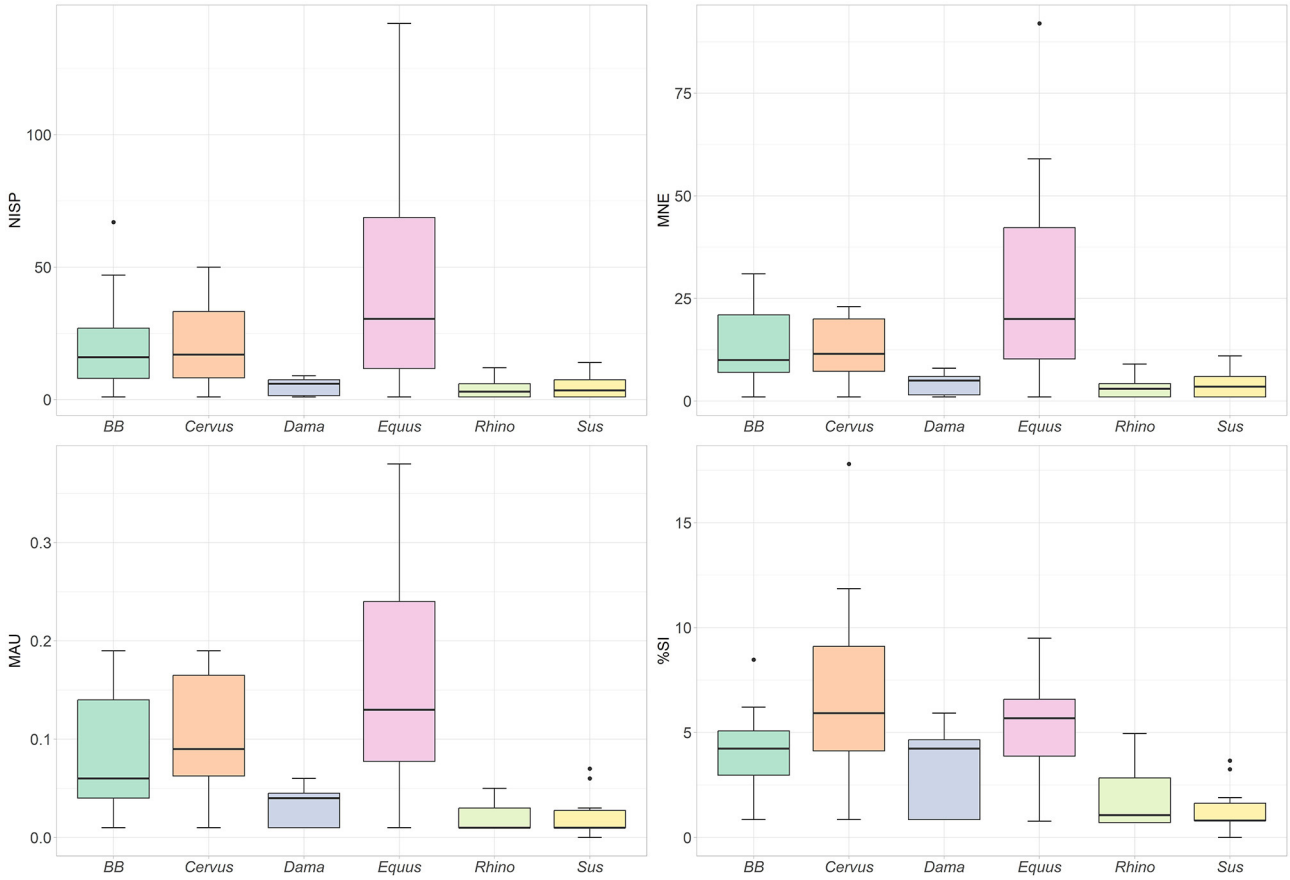

FIGURE 3
Box plots of the primary taxonomic representation across the entire stratigraphic assemblage for the four main indices.

similarity between BB, *Cervus*, and *Equus* (Group 1) (NISP: $H = 2.97$, df $= 2$, $p = 0.226$, $\eta^2 = 0.0129$; MNE: $H = 3.68$, df $= 2$, $p = 0.159$, $\eta^2 = 0.0223$; MAU: $H = 3.81$, df $= 2$, $p = 0.149$, $\eta^2 = 0.0242$) and between *Dama*, *Sus*, and *Rhino* (Group 2) (NISP: $H = 0.34$, df $= 2$, $p = 0.843$, $\eta^2 = -0.0221$; MNE: $H = 0.62$, df $= 2$, $p = 0.734$, $\eta^2 = -0.0184$; MAU: $H = 2.87$, df $= 2$, $p = 0.238$, $\eta^2 = 0.0116$). In summary, we can assume two main distinct groups based on their representativity in the stratigraphic sequence, with the first group showing significantly higher representativity compared to the second (Figure 4).

The results indicate that Group 1 forms the core trio of species with the highest taxonomic and anatomical representation within the assemblage and throughout the entire stratigraphic sequence. This does not imply that there are no differences between stratigraphic levels, as it is clear that in some levels the representation of these taxa is higher than others, but they always maintain a similar presence per level, comparable to the rest of the layers. Group 2 behaves similarly according to the data, but with a much lower representation. When we applied the same test for the survival index (%SI), which takes into account the MNI, it confirmed the similarity within the first group (%SI: $H = 4.73$, df $= 2$, $p = 0.94$, $\eta^2 = 0.0364$), and within the second group (%SI: $H = 8.06$, df $= 2$, $p = 0.0177$, $\eta^2 = 0.0808$). However, there is greater similarity between *Rhino* and *Sus*. This is because the skeletal survival of *Dama* is more similar to that of BB.

The overall skeletal representation based on MNE is dominated by long bones (37.51%), cranial remains including isolated teeth and antlers (31.81%), and axial skeleton elements (12.2%), followed by articular bones, girdles, and phalanges. However, the MAU (Figure 5) indicates a slightly different distribution, where long bones still dominate (57.57%) along with cranial remains (24.70%), but these are followed by girdles (9.66%), articular bones (3.14%), phalanges (2.84%), and axial elements (2.10%). This same distribution is reflected in the skeletal survival index, although the representation of phalanges (2.8%) is slightly higher than that of articular bones (2.4%).

When comparing the MAU by taxa (Figure 5), the same general distribution is observed, with long bones predominating, followed by cranial elements, phalanges, or articular and axial bones, except for *Sus scrofa*. The wild boar shows a different pattern, where cranial elements dominate (75%) compared to long bones (20.3%), followed by articular bones (2.5%), phalanges (1.9%), and axial elements (0.2%).

According to the MAU by anatomical elements (Figure 4, Supplementary Figure S1), metapodials are the most represented (16.7%), followed by tibiae (10.40%), humeri (8.73%), femora (8.36%), radii (7.61%), and ulnae (5.57%). However, if we

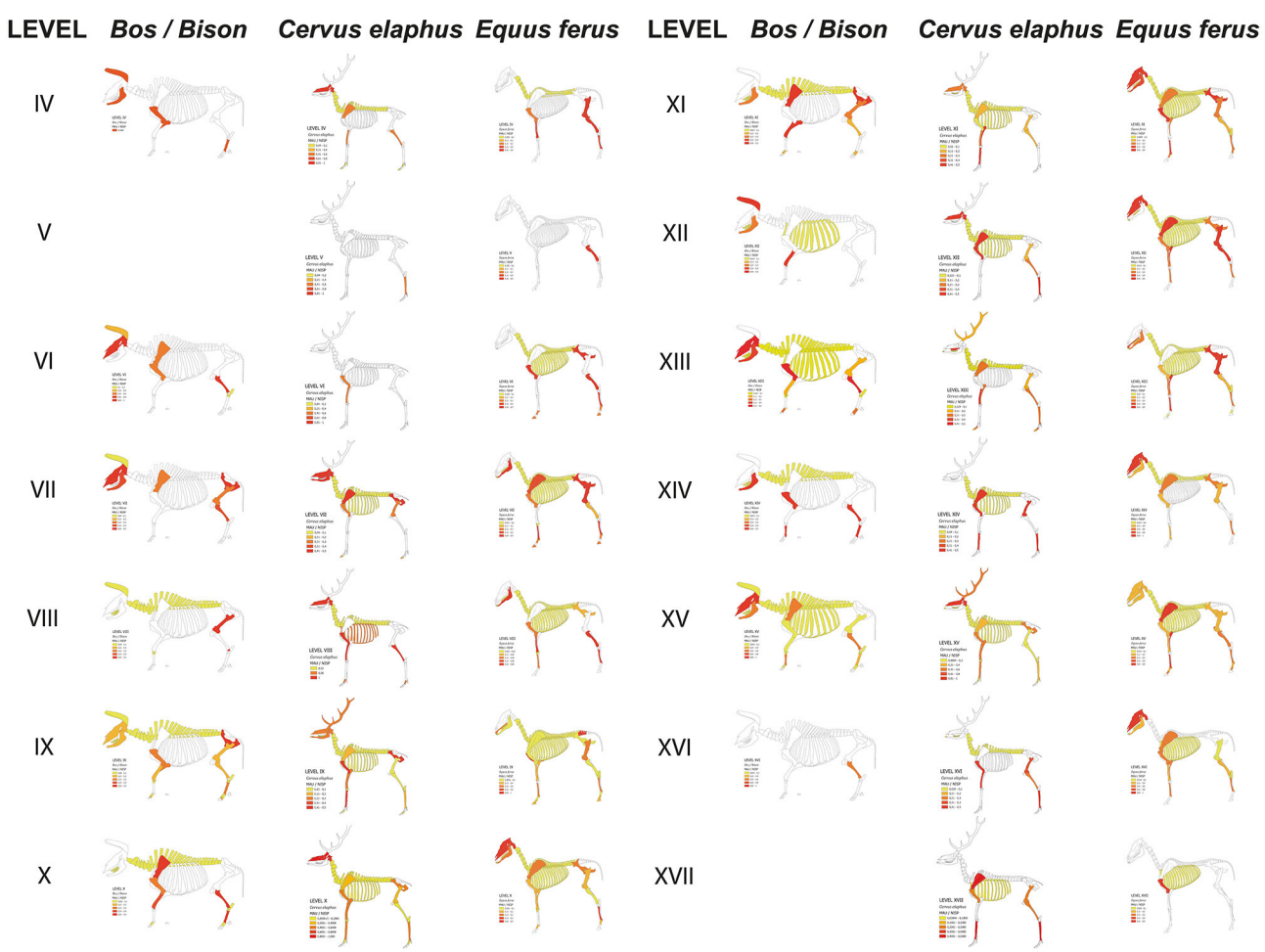

FIGURE 4
Anatomical distribution of the three main taxa (group 1) across the stratigraphic sequence (all taxa in Supplementary Figure S1). The representativity of each element (ribs and vertebrae have been generalized) is measured using the MAU and NISP to normalize the color gradient (Vector templates from https://www.archeozoo.org/).

break down all the elements, tibiae (10.28%) are the best represented, followed by cranial elements (9.92%), mandibles (9.00%), metatarsals (8.88%), humeri (8.63%), femora (8.26%), radii (7.53%), scapulae (5.51%), ulnae (5.51%), metacarpals (4.34%), and coxae (4.04%). The remaining elements are below 2%.

At the stratigraphic level, most layers contain skewed (non-symmetrical) data. Only levels X, XI, and XV show data symmetry. However, when we analyse the MAU (Figure 5) as a contrast index, we confirm that there is no statistically significant difference between them, based on the K–W test ($H = 14.904$, df $= 13$, $p = 0.3134$, $\eta^2 = 0.00362$) and the two-sided Jonckheere-Terpstra test (JT $= 65{,}792$, $p = 0.8461$). In contrast, the %SI (Figure 5) shows significant differences ($H = 29.878$, df $= 13$, $p = 0.005$, $\eta^2 = 0.0321$), although the effect size is very close. This is because the differences are solely related to layer X. Thus, the JT test, which is more robust and takes into account the order of the stratigraphic sequence, indicates similarity (JT $= 68{,}622$, $p = 0.24$). This result supports the feasibility of conducting analyses to identify differences and similarities between species groups and anatomical categories for the entire assemblage. In fact, the correspondence analysis between anatomical categories throughout the sequence shows how most levels cluster around the long bones and near the origin of the coordinates, indicating little variation (Figure 6B).

The species with the highest number of elements are *Equus*, *Cervus*, BB, *Sus*, and *Dama*. However, as we have seen, *Sus* presents a different skeletal configuration (Supplementary Figure S1). When comparing the total anatomical representation of the four taxa based on the MAU, there are also significant differences ($H = 229.56$, df $= 5$, $p < 2.2\text{e-}16$, $\eta^2 = 0.488$), although *post-hoc* tests indicate a potential similarity between BB, *Cervus*, and *Equus*, and *Dama* with *Cervus*. However, when pairwise tests are conducted, no correspondence is found. This is due to a certain variability in combinations of categories by elements. When analyzing these skeletal categories for the four mentioned taxa, there is statistically significant similarity between skulls, long bones, and girdles ($H = 2.6531$, df $= 2$, $p = 0.2654$, $\eta^2 = 0.00197$), with the distribution of skulls and girdles being much more similar between BB, *Cervus*, and *Equus* ($H = 2.0769$, df $= 2$, $p = 0.354$, $\eta^2 = 0.000254$). These results indicate a similar configuration among the species in Group 1, with a predominance of long bones, followed by skulls and girdles and mandibles in similar proportions (Figure 6A). As we have seen, *Dama* presents a distribution approaching that of Group 1, but

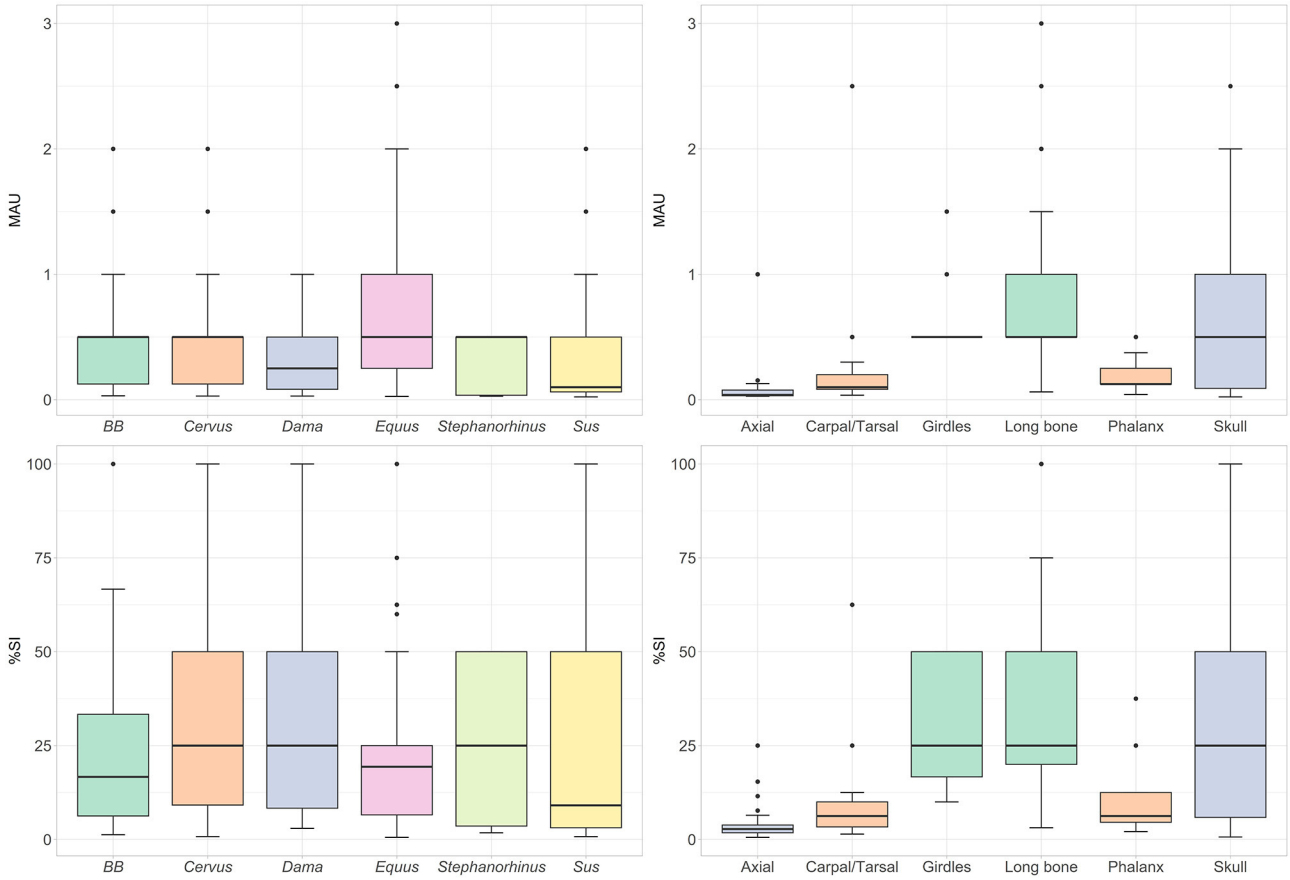

FIGURE 5
Box plots of the anatomical representation of the main taxa **(left)** and skeletal element categories **(right)** according to the MAU and %SI.

its lower representation, for now, does not allow it to be fully included in that group and instead places it in Group 2, as noted earlier. Group 2 shows statistical similarity between articular bones and phalanges ($H = 0.15342$, df $= 1$, $p = 0.6953$, -$\eta^2 = 0.0470$), long bones and girdles ($H = 0.32613$, df $= 1$, $p = 0.5679$, $\eta^2 = -0.0157$), and skulls and girdles ($H = 1.3651$, df $= 1$, $p = 0.2427$, $\eta^2 = 0.00936$).

The survival index for the entire assemblage (Table 1) shows that the red deer has the highest skeletal survival (34%), followed by the horse (24.3%) and BB (17.5%). In Group 2, with lower indices, the best represented is the fallow deer (11.2%), followed by the rhinoceros (7%) and the wild boar (6.1%). At the skeletal level (Figure 5), long bones are the best represented (58.1%) for all taxa except for the wild boar, where cranial remains predominate. Cranial remains are the second most represented (25.5%) for the other taxa, followed by girdles (9.2%), phalanges (2.8%), and articular bones (2.4%). Among the long bones, metapodials have the highest survival (15.5%), followed by tibiae and humeri (10.5%). These are followed by femora (8.3%), radii (7.4%), and ulnae (5.4%). Scapulae (5.9%) are better represented than pelves (3.3%), and phalanges (2.8%) are better represented than articular bones (2.4%), although the difference is minimal. As can be seen, the survival of the girdles is consistent with that of humeri and femora, considering their anatomical connection. Additionally, it indicates a higher representativity of anterior stylopodia and posterior zeugopodia, although the MAU is similar for the stylopodia, and the tibia stands out more than the radius among the zeugopodia.

Lastly, we conducted an analysis of the distribution of forelimbs and hindlimbs based on the MNE. At first glance, the frequency of elements is markedly uneven between Groups 1 and 2 (Figure 7A). As a preliminary approach, we calculated the Log (Forelimb/Hindlimb) ratio for all species with at least two elements within the same level. The overall average for the entire dataset is $\bar{x} = -0.16$, $\sigma = 0.54$, min $= -1.39$, max $= 0.85$, indicating a near balance between forelimbs and hindlimbs, though with a slight tendency toward the hindlimb. Some taxa, such as *Cervus*, lean toward the forelimb (Figures 7B, C), while others, like *Equus* and *Sus*, show a preference for the hindlimb.

This distribution is particularly apparent in the density plots (Figures 7C, D), where a clear balance can be observed in taxa such as BB and *Stephanorhinus*, though with a predominance toward the hindlimb, especially in the case of *Equus*. Stratigraphically, although there is variability and extreme values in some species like BB in Levels IV or VII, the differences are not statistically significant, even though *Equus* and *Cervus* exhibit the highest variability throughout the sequence. Taxa in Group 2 are dominated by the hindlimb at all levels, except for *Dama*, which shows a predominance of the forelimb in Level XV.

Since Group 2 exceeds 50% missing values, we do not consider it suitable for further analyses, as these cannot be interpreted as

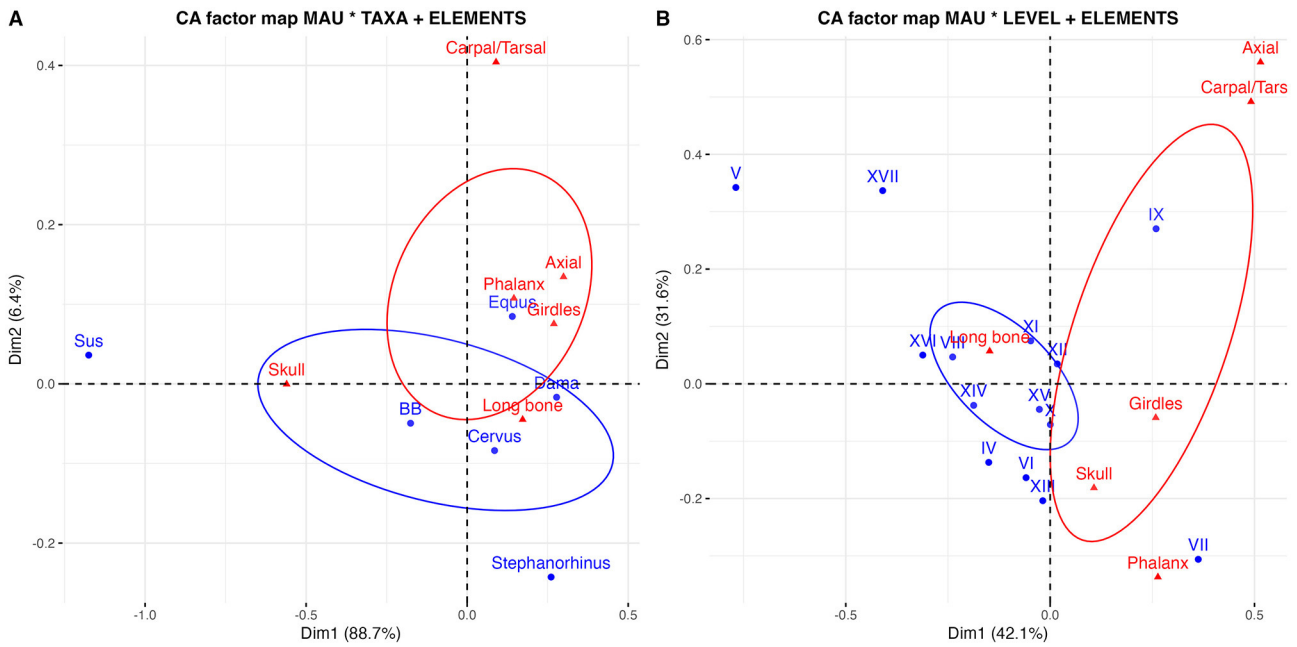

FIGURE 6
Graphical output of the correspondence analysis between the main taxa **(A)** and levels **(B)** by anatomical element categories based on the MAU. The ellipses represent 95% confidence intervals for taxa and levels (blue) and elements (red).

absences (value 0) given the current sample size and excavated area. Likewise, data imputation in this case would not provide reliable results, so we focused on Group 1 for a more detailed exploration. Missing values (*BB*: 15%; *Cervus* and *Equus*: 3.8%) were imputed using the "mice" algorithm ($m = 5$, method = "pmm", maxit = 50) (van Buuren and Groothuis-Oudshoorn, 2011), which is robust and flexible for such distributions (*BB*: $W = 0.94$, $p = 0.45$; *Cervus*: $W = 0.94$, $p = 0.46$; *Equus*: $W = 0.95$, $p = 0.545$). Levene's test [$\Pr(>F) = 0.19$, $p = 0.83$] indicates homogeneity of variances among species. The analysis ($H = 2.29$, df = 2, $p = 0.32$) suggests no statistically significant differences between the ratios of the three species. However, the correlations between species are low, indicating little direct relationship in terms of the forelimb-hindlimb ratio. This could suggest that their representation across stratigraphic levels is independent or influenced by different factors.

The analysis of ratios across stratigraphic levels ($H = 10.82$, df = 12, $p = 0.54$) also indicates no statistically significant differences between levels. The distributions are evenly spread and independent of stratigraphic level. However, while the variability is not statistically significant, it may still provide some stratigraphic insights.

The principal component analysis between species (Figure 8A) reveals a distinct behavior of *Equus* compared to BB and *Cervus*. Component 1 explains forelimb representation. As a result, *Equus* contributes very little to this component, appearing mainly in Levels VII, VIII, and XII. The distribution of BB and *Cervus* is the most similar throughout the sequence, showing a tendency toward the forelimb but with opposing differences in certain levels, such as XI and XVI. In this context, BB exhibits the greatest balance in forelimb-hindlimb proportions throughout the sequence, while *Cervus* shows a stronger tendency toward the forelimb (Figure 7C). Component 2, which explains hindlimb representation, is strongly dominated by *Equus*, contributing hindlimb elements across all levels except the three mentioned earlier. Except for Level VIII, entirely dominated by forelimb elements, the remaining levels tend, to varying degrees, toward the hindlimb.

To better understand the association between species elements and stratigraphic levels, we performed a correspondence analysis (Figure 8B). Most levels cluster near the origin, suggesting a balance between forelimb and hindlimb, though with a tendency toward the hindlimb. Some levels are outliers, such as Level VIII, composed solely of forelimb elements dominated by *Equus*, and its opposite, Level XVII (imputed data), composed entirely of hindlimb elements dominated by BB.

There does not appear to be a clear pattern in the representation of forelimbs and hindlimbs throughout the sequence. What we can deduce is that *Equus* is the dominant species, with a strong representation of hindlimbs, while *Cervus* shows a slight tendency toward forelimbs, often contrasting with *Equus* at various levels. Considering that BB tends toward anatomical balance, while *Equus* and *Cervus* show opposing tendencies, the overall dataset generally reflects a balanced representation between forelimbs and hindlimbs, as indicated by the global mean and statistical tests performed.

4.2 Integrity and fragmentation of the assemblage

A total of 98.6% of the remains included in this study are fragmented, and 97.3% retain less than half of their original size

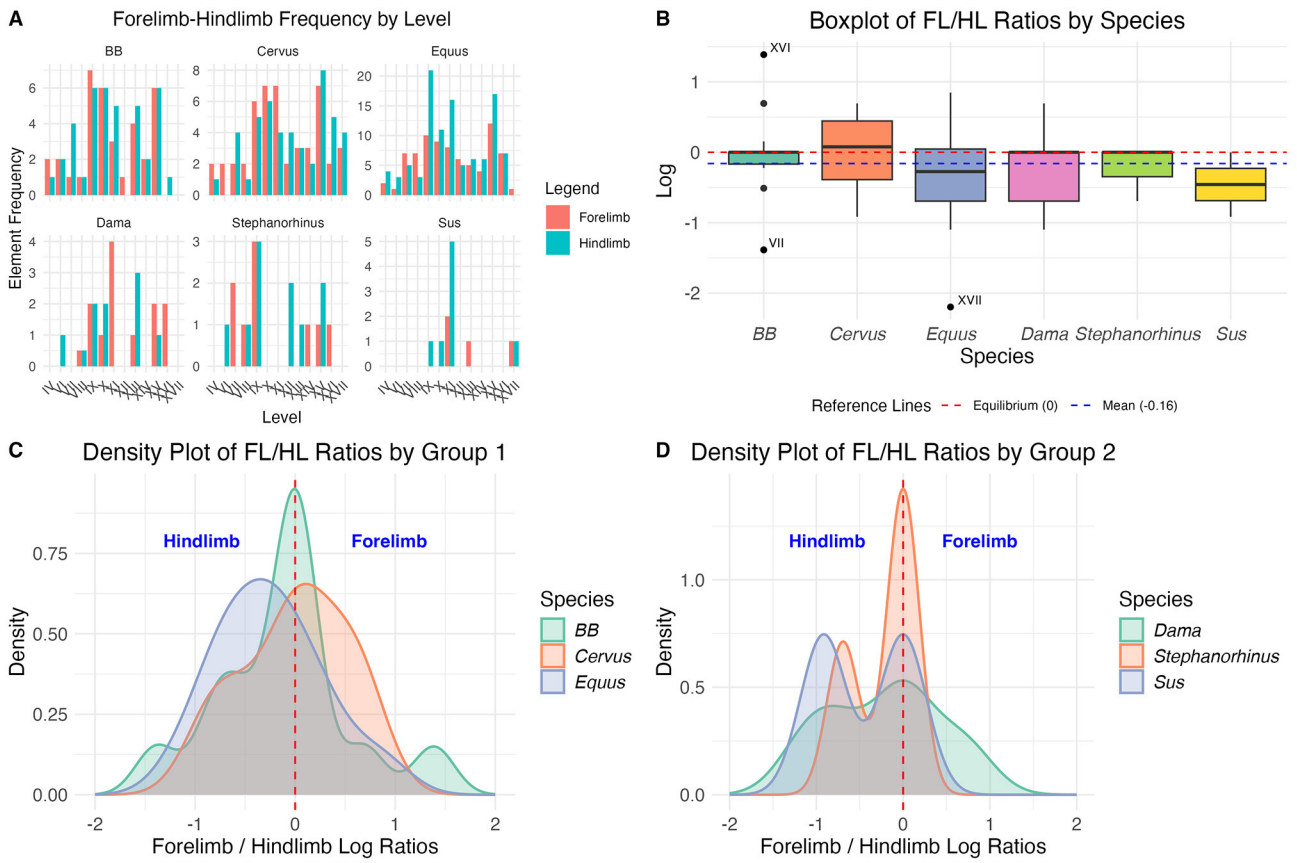

FIGURE 7
Exploración estadística de la relacion forelimb hindlimb. **(A)** Distribución de la frecuencia absoluta de elementos de forelimb y hindlimb para cada especie por nivel estratigráfico. **(B)** Boxplot de la ratio log(forelimb/hindlimb) por especie. **(C)** Gráfico de densidad de la log ratio forelimb/hindlimb por especies del grupo 1. **(D)** Gráfico de densidad de la log ratio forelimb/hindlimb por especies del grupo 2.

(Table 2). Moreover, the vast majority (91.9%) retain between 0 and 25% of their size. Their distribution across the sequence is very homogeneous ($\bar{x} = 90.3$, $\sigma = 6.4$, CV = 7.1), with hardly any differences in terms of integrity between stratigraphic levels. However, when analyzing the length of ungulate remains, we do find significant variability (min = 2 mm, max = 283 mm, $\bar{x} = 49.9$, $\sigma = 30.2$, CV = 60.6). The overall average for all levels is between 4.5 and 6 cm, except for layer V, which has an average length of 23 mm. These results already point to a high degree of fragmentation. In fact, the circumference of long bones is $<180°$ in 94% of the cases ($\bar{x} = 93.2$, $\sigma = 8.1$, CV = 8.7), and in 60% for those $<90°$ ($\bar{x} = 55.2$, $\sigma = 13.6$, CV = 8.7). The ratio of fractured remains is 19.9 for each complete element in the entire assemblage. An increase in this ratio is observed from the lower levels to the upper ones, but with some variability in the central levels.

The highest degree of fragmentation is observed in Group 1, with MNE/NISP averages (Table 3) around 0.7, in the following order: *Equus*, BB, and *Cervus*. In contrast, Group 2 has values above 0.9: *Rhino*, *Dama*, and *Sus*. Among skeletal categories, cranial elements and long bones are the most fragmented (0.76), followed by girdles (0.79), axial elements (0.8), and phalanges (0.9). Horns and antlers (0.49), along with femora (0.59), exhibit the highest degree of fragmentation, followed by tibiae (0.7) and radii (0.72). Next are skull remains, humeri, scapulae, ribs, and vertebrae (0.74–0.82). A third group consists of pelvises, teeth, metapodials, ulnae, and phalanges (0.83–0.90), and finally, articular bones, which are mostly complete (0.97). If we compare the index solely for long bones, again the horse, BB, and red deer show values between 0.7 and 0.76, followed by the fallow deer (0.86), with wild boar and rhinoceros above 0.96. However, when we analyse the intensity of fragmentation using the %IFOin (Table 2), which considers whole elements, we observe that red deer and fallow deer have the highest values, followed by the horse, BB, and rhinoceros. The wild boar shows the lowest fragmentation intensity, as its anatomical configuration, dominated by teeth and largely complete articular bones, reduces the proportion of fractured elements.

Long bones are the most represented in the assemblage (n = 1,817). Of these, 35.88% have been identified (NISP = 652), with an MNE of 328. Within this group, we found only two complete elements (metatarsals), two complete shafts (humerus and metatarsal), and 26 complete epiphyses (1.6%). The remainder consists of diaphyses (83.1%) and fragmented epiphyses (14.9%). The overall ratio between shafts and epiphyses is 5.56. Among the identified elements, tibiae and femora are the best represented, followed by radii-ulnae and humeri. Metapodials, as a group, are well represented, with metatarsals being the most abundant.

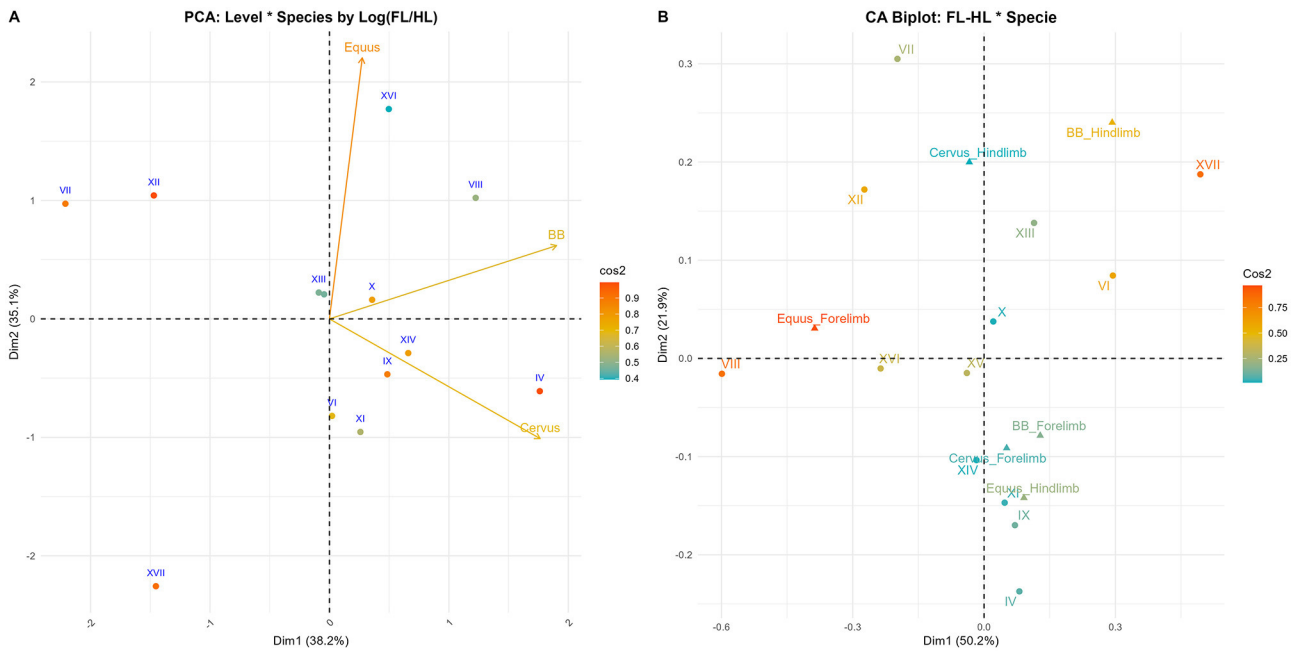

FIGURE 8
(A) Análisis de componentes principales de la log ratio forelimb/hindlimb por niveles y especies. **(B)** Análisis de correspondencias de la log ratio forelimb/hindlimb por niveles y especies.

More than half of the long bone remains (56.8%) could not be identified. At the stratigraphic level, there is considerable variability in the number of long bone remains, but there is a strong positive correlation ($\rho = 0.774$, $p = 0.001$; $\tau = 0.641$, $p = 0.001$) between the number of shafts and epiphyses throughout the sequence.

Fragmentation was also analyzed for phalanges and mandibles (Table 3). A total of 79 ungulate phalanges were recorded, with first phalanges being the most abundant (50.6%). Of these, 77% are fractured, and 6.3% are longitudinally fractured, primarily first phalanges. Although the index of longitudinally fractured phalanges suggests similarities between first and third phalanges, complete phalanges account for 16.4%, with third phalanges being the most common. The taxa with the highest incidence of longitudinally fractured phalanges are the red deer, BB, and the horse. As for mandibles, the NR is slightly higher than that of phalanges. All mandibles are fractured, and of these, 39.4% are longitudinally fractured, significantly raising the longitudinal fracture index (64.9%). Like the phalanges, the taxa from Group 1 show the highest proportion of this fracture type. At the stratigraphic level, they exhibit the same variability as the other indices.

Regarding skeletal preservation, there is a marked bias against the axial skeleton, basipodia, and acropodia. To a lesser extent, but still with significant bias, the girdles and even the metapodia are affected. In contrast, the regions with the highest survival are the stylopodia, zeugopodia, and cranial skeleton. Long bones are the elements that have been best preserved, particularly the diaphyses. The relationship between diaphyses and epiphyses shows a considerable difference, with a significant bias against epiphyses, especially the distal ones. Differential preservation is evident, but it is not related to bone density and therefore not to post-depositional processes. However, there are other significant taphonomic factors, such as fire, that have undoubtedly contributed to the differential preservation of the assemblage (Solano García, 2024).

4.3 Anthropogenic and carnivore modifications

The anatomical regions with the highest frequency of cut marks in the assemblage are the axial skeleton and the stylopodia, followed by the zeugopodia and girdles. Cut marks on metapodia and acropodia are present but less frequent, and are almost absent on basipodia. The distribution of cut marks and their various attributes on the represented elements are very similar across all stratigraphic units. Virtually the entire butchery processing sequence is present in all stratigraphic units, except for periosteum scraping, which shows greater variability.

Intentional fracturing evidence is present across all units and species, but occurs most frequently in Group 1. Throughout the sequence, the predominant fracture profiles are longitudinal, with a prevalence of pointed and oblique types. These are followed by spiral and pointed spiral fractures. The predominant fracture angle at all levels is right, except in level IX, where acute angles prevail. Acute angles are the second most common in all units, while mixed angles are less frequent (Solano García, 2024).

The proportion of burnt remains throughout the J/K profile is remarkably high (82.51; Table 4). The analysis of their distribution along the sequence reveals a clear difference between Complex

TABLE 2 Quantification of bone fragmentation for the entire analyzed ungulate assemblage based on various indices.

Level	Total NR				MNE/NISP						% IFOin						Integrity	Long bone circumference			Bone length					
	Fragments	Complete	F/C	S/E	*BB*	*CE*	*DD*	*SS*	*EF*	*SH*	*BB*	*CE*	*DD*	*SS*	*EF*	*SH*	0–25%	<90°	90°-180°	0–180°	Min (mm)	Max (mm)	Mean (mm)	SD	Median	CV
IV	46	2	23	3.5	1.00	1.00	1.00	1.00	0.90	1.00	100	100	100	50	100	100	86.96	57.14	42.86	100	8	180	49.47	33.20	39	67.10
V	173			26.5	1.00	1.00		1.00	1.00		100	100		100	100		97.65	33.33	66.67	100	6	90	23.18	16.88	18	72.84
VI	43	1	43	2.3	0.88	1.00	1.00	1.00	1.00	1.00	87.5	100	100	100	100	100	81.25	37.50	62.50	100	16	130	53.13	23.56	50	44.34
VII	159	10	15.9	7.6	0.40	0.78		1.00	0.59	0.63	100	81.48		100	84.375	100	86.25	68.97	31.03	100	4	190	59.31	35.04	52	59.08
VIII	80	3	26.7	2.5	0.44	0.70	1.00	1.00	0.68	0.67	100	100	100	100	86.36	100	96.55	69.23	19.23	88.46	4	124	53.40	25.46	46.00	47.67
IX	659	21	31.4	6.4	0.45	0.41	0.67	0.89	0.42	0.75	92.42	96.30	88.89	77.78	94.89	91.67	94.72	58.54	37.56	96.10	4	190	53.84	27.94	49.00	51.89
X	387	23	16.8	6.6	0.72	0.59	1.00	0.57	0.47	1.00	82.76	94.59	83.33	92.86	87.88		90.15	57.47	34.48	91.95	2	276	52.80	32.23	48.00	61.05
XI	415	26	16.0	4.8	0.64	0.37	0.67	0.79	0.57	0.57	88	97.67	100	85.71	85.71	100	89.32	42.11	45.61	87.72	3	258	47.84	28.58	42.00	59.74
XII	214	10	21.4	11.1	0.78	0.60	1.00	0.75	0.60	0.83	88.89	100	100	62.5	91.43	100	90	61.29	29.03	90.32	6	150	44.60	24.27	40.00	54.41
XIII	429	17	25.2	2.3	0.69	0.60	0.80	0.80	0.58	0.75	77.78	100	90	80	97.5	100	93.6	60.87	28.99	89.86	5	153	44.88	26.20	36.00	58.38
XIV	153	3	51	8.5	0.77	0.88		1.00	0.64	0.50	92.31	100		75	100	100	94.31	68.35	27.85	96.20	5	150	48.65	28.15	41.00	57.88
XV	536	41	13.1	5.1	0.50	0.55	1.00	1.00	0.63	0.67	92.31	95.24	83.33	100	80.56	100	90.81	61.26	32.98	94.24	2	283	51.96	36.13	44.00	69.55
XVI	144	14	10.3	4.3	1.00	0.69	0.83	1.00	0.65	1.00	100	100	100	100	100	100	97.22	66.67	33.33	100	5	142	49.60	27.33	40	55.09
XVII	46	4	11.5	2.3		0.69	1.00	1.00	1.00			100	100	66.67	100		75	30	40	70	10	105	45.43	20.39	45	44.87
Total | mean	3,484	175	19.9	5.6	0.71	0.70	0.91	0.91	0.70	0.78	92.46	97.52	95.05	85.04	93.48	99.24	90.27	55.19	38.01	93.20	2	283	49.89	30.22	44	60.58

NR, number of remains; F/C, fragmented/complete; S/E, shafts/epiphyses; % IFOin, intensity of fragmentation.

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TABLE 3 Quantification of the fragmentation of long bones, phalanges, and mandibles of ungulates.

Elements	Shafts	Epiphysis	Completes	Full shafts	Full epiphysis	Total
Humerus	75	25	0	1	1	100
Radio-ulna	64	46	0	0	7	110
Metacarpal	9	18	0	0	4	27
Femur	93	29	0	0	0	122
Tibia	104	33	0	0	4	137
Metatarsal	43	27	2	1	6	72
Metapodial	57	22	0	0	4	79
Long bones	855	34	0	0	0	889
Total	1,300	234	2	2	26	1,536
Elements	**Fractured**	**F. lengthwise**	**% FI**	**Complete**	**C/F**	**Total**
Phalanx I	33	3	9.09	4	0.12	40
Phalanx II	13	1	7.69	3	0.23	17
Phalanx III	11	1	9.09	6	0.55	18
Phalanx ind.	4		0		0	4
Total phalanx	61	5	8.20	13	0.21	79
Mandibles	57	37	64.91	0		94

%FI, percentage of longitudinal fractures; C/F, ratio of complete elements.

III ($\bar{x}$ = 82.3%, σ = 10.3%) and Complexes II ($\bar{x}$ = 96%, σ = 3.3%) and I ($\bar{x}$ = 96.1%, σ = 3%), which share the same proportion. Therefore, from Level XIII onwards, an increase in thermally altered elements is observed, persisting up to the top of the sequence.

In this analysis, all bone remains showing cut marks, green fractures, percussion marks, and evidence of burning were recorded (Table 4). Additionally, remains with carnivore tooth marks were included as complementary information. From this count, we observe that 7.62% of the remains bear cut marks, 12.9% show green fractures, 1.58% display percussion marks, and 82.5% of the remains exhibit evidence of fire. Carnivore tooth marks were recorded at a relatively low rate (0.79%) across the entire J/K assemblage. At the stratigraphic level, as in previous analyses, there is variability in the number of remains with anthropogenic modifications per level, due to the density of remains per excavated surface. However, there is a strong correlation between the various types of modification and the total number of remains without teeth for each stratigraphic level (cutmarks: $\rho = 0.877$, $p < 0.01$; percussion: $\rho = 0.822$, $p = 0.002$; burnt: $\rho = 0.972$, $p < 0.01$; fractures: $r_s = 0.832$, $p < 0.01$), except for the few carnivore tooth marks ($r_s = 0.557$, $p < 0.06$). Therefore, the results are consistent and proportional throughout the stratigraphic sequence. In other words, where there is a higher number of remains, it is reasonable to expect a higher number of anthropogenic modifications. Thus, given that the highest number of elements is found in the central levels, it is also here where the greatest number of modifications is located.

Nearly 90% of the remains are burnt, with greater representation in levels XVII–X and level IX. There is no preferential burning pattern by taxon, as around 90% of their remains also show signs of burning. However, this is not the case for the rest of the surface modifications. As expected, the taxa from Group 1 show the highest incidence of anthropogenic modifications. When we analyse the relationship between the six main taxa and cut marks, percussion marks, fractures, and carnivore tooth marks, there is a statistically significant association ($X^2 = 25.124$, df = 15, $p = 0.04831$), given the strong association within Group 1 (Figure 9A). In fact, *Cervus* and *Equus* show a strong association with cut marks and fractures, while BB is more associated with fracturing (19.8%). The red deer has a stronger relationship with percussion (24%), cut marks (20.5%), and fracturing (18.4%). The horse shows an almost equal association (~60%) with percussion, fracturing, and cut marks. Interestingly, fallow deer shows a low incidence of inflicted modifications, distancing it from the main group, while the rhinoceros shows some association primarily with fractures. In the case of the wild boar, with only two recorded cut marks and one percussion mark, it stands out as an atypical species within the assemblage. Carnivore activity is mostly associated with *Cervus* (50%) and *Equus* (30%).

Anatomical categories show a strong association with surface modifications ($X^2 = 92.0623$, df = 21, $p = 7.0971e\text{-}11$). Long bones are highly associated with percussion activities (92%), fracturing (90.3%), and cut marks (59.8%), while axial elements (18.2%), girdles (10.6%), and mandibles (6.8%) are primarily associated with cut marks (Figure 9B). Phalanges show a stronger correlation with percussion (8%) and fractures (3.7%) than with other modifications. Finally, cranial elements are distanced from the main group, with a low connection to cut marks (0.8%)

TABLE 4 Cross tables of surface bone modifications by stratigraphic levels, taxa, and anatomical categories.

Level	Cutmarks	%	Percussion	%	Green fractures	%	Burnt	%	C. toothmarks	%
IV	3	6.5	1	2.2	5	10.9	42	95.5	1	2.2
V*	2	1.2	1	0.6	1	0.6	170	99.4		
VI	2	4.5			4	9.1	40	97.6	1	2.3
VII	25	15.3	5	3.1	25	15.3	154	91.7	3	1.8
VIII	8	10.1			8	10.1	75	93.8	1	1.3
IX	75	11.7	11	1.7	152	23.7	625	92.0	5	0.8
X	31	8.1	7	1.8	55	14.4	368	98.4	5	1.3
XI	13	3.2	8	2.0	31	7.6	400	98.8	2	0.5
XII	19	9.2	2	1.0	18	8.7	196	97.5	4	1.9
XIII	24	5.6	3	0.7	45	10.6	358	94.2	2	0.5
XIV	4	2.7	2	1.4	12	8.1	119	81.5		
XV	46	8.9	13	2.5	54	10.5	332	70.3	3	0.6
XVI	8	6.1	1	0.8	23	17.4	99	74.4	2	1.5
XVII					7	15.2	41	91.1		
Total	260	7.6	54	1.6	440	12.9	3,019	82.5	29	0.8
	Cutmarks	%	Green fractures	%	Percussion	%	Toothmarks	%	Total	
Taxa										
BB	20	15.2	43	19.8	3	12.0	0	0.0	66	
Cervus	27	20.5	40	18.4	6	24.0	5	50.0	78	
Dama	3	2.3	2	0.9	0	0.0	1	10.0	6	
Equus	76	57.6	128	59.0	15	60.0	3	30.0	222	
Stephanorhinus	4	3.0	4	1.8	0	0.0	1	10.0	8	
Sus	2	1.5	0	0.0	1	4.0	0	0.0	3	
Total	132		217		25		10		384	
Element										
Axial	24	18.2	1	0.5	0	0	1	10	26	
Flat bone	0	0.0	1	0.5	0	0	0	0	1	
Girdles	14	10.6	4	1.8	0	0	2	20	20	
Long bone	79	59.8	196	90.3	23	92	5	50	303	
Mandible	9	6.8	4	1.8	0	0	0	0	13	
Phalanx	3	2.3	8	3.7	2	8	1	10	14	
Short bones	2	1.5	2	0.9	0	0	0	0	4	
Skull	1	0.8	1	0.5	0	0	1	10	3	
Total	132		217		25		10		384	

Percentages for the stratigraphic levels were calculated using the total NR without teeth from the layer.

and fractures (0.5%). Carnivore tooth marks are predominantly associated with long bones (50%) and girdles (20%) from red deer and horse.

In summary, the presence of the three main species throughout the sequence reflects the exploitation of meat, marrow, and fat, as indicated by the fracturing and its correlation with utility indices, and the systematic distribution of predominant cut marks on ribs and long bone diaphyses (Solano García, 2024).

5 Discussion

The sample from the J/K profile that we analyzed shows a significant bias, as previously mentioned, in terms of the number of remains in units IV, V, VI, and XVII, due to the smaller volume of excavated surface. Nevertheless, the results appear to be consistent with the analyses conducted. This allows us to make the first diachronic approximation regarding ungulate exploitation at

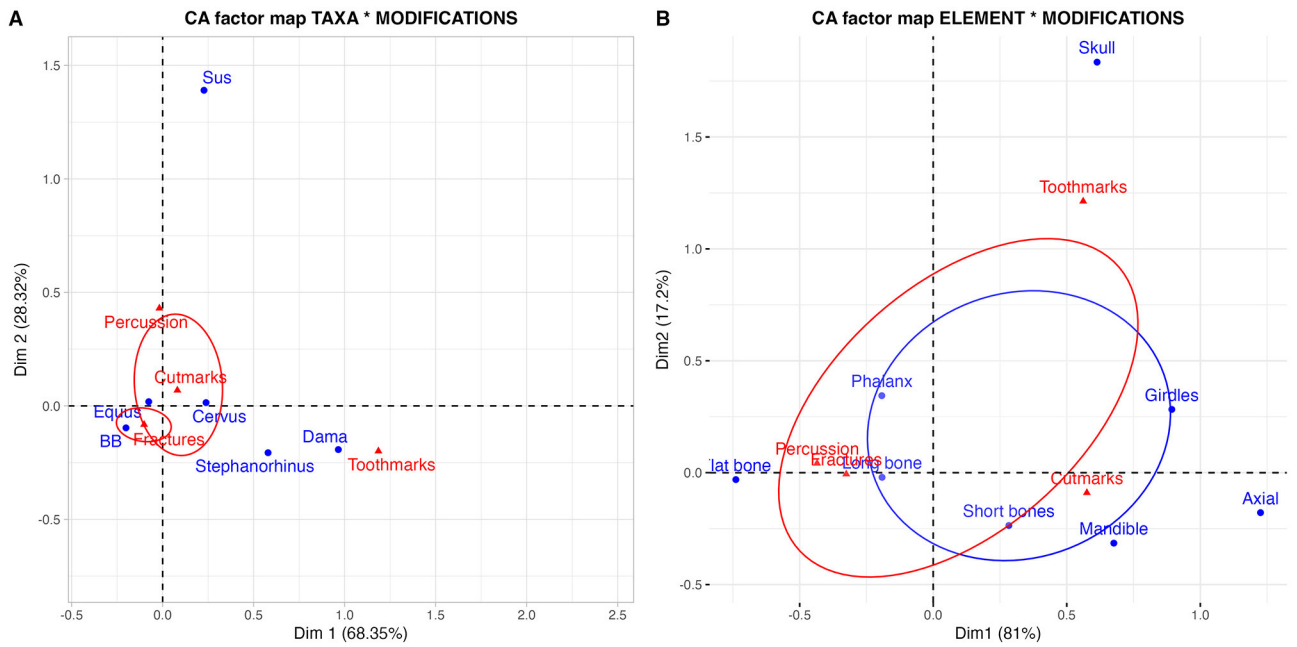

FIGURE 9
Graphical output of the correspondence analysis based on surface bone modifications between the main taxa **(A)** and elements categories **(B)**. The ellipses represent 95% confidence intervals for taxa (blue) and modifications (red).

Cueva del Ángel. Initially, we operate under the premise that we are dealing with a residential site (Binford, 1980, 1983; Kuhn and Stiner, 2019) where various activities were carried out, including flint knapping, bone retouchers, intensive use of fire, and different butchering activities, with a very low frequency of carnivore activity (Barroso Ruíz et al., 2011; Solano García, 2024).

The origin of the accumulation is clearly anthropogenic (Solano García, 2024), considering the high proportion of burnt remains (between 80 and 90%), the intensity of fragmentation (Tables 2, 3), where 98.6% of the remains are fragmented with average lengths around 5 cm, and the surface modifications (Table 4). However, carnivores are present throughout the sequence, and along with bite marks, they may suggest various interaction scenarios (Brain, 1981; Stiner, 2002, 2004a, 2012; Blasco and Rosell, 2009; Rosell and Blasco, 2009; Rosell et al., 2010; Yravedra, 2010; Enloe, 2012; Dusseldorp, 2013; Saladié et al., 2014; Camarós et al., 2016, 2017; Sauqué and Sanchis, 2017; Arilla et al., 2020). Nonetheless, the low overall herbivore-carnivore ratio (4.89) and the low occurrence of bite marks (0.79%) (Klein and Cruz Uribe, 1984), together with the absence of digested remains or coprolites, suggest that carnivores played a very secondary and opportunistic role as accumulators or modifiers (Blumenschine, 1995; Capaldo, 1998; Marean et al., 2000; Pickering, 2002). However, without completely ruling out carnivore activity, recent research over the last decade suggests that in the Middle Paleolithic, carnivores may have played a different role as a resource source and were possibly exploited (Tagliacozzo et al., 2013; Gabucio et al., 2014; Gómez-Olivencia et al., 2018; Val et al., 2020; Smith et al., 2021; Mata-González et al., 2023; Russo et al., 2023; Verheijen et al., 2023). In Cueva del Ángel, bears, wolves, and lynxes are recurrently present throughout the sequence, like ungulates, but with relatively few remains so far. In fact, most of the carnivore remains are burned. However, in Level XIII, followed by Level XI, there is a slight increase in carnivore remains, although with very low activity in both levels (<0.5%). The highest carnivore activity, albeit always at low rates, seems to occur from Level VII onwards. For now, until the detailed taphonomic histories of all levels are known, a very oportunistic and sporadic role has been proposed for carnivores as potential scavengers-prowlers exploiting the waste from human activities in Units XVII, XVI, XIII, IX, and VII (Solano García, 2024) or perhaps an incipient synanthropic behavior (Baumann, 2023) and/or consequences arising from the use of fire.

The use of fire is well-documented throughout the site's stratigraphic sequence. Although hearth structures have not yet been delineated, preliminary sedimentological and micromorphological studies indicate their presence (Monge et al., 2020). Its use appears to be a consistent feature throughout all occupations of the Cueva del Ángel. The fact that around 90% of the recovered bone remains exhibit thermal alterations, as well as a third of the lithic industry, highlights the importance of fire as a central element in the lives of these human groups at the site. This high concentration of burned remains is uncommon in Middle Pleistocene sites (Roebroeks and Villa, 2011). In other sites with burned bone remains of similar chronologies, such as Orgnac-3, Terra Amata, Lazaret, and Payre (Moigne and Barsky, 1999; Moncel and Patou-Mathis, 2005; Valensi et al., 2005), the proportion does not exceed half of the sample. Even in records with hearths and controlled use of fire, like Hayonim Cave or Kebara (Speth and Tchernov, 2001; Stiner et al., 2001), the frequency of burned remains is low. Few sites, such as Qesem Cave (Blasco et al., 2014; Barkai et al., 2017) or Bolomor XI, IV (Blasco et al., 2013), have more than 50% of burned remains. Generally, sites

with a high frequency of burned remains are found in the Upper Pleistocene, for example: Pech de l'Azé IV (∼57%) (Dibble et al., 2009); La Quina 8–6 (∼95%) (Debénath et al., 1998); Krems-Wachtberg (90–98%) (Fladerer et al., 2012); and levels 15–30 of Esquilleu (88–99%) (Yravedra and Uzquiano, 2013). In Cueva del Ángel, the identified colors, compared with experimental studies (Lebon et al., 2008), suggest medium exposures between 200 and 400°C, although some remains show evidence of having reached temperatures of 700°C. These temperatures are typical for roasting meat (Shipman et al., 1984; Buikstra and Swegle, 1989); however, we cannot rule out other culinary or mechanical activities related to fat and bone respectively. Additionally, the presence of hundreds of small burned fragments (<2 cm) may suggest other uses of bone, such as fuel (Costamagno et al., 2009, 2010), or their disposal during cleaning activities (For in-depth discussion see, Solano García, 2024).

This study focuses on the six recurring ungulate taxa found in the fossil assemblage: *Bos/Bison*, *Cervus*, *Dama*, *Equus*, *Sus*, and *Rhino*. Although the elephant is present in three levels (VII, XII, XVII) and the ibex only in one (XVII), their representation so far is minimal, with only one remain per level. Among these taxa, the dominant species based on MNI are the horse (28.5%), BB, and red deer (19 and 17.5%, respectively). If the BB group were separated, the red deer would be the second most represented species. In fact, the taxa with the highest anatomical representation are the horse and red deer, followed by BB, fallow deer, rhinoceros, and wild boar. However, across the entire assemblage, there are more wild boar individuals (14.6%) than rhinoceros (9.5%) and fallow deer (8%). Regarding age at death, around 75% are adults, indicating an adult-dominant mortality profile (Stiner, 1990), consistent with hunting activities (Gaudzinski and Roebroeks, 2000) and the procurement of larger amounts of resources.

From the statistical analysis of the various indices, we have been able to differentiate two groups with similar patterns throughout the entire sequence. Group 1 (*Equus*, *Cervus*, BB) is the best anatomically represented and has the highest survival index. Its anatomical configuration, fragmentation, and surface modifications are very similar, thus reflecting the same exploitation processes. The higher proportion of long bones, followed by cranial and girdle remains, indicates a selection and preference for the parts richest in meat and bone marrow. This is further supported by the location of the anthropogenic modifications, although BB and *Rhino* seem to show a pattern more oriented toward fracturing and marrow extraction, consistent with the utility indices calculated by Solano García (2024). Group 2 (*Dama*, *Sus*, *Rhino*) also shows a similar distribution among its members, although *Dama* closely approaches the configuration of Group 1, as its skeletal survival is more similar to that of BB, while *Sus* shows a very different anatomical representation compared to the others. On the other hand, the data on *Rhino* indicate activities related to butchering and marrow extraction. Overall, the species in Group 2, though less abundant, are always present throughout the sequence. Therefore, they likely represent a supplementary exploitation group, where *Rhino* and fallow deer could provide additional protein and fat to the diet. However, the anatomical representation of wild boar presents an outlier in the exploitation pattern for diet, possibly indicating the use of wild boar for other resources.

The anatomical representation of the three main species is characterized by the elements richest in meat and fat, particularly evident in the higher representation of hindlimbs in *Equus* and a more balanced distribution in BB. Along with the predominance of cut marks on diaphyses, as well as on epiphysis, ribs, mandibles, pelvises, and short bones, this suggests primary access and butchery activities aimed at consumption. In the levels with the highest density of remains, the entire operational chain is documented (Solano García, 2024).

The recurrent presence of these taxa throughout almost the entire sequence suggests their importance as a resource in a favorable ecosystem for these ungulates (Filella et al., 2024), implying knowledge of hunting grounds and a preference for high-return rates (Ben-Dor and Barkai, 2021) or social prestige (Hawkes et al., 2001). In the long term, this suggests stable subsistence strategies, as has been documented at the Payre site (Ecker et al., 2013), although small-scale temporal strategic changes could be confirmed through isotopic analyses (Bocherens et al., 2016). The persistent focus on horse, red deer, and large bovids, which we might call the "Mediterranean triad," suggests a preference and therefore a selection of species within the faunal spectrum of the hunting range. When compared with nearby contemporaneous sites, the ungulate species described are almost the same. At the Solana del Zamborino site (400–300 ka): *Palaeoloxodon antiquus*, *Equus caballus*, *Stephanorhinus hemitoechus*, *Cervus elaphus*, *Capreolus capreolus*, *Dama sp.*, *Bos primigenius*, *Bison priscus*, *Hippopotamus sp.*, and *Sus scrofa* (Martín-Penela, 1988); and at Cueva Horá (Upper Acheulean-Mousterian): *Equus caballus*, *Equus hydruntinus*, *Stephanorhinus hemitoechus*, *Cervus elaphus*, *Bos/Bison*, and *Capra pyrenaica* (Martín-Penela, 1986). Therefore, it is likely that this is either the only faunal spectrum of ungulates present in the southern Iberian Peninsula or that they are exploiting the same species. We know that although there is greater representation of the group formed by equids, red deer, and BB, other taxa such as fallow deer, ibex, rhinoceros, and wild boar are exploited with the same frequency in parallel. In reality, they are exploiting nearly everything available, but with different scopes and objectives.

In Iberia, other sites with similar chronologies and the predominant exploitation of Group 1 taxa accessed primarily by hominins have been identified, such as TD10.1 in Atapuerca (Díez Fernández-Lomana et al., 1999; Rodríguez-Hidalgo et al., 2015), Bolomor Cave (Blasco et al., 2010, 2013), Cuesta de la Bajada (Domínguez-Rodrigo et al., 2015), Navalmaíllo Rockshelter (Huguet et al., 2010; Moclán et al., 2020), Galeria Pesada (Marks et al., 2002), and Gruta da Aroeira (Croitor et al., 2019). These sites indicate that by MIS 9, or even earlier as seen in TD6.2 (Saladié et al., 2011), well-established strategies for hunting and processing medium-to-large-sized animals were already in place. Within this same context, the results presented here allow us to include Cueva del Ángel.

The intensity of fragmentation is very high and highlights the anthropogenic nature of the site. The results reveal the use of percussion and green bone fracturing throughout the sequence, with a focus on marrow exploitation, especially in Group 1 (Solano García, 2024). Additionally, the intensity of marrow exploitation is evidenced by the recurrent presence of longitudinally fractured phalanges in decreasing frequency by size (Starkovich, 2017) However, their low representation so far does not allow for diachronic inferences. Fractured mandibles, though, show a noticeable increase in levels XIII and XI, which is consistent

with a possible rise in exploitation intensity from level XIII onwards (Solano García, 2024) and could be correlated with the increase in burnt remains from the same level onwards. On the other hand, the low proportion of epiphyses and the intense fragmentation of the assemblage could be related to fat exploitation (Morin, 2020b,a), but this activity does not seem sufficiently demonstrated at this time, given the taphonomic challenges (Blasco et al., 2024), especially when considering similar contexts involving the use of fire in areas configured as large hearths (Barroso Ruíz et al., 2011; Barkai et al., 2017). Nonetheless, there is a correlation between the number of diaphyses and epiphyses throughout the sequence. Regardless, there is a persistent pattern of long bone exploitation focused on protein and fat extraction. Therefore, this reflects an intense and sustained exploitation of resources from large and medium-sized ungulates.

Considering the exploitation of phalanges and mandibles (Starkovich, 2017) and the introduction of fast-moving animals as phenomena of intensification (Stiner, 2013; Jones, 2016; Lloveras et al., 2016; Starkovich and Ntinou, 2017), we might assume we are observing cases of high-rank resource depression (Betts and Friesen, 2004, 2006; Broughton et al., 2007; Lupo, 2007), climatic changes, or ecological or demographic pressures (Stiner et al., 1999; Zeder, 2012). However, it appears that the inclusion of leporids in the diet does not reflect intensification phenomena but rather density-driven ecological processes, making them more comparable to high-rank resources (Morin et al., 2020). Moreover, in our assemblage, there are no significant variations in specific or anatomical representation throughout the sequence, except for subtle changes in exploitation intensity or the introduction of small animals (Solano García, 2024). Big game hunting, while offering high return rates, involves significant costs and risks due to the low frequency of encounters, the danger posed by the prey, and the skill required from hunters. This makes it a low-success activity that must often be supplemented by gathering. However, it also confers considerable social prestige (Hawkes et al., 2001; Hawkes, 2016). Therefore, the diversified contributions of small fauna as a dietary supplement (Blasco et al., 2022) may have functioned as both an economic and social buffer, helping to sustain large game hunting activities. Additionally, the subtle variations observed—such as signs of intensification—could reflect strategic adjustments aimed at adapting to environmental fluctuations and contingencies, thereby maintaining lifestyles.

Current research into Neanderthal subsistence strategies suggests a high level of adaptability and flexibility (Romagnoli et al., 2022). These strategies appear to have incorporated methods designed to increase the predictability of food acquisition while ensuring group security and minimizing social costs (Vicent, 1991). Ultimately, their purpose was likely to stabilize group dynamics and mitigate potential risks.

6 Conclusions

The results of the study conducted at Cueva del Ángel should be interpreted within the context of recent advances in understanding subsistence strategies of Late Middle Pleistocene groups. During this time, the shift toward broad-spectrum diets and technological innovations, such as the use of fire, transformed the practices of animal resource exploitation. Although the excavated area remains limited, the findings are consistent with similar studies in western Eurasia, revealing a recurrent exploitation of medium- and large-sized ungulates throughout the sequence.

The zooarchaeological study of Cueva del Ángel reveals a persistent exploitation of *Equus*, large bovids, and *Cervus*, with clear evidence of primary access and an intensive selection of the most meat- and marrow-rich parts, highlighting their importance as dietary staples. Although less represented, fallow deer, rhinoceros, and wild boar are also present in almost all levels, contributing additional resources, with more defined exploitation patterns for fallow deer and predominantly secondary access for rhinoceros. Wild boar displays atypical patterns that require specific analysis. The low presence of carnivores, despite the recurrent occurrence of bears and lynxes, along with their minimal impact and significant anthropogenic activity, reinforces the interpretation of a human-origin accumulation. The diachronic analysis of the bone remains suggests that the Neanderthals who occupied the cave engaged in intensive hunting and exploitation of large mammals, particularly horses, red deer, and large bovids, a pattern also observed in other Mediterranean sites from the same period. This species selection pattern, with an emphasis on adult individuals, reflects a deliberate and flexible approach to hunting strategies, as well as the persistent pursuit of high-energy resources. Given the high costs of big game hunting, other animal resources, with lower energy impact and archaeological footprint—though likely not lower economic value—were also recurrently exploited. This suggests a close relationship between the various exploitation strategies adopted. In summary, it is possible that these strategies were aimed at maintaining the subsistence habits and lifestyles of the hunters of the "Mediterranean Triad."

In this study, we provide an initial diachronic approach to the subsistence base of these human groups. However, many aspects of their daily life and their relationship with the environment remain to be explored. How is it possible for them to maintain a subsistence strategy based on the same species for thousands of years in the same location? These should be addressed in the future through higher temporal resolution taphonomic and palaeoenvironmental histories of each level of this promising site.

In conclusion, the Cueva del Ángel site provides valuable insight into the evolution of Neanderthal subsistence strategies, which combined the intensive exploitation of large ungulates with a progressive diversification of resources. This adaptive behavior highlights the remarkable ability of these groups to adjust to environmental changes and ensure food security within Mediterranean ecosystems.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JS-G: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. A-MM: Data curation, Investigation, Methodology, Supervision, 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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2025.1517568/full#supplementary-material

References

Arilla, M., Rosell, J., and Blasco, R. (2020). A neo-taphonomic approach to human campsites modified by carnivores. *Sci. Rep.* 10, 1–15. doi: 10.1038/s41598-020-63431-8

Bailey, G. (2007). Time perspectives, palimpsests and the archaeology of time. *J Anthropol. Archaeol.* 26, 198–223. doi: 10.1016/j.jaa.2006.08.002

Bailey, G., and Galanidou, N. (2009). Caves, palimpsests and dwelling spaces: examples from the Upper Palaeolithic of south-east Europe. *World Archaeol.* 41, 215–241. doi: 10.1080/00438240902843733

Barkai, R., Rosell, J., Blasco, R., and Gopher, A. (2017). Fire for a reason: barbecue at Middle Pleistocene Qesem Cave, Israel. *Curr. Anthropol.* 58, S314–S328. doi: 10.1086/691211

Barone, R. (2010). *Anatomie comparée des mammifères domestiques. Tome 1, Ostéologie*., 5e édition. Paris: Vigot Freres.

Barroso Ruíz, C., Botella Ortega, D., Caparrós, M., Moigne, A. M., Celiberti, V., Testu, A., et al. (2011). The Cueva del Angel (Lucena, Spain): an Acheulean hunters habitat in the South of the Iberian Peninsula. *Quat. Int.* 243, 105–126. doi: 10.1016/j.quaint.2011.02.021

Baumann, C. (2023). The paleo-synanthropic niche: a first attempt to define animal's adaptation to a human-made micro-environment in the Late Pleistocene. *Archaeol. Anthropol. Sci.* 15:63. doi: 10.1007/s12520-023-01764-x

Behrensmeyer, A. K. (1978). Taphonomic and Ecologic Information from Bone Weathering. *Paleobiology* 4, 150–162.

Ben-Dor, M., and Barkai, R. (2021). Prey size decline as a unifying ecological selecting agent in Pleistocene human evolution. *Quaternary* 4:7. doi: 10.3390/quat4010007

Berlioz, E., Capdepon, E., and Discamps, E. (2023). A long-term perspective on Neanderthal environment and subsistence: insights from the dental microwear texture analysis of hunted ungulates at Combe-Grenal (Dordogne, France). *PLoS ONE* 18:e0278395. doi: 10.1371/journal.pone.0278395

Bermúdez, F. J., Martínez de Pinillos, M., Medina-Lara, F., Barroso-Medina, C., Cabral-Mesa, A. L., Santiago-Pérez, A., et al. (2023). A human lower third molar from the Acheulean site of Cueva del Ángel (Lucena, Córdoba, Spain). *Am. J. Biol. Anthropol.* 180, 386–400. doi: 10.1002/ajpa.24677

Betts, M. W., and Friesen, T. M. (2004). Quantifying hunter–gatherer intensification: a zooarchaeological case study from Arctic Canada. *J. Anthropol. Archaeol.* 23, 357–384. doi: 10.1016/J.JAA.2004.07.001

Betts, M. W., and Friesen, T. M. (2006). Declining foraging returns from an inexhaustible resource? Abundance indices and beluga whaling in the western Canadian Arctic. *J. Anthropol. Archaeol.* 25, 59–81. doi: 10.1016/J.JAA.2005.11.001

Binford, L. R. (1980). Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formation. *Am. Antiq.* 45, 4–20.

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths*. New York, NY: Academic Press.

Binford, L. R. (1983). *In Pursuit of the Past: Decoding the Archaeological Record*. New York, NY: Thames and Hudson.

Blain, H.-A., Fagoaga, A., Ruiz-Sánchez, F. J., García-Medrano, P., Ollé, A., and Jiménez-Arenas, J. M. (2021). Coping with arid environments: a critical threshold for human expansion in Europe at the Marine Isotope Stage 12/11 transition? The case of the Iberian Peninsula. *J. Hum. Evol.* 153:102950. doi: 10.1016/j.jhevol.2021.102950

Blasco, R. (2008). Human consumption of tortoises at level IV of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839–2848. doi: 10.1016/J.JAS.2008.05.013

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Amsterdam: Elsevier), 123–143. doi: 10.1016/B978-0-12-821428-2.00010-X

Blasco, R., Fernández Peris, J., and Rosell, J. (2010). Several different strategies for obtaining animal resources in the late Middle Pleistocene: the case of level XII at Bolomor Cave (Valencia, Spain). *C. R. Palevol.* 9, 171–184. doi: 10.1016/j.crpv.2010.05.004

Blasco, R., and Peris, J. F. (2009). Middle Pleistocene bird consumption at level XI of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 36, 2213–2223. doi: 10.1016/J.JAS.2009.06.006

Blasco, R., and Rosell, J. (2009). Who was the first? An experimental application of carnivore and hominid overlapping marks at the Pleistocene archaeological sites. *C. R. Palevol.* 8, 579–592. doi: 10.1016/j.crpv.2009.06.003

Blasco, R., Rosell, J., Assaf, E., Barkai, R., and Gopher, A. (2024). Exploring the lack of articular ends at the Middle Pleistocene site of Qesem Cave, Israel. *J. Hum. Evol.* 189:103509. doi: 10.1016/J.JHEVOL.2024.103509

Blasco, R., Rosell, J., Domínguez-Rodrigo, M., Lozano, S., Pastó, I., Riba, D., et al. (2013). Learning by heart: cultural patterns in the faunal processing sequence during the Middle Pleistocene. *PLoS ONE* 8:e55863. doi: 10.1371/journal.pone.0055863

Blasco, R., Rosell, J., Gopher, A., and Barkai, R. (2014). Subsistence economy and social life: a zooarchaeological view from the 300 kya central hearth at Qesem Cave, Israel. *J. Anthropol. Archaeol.* 35, 248–268. doi: 10.1016/j.jaa.2014.06.005

Blasco, R., Rosell, J., Smith, K. T., Maul, L. C., Sañudo, P., Barkai, R., et al. (2016). Tortoises as a dietary supplement: a view from the Middle Pleistocene site of Qesem Cave, Israel. *Quat. Sci. Rev.* 133, 165–182. doi: 10.1016/j.quascirev.2015.12.006

Blumenschine, R. J. (1995). Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29, 21–51. doi: 10.1006/jhev.1995.1046

Blumenschine, R. J., Marean, C. W., and Capaldo, S. D. (1996). Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *J. Archaeol. Sci.* 23, 493–507. doi: 10.1006/jasc.1996.0047

Blumenschine, R. J., and Selvaggio, M. M. (1988). Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 333, 763–765. doi: 10.1038/333763a0

Bocherens, H., Díaz-Zorita Bonilla, M., Daujeard, C., Fernandes, P., Raynal, J.-P., and Moncel, M.-H. (2016). Direct isotopic evidence for subsistence variability in Middle Pleistocene Neanderthals (Payre, southeastern France). *Quat. Sci. Rev.* 154, 226–236. doi: 10.1016/j.quascirev.2016.11.004

Botella Ortega, D., Barroso Ruiz, C., Riquelme Cantal, J. A., Abdessadok, S., Caparrós, M., Verdú Bermejo, L., et al. (2006). La Cueva del Ángel (Lucena, Córdoba), a site of the Middle and Early Upper Pleistocene in the South of the Iberian Peninsula. *Trabajos Prehist.* 63, 153–165. doi: 10.3989/tp.2006.v63.i2.22

Brain, C. (1981). *The hunters or the hunted?: an introduction to African cave taphonomy*. University of Chicago Press. Available online at: https://books.google.com/books?hl=esandlr=andid=E4JyZgr8y50Candoi=fndandpg=PR9andots=5ho5dhQLCpandsig=RNBc4bvf-s3tknjrt6XVfRTMB7k (accessed September 25, 2024).

Broughton, J. M., Mullins, D., and Ekker, T. (2007). Avian resource depression or intertaxonomic variation in bone density? A test with San Francisco Bay avifaunas. *J. Archaeol. Sci.* 34, 374–391. doi: 10.1016/J.JAS.2006.05.013

Brugal, J.-P. (1984). Le Bos primigenius boj 1827 du pleistocene moyen des grottes de lunel-viel (herault). *Bull. Musee D'Anthropol. Prehist. Monaco* 28, 7–62.

Buikstra, J., and Swegle, M. (1989). "Bone modification due to burning: experimental evidence," in *Bone Modification*, eds. R. Bonnichsen and M. S. (ed) (Orono, Maine: Center for the Study of the First Americans, Institute for Quaternary Studies, Universtiy of Maine), 247–258.

Bunn, H. T. (1981). Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291, 574–577.

Bunn, H. T., Kroll, E. M., Ambrose, S. H., Behrensmeyer, A. K., Binford, L. R., Blumenschine, R. J., et al. (1986). Systematic butchery by Plio/Pleistocene Hominids at Olduvai Gorge, Tanzania [and Comments and Reply]. *Curr. Anthropol.* 27, 431–452.

Cain, C. R. (2005). Using burned animal bone to look at Middle Stone Age occupation and behavior. *J. Archaeol. Sci.* 32, 873–884. doi: 10.1016/j.jas.2005.01.005

Camarós, E., Cueto, M., Teira, L., Münzel, S. C., Plassard, F., Arias, P., et al. (2017). Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior. *Quat. Int.* 435, 237–246. doi: 10.1016/j.quaint.2015.11.027

Camarós, E., Münzel, S. C., Cueto, M., Rivals, F., and Conard, N. J. (2016). The evolution of Paleolithic hominin–carnivore interaction written in teeth: stories from the Swabian Jura (Germany). *J. Archaeol. Sci. Rep.* 6, 798–809. doi: 10.1016/j.jasrep.2015.11.010

Capaldo, S. D. (1998). Methods, marks, and models for inferring hominid and carnivore behavior. *J. Hum. Evol.* 35, 323–326.

Chazan, M. (2009). "Assessing the Lower to Middle Paleolithic transition," in *Sourcebook of Paleolithic Transitions*, eds. M. Camps, and P. Chauhan (New York, NY: Springer), 237–243. doi: 10.1007/978-0-387-76487-0_14

Costamagno, S., Théry-Parisot, I., Castel, J. C., and Brugal, J. P. (2009). "Combustible ou non? Analyse multifactorielle et modèles explicatifs sur des ossements brûlés paléolithiques," in *Gestion des Combustibles au Paléolithique et au Mésolithique: Nouveaux Outils, Nouvelles Interprétations*, eds. C. S. Théry-Parisot, and I. A. Henry (Oxford: Proceedings of workshop 21. XVe Congrès de l'UISPP, Lisbonne, 4-9 septembre 2006. BAR International Series 1914, Archaeopress), 47–60.

Costamagno, S., Théry-Parisot, I., Kuntz, D., Bon, F., and Mensan, R. (2010). "Impact taphonomique d'une combustion prolongée sur des ssements utilisés comme combustible ," in *Taphonomie de la Combustion des Résidus Organiques et des Structures de Combustion en Contexte Archéologique*, eds. L. Chabal, S. Costamagno, and I. Théry (Nice: Actes de la table ronde, 27-29 mai 2008, CEPAM.P@lethnologie), 173–188.

Crater Gershtein, K. M., Zaidner, Y., and Yeshurun, R. (2022). A campsite on the open plain: zooarchaeology of Unit III at the Middle Paleolithic site of Nesher Ramla, Israel. *Quat. Int.* 624, 49–66. doi: 10.1016/j.quaint.2020.01.026

Croitor, R., Sanz, M., and Daura, J. (2019). Deer remains from the Middle Pleistocene site of Gruta da Aroeira (Portugal): Iberian faunal endemism and implications for hominin paleobiogeography. *Quat. Sci. Rev.* 225:106022. doi: 10.1016/j.quascirev.2019.106022

Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., et al. (2019). Neanderthal selective hunting of reindeer? The case study of Abri du Maras (South-Eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011. doi: 10.1007/s12520-017-0580-8

De Juana, S., and Domínguez-Rodrigo, M. (2011). Testing analogical taphonomic signatures in bone breaking: a comparison between hammerstone-broken equid and bovid bones. *Archaeometry* 53, 996–1011. doi: 10.1111/j.1475-4754.2010.00576.x

Debénath, A., Jelinek, A. J., Armand, D., Chase, P. G., Dibble, H. L., Mercier, N., et al. (1998). Nouvelles fouilles à La Quina (Charente) : résultats préliminaires. *Gallia Préhist.* 40, 29–74. doi: 10.3406/galip.1998.2400

Dibble, H. L., Berna, F., Goldberg, P., Mcpherron, S. P., Mentzer, S., Niven, L., et al. (2009). A preliminary report on Pech de l'Azé IV, Layer 8 (Middle Paleolithic, France). *Paleoanthropology* 2019, 182–219. doi: 10.4207/PA.2009.ART30

Diedrich, C. G. (2010). Specialized horse killers in Europe: foetal horse remains in the Late Pleistocene Srbsko Chlum-Komín Cave hyena den in the Bohemian Karst (Czech Republic) and actualistic comparisons to modern African spotted hyenas as zebra hunters. *Quat. Int.* 220, 174–187. doi: 10.1016/j.quaint.2010.01.023

Díez Fernández-Lomana, J. C., Fernández Jalvo, Y., Rosell, J., and Cáceres, I. (1999). Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). *J. Hum. Evol.* 37, 623–652. doi: 10.1006/jhev.1999.0346

Domínguez-Rodrigo, M., Barba, R., Soto, E., Sesé, C., Santonja, M., Pérez-González, A., et al. (2015). Another window to the subsistence of Middle Pleistocene hominins in Europe: a taphonomic study of Cuesta de la Bajada (Teruel, Spain). *Quat. Sci. Rev.* 126, 67–95. doi: 10.1016/j.quascirev.2015.08.020

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B., and Rodríguez, M. (2009). A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654. doi: 10.1016/j.jas.2009.07.017

Dusseldorp, G. L. (2013). "Neanderthals and cave hyenas: co-existence, competition or conflict?" in *Vertebrate Paleobiology and Paleoanthropology*, eds. J. Clark, and J. Speth (Cham: Springer), 191–208. doi: 10.1007/978-94-007-6766-9_12

Ecker, M., Bocherens, H., Julien, M.-A., Rivals, F., Raynal, J.-P., and Moncel, M.-H. (2013). Middle Pleistocene ecology and Neanderthal subsistence: insights from stable isotope analyses in Payre (Ardèche, southeastern France). *J. Hum. Evol.* 65, 363–373. doi: 10.1016/j.jhevol.2013.06.013

Enloe, J. G. (2012). Neanderthals, bears and hyenas, oh my! competition for exclusive use of space. *J. Taphonomy* 10, 185–195.

ESRI Inc (2023). *ArcGIS Pro (Version 3.1)*. Esri Inc. Available at: https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

Falguères, C., Ghaleb, B., Tombret, O., Ben Arous, E., Richard, M., Moigne, A. M., et al. (2019). ESR/U-series dates on equus teeth from the Middle Pleistocene Acheulean site of Cueva del Angel, Spain. *Quat. Geochronol.* 49, 297–302. doi: 10.1016/j.quageo.2018.02.003

Filella, J. B., Morán, F., Kemp, Y. J. M., Munir, H., Gort-Esteve, A., and Cassinello, J. (2024). Diet comparison between sympatric European bison, red deer and fallow deer in a Mediterranean landscape. *Biodivers. Conserv.* 33, 1775–1791. doi: 10.1007/S10531-024-02832-X/TABLES/3

Fisher, J. (1995). Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory* 2, 7–68. doi: 10.1007/bf02228434

Fladerer, F. A., Salcher-Jedrasiak, T. A., and Händel, M. (2012). Hearth-side bone assemblages within the 27 ka BP Krems-Wachtberg settlement: fired ribs and the mammoth bone-grease hypothesis. *Quat. Int.* 351, 115–133. doi: 10.1016/j.quaint.2012.06.030

Forsten, A., and Moigne, A. M. (1998). The horse from the middle Pleistocene of Orgnac-3 (Ardèche, France) [Les chevaux du site du Pléistocène moyen d'Orgnac 3 (Ardèche, France)]. *Quaternaire* 9, 315–323. doi: 10.3406/QUATE.1998.1613

Gabucio, M. J., Cáceres, I., Rodríguez-Hidalgo, A., Rosell, J., and Saladié, P. (2014). A wildcat (Felis silvestris) butchered by Neanderthals in Level O of the Abric Romaní site (Capellades, Barcelona, Spain). *Quat. Int.* 326–327, 307–318. doi: 10.1016/j.quaint.2013.10.051

García-Medrano, P., Cáceres, I., Ollé, A., and Carbonell, E. (2017). The occupational pattern of the Galería site (Atapuerca, Spain): a technological perspective. *Quat. Int.* 433, 363–378. doi: 10.1016/j.quaint.2015.11.013

Gaudzinski, S. (2006). Monospecific or species-dominated faunal assemblages during the middle Paleolithic in Europe. *Interdisciplinary Contributions to Archaeology*, eds. E. Hovers, and S. L. Kuhn (Cham: Springer), 137–147. doi: 10.1007/0-387-24661-4_8

Gaudzinski, S., and Roebroeks, W. (2000). Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, Northern Germany. *J. Hum. Evol.* 38, 497–521. doi: 10.1006/jhev.1999.0359

Gaudzinski-Windheuser, S., and Kindler, L. (2012a). Research perspectives for the study of Neandertal subsistence strategies based on the analysis of archaeozoological assemblages. *Quat. Int.* 247, 59–68. doi: 10.1016/j.quaint.2010.11.029

Gaudzinski-Windheuser, S., and Kindler, L. (2012b). The evolution of hominin food resource exploitation in Pleistocene Europe: recent studies in Zooarchaeology. *Quat. Int.* 252, 1–2. doi: 10.1016/j.quaint.2011.10.017

Gaudzinski-Windheuser, S., and Niven, L. (2009). "Hominin Subsistence Patterns During the Middle and Late Paleolithic in Northwestern Europe," in *The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*, eds. J.-J. Hublin, and M. P. Richards (Cham: Springer Science + Business Media B.V.), 97–109.

Gaudzinski-Windheuser, S., Noack, E. S., Pop, E., Herbst, C., Pfleging, J., Buchli, J., et al. (2018). Evidence for close-range hunting by last interglacial Neanderthals. *Nat. Ecol. Evol.* 2, 1087–1092. doi: 10.1038/s41559-018-0596-1

Gee, H. (1993). The distinction between postcranial bones of *Bos primigenius* Bojanus, 1827 and *Bison priscus* Bojanus, 1827 from the British pleistocene and the taxonomic status of *Bos* and *Bison*. *J. Quat. Sci.* 8, 79–92. doi: 10.1002/jqs.3390080107

Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., and Rios-Garaizar, J. (2018). First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* 8, 1–14. doi: 10.1038/s41598-018-28377-y

Gowlett, J. A. J. (2006). The early settlement of northern Europe: fire history in the context of climate change and the social brain. *Palevol* 5, 299–310. doi: 10.1016/j.crpv.2005.10.008

Grayson, D. K. (1984). *Quantitative Zooarchaeology : Topics in the Analysis of Archaeological Faunas*. Orlando, FL: Academic Press.

Guadelli, J.-L. (1998). Détermination de l'âge des chevaux fossiles et établissement des classes d'âge/age determination of fossil horses and the establishment of age classes. *Paléo Rev. d'Archéol. Préhist.* 10, 87–93. doi: 10.3406/PAL.1998.1130

Hardy, B. L., and Moncel, M.-H. (2011). Neanderthal use of fish, mammals, birds, starchy plants and wood 125-250,000 years ago. *PLoS ONE* 6:e23768. doi: 10.1371/journal.pone.0023768

Hardy, K., Bocherens, H., Miller, J. B., and Copeland, L. (2022). Reconstructing Neanderthal diet: the case for carbohydrates. *J. Hum. Evol.* 162:103105. doi: 10.1016/J.JHEVOL.2021.103105

Hawkes, K. (2016). Ethnoarchaeology and Plio-Pleistocene sites: some lessons from the Hadza. *J. Anthropol. Archaeol.* 44, 158–165. doi: 10.1016/j.jaa.2016.07.005

Hawkes, K., O'Connell, J. F., and Jones, N. G. B. (2001). Hadza meat sharing. *Evol. Hum. Behav.* 22, 113–142. doi: 10.1016/S1090-5138(00)00066-0

Heintz, E. (1970). *Les cervidés villafranchiens de France et d'Espagne. Volume I. Texte et planches.* Paris: Editions du Muséum, Mémoires du Muséum national d'histoire naturelle, Nouvelle série, C, Sciences de la Terre.

Hillson, S. (2005). *Teeth., 2nd ed.* Cambridge: Cambridge University Press.

Huguet, R., Arsuaga, J. L., Pérez-González, A., Arriaza, M. C., Sala-Burgos, N., Laplana, C., et al. (2010). Homínidos y hienas en el Calvero de la Higuera (Pinilla del Valle, Madrid) durante el Pleistoceno Superior: resultados preliminares. *Zona Arqueol.* 13, 444–458. Available at: https://hdl.handle.net/20.500.14352/45299

Hutson, J. M., Aritza Villaluenga, ·, García-Moreno, A., Turner, E., and Gaudzinski-Windheuser, S. (2020). "A zooarchaeological and taphonomic perspective of hominin behaviour from the Schöningen 13II-4 'Spear Horizon,"' in *Human Behavioural Adaptations to Interglacial Lakeshore Environments*, eds. A. García-Moreno, J. M. Hutson, G. M. Smith, L. Kindler, E. Turner, A. Villaluenga, et al. (Heidelberg: RGZM – Tagungen), 43–66. doi: 10.11588/propylaeum.647

Jaouen, K., Richards, M. P., Le Cabec, A., Welker, F., Rendu, W., Hublin, J. J., et al. (2019). Exceptionally high δ15N values in collagen single amino acids confirm Neandertals as high-trophic level carnivores. *Proc. Natl. Acad. Sci. USA.* 116, 4928–4933. doi: 10.1073/pnas.1814087116

Jaubert, J., Lorblanchet, M., Laville, H., Slott-Moller, R., Turq, A., and Brugal, J.-P. (1990). *Les chasseurs d'aurochs de La Borde: un site du Paléolithique moyen (Livernon, Lot).* Paris: Documents d'Archéologie Francaise, Editions de la Maison Les Sciences de l'Homme. doi: 10.2307/282214

Jones, E. L. (2016). *In search of the broad spectrum revolution in Paleolithic Southwest Europe*. Available online at: https://link.springer.com/content/pdf/10.1007/978-3-319-22351-3.pdf (accessed September 29, 2024).

Karkanas, P., Shahack-Gross, R., Ayalon, A., Bar-Matthews, M., Barkai, R., Frumkin, A., et al. (2007). Evidence for habitual use of fire at the end of the Lower Paleolithic: site-formation processes at Qesem Cave, Israel. *J. Hum. Evol.* 53, 197–212. doi: 10.1016/j.jhevol.2007.04.002

Klein, R. G., and Cruz Uribe, K. (1984). *The Analysis of Animal Bones from Archeological Sites*. Chicago, IL: University of Chicago Press.

Kuhn, S., Moncel, M. H., Weinstein-Evron, M., and Zaidner, Y. (2021). Introduction to special issue the Lower to Middle Paleolithic boundaries: evolutionary threshold or continuum? *J. Hum. Evol.* 159:103054. doi: 10.1016/j.jhevol.2021.103054

Kuhn, S. L., and Stiner, M. C. (2019). Hearth and home in the Middle Pleistocene. *J. Anthropol. Res.* 75, 305–327. doi: 10.1086/704145

Lebon, M., Reiche, I., Fröhlich, F., Bahain, J. J., and Falguères, C. (2008). Characterization of archaeological burnt bones: contribution of a new analytical protocol based on derivative FTIR spectroscopy and curve fitting of the ν 1 ν 3 PO4 domain. *Anal. Bioanal. Chem.* 392, 1479–1488. doi: 10.1007/s00216-008-2469-y

Lebreton, L., Moigne, A.-M., Filoux, A., and Perrenoud, C. (2017). A specific small game exploitation for Lower Paleolithic: the beaver (Castor fiber) exploitation at the Caune de l'Arago (Pyrénées-Orientales, France). *J. Archaeol. Sci. Rep.* 11, 53–58. doi: 10.1016/j.jasrep.2016.11.023

Lee-Thorp, J., Katzenberg, M. A., Morin, E., and Speth, J. D. (2015). "Middle Palaeolithic diets: a critical examination of the evidence," in *The Oxford Handbook of the Archaeology of Diet*, eds. J. Lee-Thorp and M. A. Katzenberg (Oxford: Oxford Academic), 192–216. doi: 10.1093/oxfordhb/9780199694013.013.24

Linares-Matás, G. J., and Yravedra, J. (2024). Competing forces: subsistence strategies and human-carnivore interactions during the middle to Upper Palaeolithic transition in Northern Iberia. *Quat. Sci. Rev.* 334:108703. doi: 10.1016/j.quascirev.2024.108703

Lloveras, L., Maroto, J., Soler, J., Thomas, R., Moreno-García, M., Nadal, J., et al. (2016). The role of small prey in human subsistence strategies from Early Upper Palaeolithic sites in Iberia: the rabbits from the Evolved Aurignacian level of Arbreda Cave. *J. Quat. Sci.* 31, 458–471. doi: 10.1002/jqs.2869

Lupo, K. D. (2007). Evolutionary foraging models in zooarchaeological analysis: recent applications and future challenges. *J. Archaeol. Res.* 15, 143–189. doi: 10.1007/s10814-007-9011-1

Lyman, R. L. (1994a). Quantitative units and terminology in zooarchaeology. *Am. Antiq.* 59, 36–71. doi: 10.2307/3085500

Lyman, R. L. (1994b). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9781139878302

Lyman, R. L. (2008). *Quantitative Paleozoology*. Cambridge: Cambridge University Press.

Marean, C. W., Abe, Y., Frey, C. J., and Randall, R. C. (2000). Zooarchaeological and taphonomic analysis of the Die Kelders Cave 1 Layers 10 and 11 Middle Stone Age larger mammal fauna. *J. Hum. Evol.* 38, 197–233. doi: 10.1006/jhev.1999.0356

Mariezkurrena, K. (1983). Contribución al conocimiento del desarrollo de la dentición y el esqueleto postcraneal de Cervus elaphus*. *Munibe* 35, 149–202.

Marín, J., Daujeard, C., Saladié, P., Rodríguez-Hidalgo, A., Vettese, D., Rivals, F., et al. (2020). Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). *Quat. Sci. Rev.* 243:106472. doi: 10.1016/j.quascirev.2020.106472

Marks, A., Brugal, J.-Ph., Chabai, V., Monigal, K., Goldberg, P., Hockett, B., et al. (2002). Le gisement pléistocène moyen de Galeria Pesada (Estrémadure, Portugal) : premiers résultats. *PALEO Rev. d'Archéol. Préhist.* 14, 77–100. doi: 10.4000/paleo.1408

Martín-Penela, A. (1986). Los grandes mamíferos del yacimiento Pleistoceno Superior de Cueva Horá (Darro, Granada, España). *Antropol. Paleoecol. Humana* 4, 107–130.

Martín-Penela, A. J. (1988). Los grandes mamíferos del yacimiento achelense de la Solana del Zamborino, Fonelas (Granada, España). *Antropol. Paleoecol. Humana* 5, 29–188.

Mata-González, M., Starkovich, B. M., Zeidi, M., and Conard, N. J. (2023). Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). *Sci. Rep.* 13:19006. doi: 10.1038/s41598-023-45974-8

Moclán, A., Huguet, R., Márquez, B., Laplana, C., Arsuaga, J. L., Pérez-González, A., et al. (2020). Identifying the bone-breaker at the Navalmaíllo Rock Shelter (Pinilla del Valle, Madrid) using machine learning algorithms. *Archaeol. Anthropol. Sci.* 12:46. doi: 10.1007/s12520-020-01017-1

Moigne, A.-M., and Barsky, D. (1999). "Large mammal assemblages from Lower Paleolithic sites in France: La Caune de l'Arago, Terra-Amata, Orgnac 3 and Cagny l'Epinette," in *The Role of Early Humans in the Accumulation of European Lower and Middle Paleolithic bone assemblages*, eds. S. Gaudzinski, and E. Turner (Mainz: Monographien des Römisch-Germanischen Zentralmuseums), 219–235.

Moigne, A.-M., Celiberti, V., and Campmas, É. (2023). L'utilisation et la consommation des bivalves par les néandertaliens de la grotte des Ramandils (Port-La Nouvelle, Aude, France). *PALEO* 2023, 26–49. doi: 10.4000/PALEO.7671

Moigne, A.-M., Valensi, P., Auguste, P., García-Solano, J., Tuffreau, A., Lamotte, A., et al. (2016). Bone retouchers from Lower Palaeolithic sites: Terra Amata, Orgnac 3, Cagny-l'Epinette and Cueva del Angel. *Quat. Int.* 409, 195–212. doi: 10.1016/j.quaint.2015.06.059

Moncel, M.-H., Ashton, N., Lamotte, A., Tuffreau, A., Cliquet, D., and Despriée, J. (2015). The early Acheulian of north-western Europe. *J. Anthropol. Archaeol.* 40, 302–331. doi: 10.1016/j.jaa.2015.09.005

Moncel, M.-H., García-Medrano, P., Despriée, J., Arnaud, J., Voinchet, P., and Bahain, J.-J. (2021). Tracking behavioral persistence and innovations during the Middle Pleistocene in Western Europe. Shift in occupations between 700 and 450 ka at la Noira site (Centre, France). *J. Hum. Evol.* 156:103009. doi: 10.1016/j.jhevol.2021.103009

Moncel, M.-H., and Patou-Mathis, M. (2005). "Site de Payre (Ardèche): les différentes occupations humaines dans leur contexte biochronologique et paléoclimatique," in *Données récentes sur les modalités de peuplement et sur le cadre chronostratigraphique, géologique et paléoanthropologique des industries du Paléolithique inférieur et moyen en Europe*, eds. N. Molines, M.-H. Moncel, and J. L. Monnier (Oxford: British Archaeological Reports S1364), 159–173.

Monge, G., Carretero, M. I., Pozo, M., and Barroso, C. (2014). Mineralogical changes in fossil bone from Cueva del Angel, Spain: archaeological implications and occurrence of whitlockite. *J. Archaeol. Sci.* 46, 6–15. doi: 10.1016/j.jas.2014.02.033

Monge, G., Carretero, M. I., Pozo, M., Rubio, G., Barroso, C., González-Regalado, M. L., et al. (2020). Clay mineral assemblages as tracers of fireplaces in Pleistocene archaeological sites (Cueva del Ángel, Spain). *Appl. Clay Sci.* 192:105643. doi: 10.1016/j.clay.2020.105643

Monge, G., Jimenez-Espejo, F. J., Pozo, M., Carretero, M. I., and Barroso, C. (2016). A geochemical multi-proxy approach for anthropogenic processes in a Middle–Upper Pleistocene endokarstic deposit. *Quat. Int.* 407, 140–149. doi: 10.1016/j.quaint.2016.02.004

Morin, E. (2020a). Rethinking the emergence of bone grease procurement. *J. Anthropol. Archaeol.* 59:101178. doi: 10.1016/j.jaa.2020.101178

Morin, E. (2020b). Revisiting bone grease rendering in highly fragmented assemblages. *Am. Antiq.* 85, 535–553. doi: 10.1017/aaq.2020.29

Morin, E., Bliege Bird, R., and Bird, D. (2020). Mass procurement and prey rankings: insights from the European rabbit. *Archaeol. Anthropol. Sci.* 12:262. doi: 10.1007/s12520-020-01212-0

Morin, E., Meier, J., El Guennouni, K., Moigne, A. M., Lebreton, L., Rusch, L., et al. (2019). New evidence of broader diets for archaic Homo populations in the northwestern Mediterranean. *Sci. Adv.* 5:eaav9106. doi: 10.1126/sciadv.aav9106

Nabais, M., Dupont, C., and Zilhão, J. (2023a). The exploitation of crabs by Last Interglacial Iberian Neanderthals: the evidence from Gruta da Figueira Brava (Portugal). *Front. Environ. Archaeol.* 2:1097815. doi: 10.3389/fearc.2023.1097815

Nabais, M., Pimenta, C., and Zilhão, J. (2023b). Human-bird interaction in last Interglacial Iberia: a combined approach using skeletal part analysis, bone surface modification, bird ethology and ethnography. *J. Archaeol. Sci. Rep.* 49:104023. doi: 10.1016/J.JASREP.2023.104023

Nabais, M., and Zilhão, J. (2019). The consumption of tortoise among Last Interglacial Iberian Neanderthals. *Quat. Sci. Rev.* 217, 225–246. doi: 10.1016/j.quascirev.2019.03.024

Negro, J. J., Blasco, R., Rosell, J., and Finlayson, C. (2016). Potential exploitation of Avian resources by fossil hominins: an overview from ethnographic and historical data. *Quat. Int.* 421, 6–11. doi: 10.1016/j.quaint.2015.09.034

Niven, L. (2013). "A diachronic evaluation of Neanderthal cervid exploitation and site use at Pech de l'Azé IV, France," in *Vertebrate Paleobiology and Paleoanthropology*, eds. J. Clark, and J. Speth (Dordrecht: Springer), 151–161. doi: 10.1007/978-94-007-6766-9_9

Orton, D. C. (2010). A new tool for zooarchaeological analysis: ArcGIS skeletal templates for some common mammalian species. *Internet Archaeol.* 28. doi: 10.11141/ia.28.4

Pales, L., Lambert, C., and M. A. García (1971). *Atlas ostéologique pour servir à l'identification des mammifères du quaternaire*. Paris: Centre National de la Recherche Scientifique.

Pickering, T. R. (2002). Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *Int. J. Osteoarchaeol.* 12, 127–141. doi: 10.1002/oa.594

Pickering, T. R., and Egeland, C. P. (2006). Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33, 459–469. doi: 10.1016/j.jas.2005.09.001

Pickering, T. R., Marean, C. W., and Dominguez-Rodrigo, M. (2003). Importance of limb bone shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate body part profiles" (2002), by M.C. *Stiner. J. Archaeol. Sci.* 30, 1469–1482. doi: 10.1016/S0305-4403(03)00042-6

Pope, M., Roberts, M., and Parfitt, S. (2020). *The Horse Butchery Site GTP17: A High-Resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove, UK*. London: SpoilHeap Publications, University College London.

R Core Team (2024). *_R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rendu, W. (2022). Selection versus opportunism: a view from Neanderthal subsistence strategies. *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Amsterdam: Academic Press), 109–122. doi: 10.1016/B978-0-12-821428-2.00013-5

Rendu, W., Renou, S., Koliasnikova, A., Baumann, M., Plisson, H., Discamps, E., et al. (2023). Neanderthal subsistence at Chez-Pinaud Jonzac (Charente-Maritime, France): a kill site dominated by reindeer remains, but with a horse-laden diet? *Front. Ecol. Evol.* 10:1085699. doi: 10.3389/fevo.2022.1085699

Rivière, M., Rendu, W., and Jaubert, J. (2023). Les chasseurs néandertaliens d'aurochs de La Borde (Livernon, Lot): apport de l'archéozoologie. *Bull. Soc. Préhist. Française* 2023, 7–27. Available at: https://hal.science/hal-04057987v1

Roditi, E., and Starkovich, B. M. (2022). Investigating Middle Palaeolithic subsistence: zooarchaeological perspectives on the potential character of hominin climate refugia in Greece. *J. Quat. Sci.* 37, 181–193. doi: 10.1002/jqs.3371

Rodríguez-Hidalgo, A., Rivals, F., Saladié, P., and Carbonell, E. (2016). Season of bison mortality in TD10.2 bone bed at Gran Dolina site (Atapuerca): integrating tooth eruption, wear, and microwear methods. *J. Archaeol. Sci. Rep.* 6, 780–789. doi: 10.1016/j.jasrep.2015.11.033

Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., and Carbonell, E. (2015). Hominin subsistence and site function of TD10.1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. *J. Quat. Sci.* 30, 679–701. doi: 10.1002/jqs.2815

Roebroeks, W., and Villa, P. (2011). On the earliest evidence for habitual use of fire in Europe. *Proc. Natl. Acad. Sci. USA.* 108, 5209–5214. doi: 10.1073/pnas.1018116108

Rolland, N. (2000). Cave occupation, fire-making, hominid/carnivore coevolution, and Middle Pleistocene emergence of home-base settlement systems. *Acta Anthropol. Sin.* 19, 209–217.

Romagnoli, F., Rivals, F., and Benazzi, S. (2022). *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*. Amsterdam: Academic Press, 1–361. doi: 10.1016/C2019-0-03240-2

Rosell, J., and Blasco, R. (2009). Home sharing: carnivores in anthropogenic assemblages of the Middle Pleistocene. *J. Taphonomy* 7, 305–324.

Rosell, J., and Blasco, R. (2019). The early use of fire among Neanderthals from a zooarchaeological perspective. *Quat. Sci. Rev.* 217, 268–283. doi: 10.1016/j.quascirev.2019.03.002

Rosell, J., Blasco, R., van der Made, J., Cáceres, I., Campeny, G., Díez, J. C., et al. (2010). Acumulaciones producidas por carnívoros en el Pleistoceno medio inicial: una reconstrucción a partir del conjunto faunístico del nivel TD8 de Gran Dolina (Sierra de Atapuerca, Burgos). *Zona Arqueol.* 13, 158–172.

Ruebens, K., Smith, G. M., Fewlass, H., Sinet-Mathiot, V., Hublin, J., and Welker, F. (2023). Neanderthal subsistence, taphonomy and chronology at Salzgitter-Lebenstedt (Germany): a multifaceted analysis of morphologically unidentifiable bone. *J. Quat. Sci.* 38, 471–487. doi: 10.1002/jqs.3499

Russo, G., Milks, A., Leder, D., Koddenberg, T., Starkovich, B. M., Duval, M., et al. (2023). First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals. *Sci. Rep.* 13, 1–13. doi: 10.1038/s41598-023-42764-0

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., et al. (2011). Carcass transport decisions in Homo antecessor subsistence strategies. *J. Hum. Evol.* 61, 425–446. doi: 10.1016/j.jhevol.2011.05.012

Saladié, P., Rodríguez-Hidalgo, A., Huguet, R., Cáceres, I., Díez, C., Vallverdú, J., et al. (2014). The role of carnivores and their relationship to hominin settlements in the TD6-2 level from Gran Dolina (Sierra de Atapuerca, Spain). *Quat. Sci. Rev.* 93, 47–66. doi: 10.1016/j.quascirev.2014.04.001

Sauqué, V., and Sanchis, A. (2017). Leopards as taphonomic agents in the Iberian Pleistocene, the case of Racó del Duc (Valencia, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 472, 67–82. doi: 10.1016/j.palaeo.2017.01.016

Schmid, E. (1972). *Atlas of Animal Bones for Prehistorians, Archaeologists and Quaternary Geologists*. Amsterdam: Elsevier Publishing Company.

Shimelmitz, R., Kuhn, S. L., Jelinek, A. J., Ronen, A., Clark, A. E., and Weinstein-Evron, M. (2014). 'Fire at will': the emergence of habitual fire use 350,000 years ago. *J. Hum. Evol.* 77, 196–203. doi: 10.1016/j.jhevol.2014.07.005

Shipman, P., Foster, G., and Schoeninger, M. (1984). Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. *J. Archaeol. Sci.* 11, 307–325.

Silvestrini, S., Real, C., Lugli, F., Delpiano, D., Harvati, K., Collina, C., et al. (2024). Hunting game: new data on the subsistence strategies during the Uluzzian in Italy. *J. Archaeol. Sci. Rep.* 57:104575. doi: 10.1016/j.jasrep.2024.104575

Smith, G. M., Spasov, R., Martisius, N. L., Sinet-Mathiot, V., Aldeias, V., Rezek, Z., et al. (2021). Subsistence behavior during the Initial Upper Paleolithic in Europe: site use, dietary practice, and carnivore exploitation at Bacho Kiro Cave (Bulgaria). *J. Hum. Evol.* 161:103074. doi: 10.1016/j.jhevol.2021.103074

Solano García, J. A. (2024). *Paleoeconomía y subsistencia durante el Pleistoceno medio en el sur de Iberia. Zooarqueología y tafonomía de la cueva del Ángel (Lucena, Córdoba)*, International Series. Oxford: BAR publishing. Available online at: https://www.barpublishing.com/paleoeconomia-y-subsistencia-durante-el-pleistoceno-medio-en-el-sur-iberia.html (accessed April 10, 2024).

Speth, J. D., and Tchernov, E. (2001). "Neandertal Hunting and Meat-Processing in the Near East Evidence from Kebara Cave (Israel)," in *Meat-Eating and Human Evolution*, eds. C. B. Stanford, and H. T. Bunn (Oxford: Oxford University Press), 52–72.

Starkovich, B. M. (2017). Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). *J. Hum. Evol.* 111, 63–84. doi: 10.1016/j.jhevol.2017.04.005

Starkovich, B. M., and Ntinou, M. (2017). Climate change, human population growth, or both? Upper Paleolithic subsistence shifts in southern Greece. *Quat. Int.* 428, 17–32. doi: 10.1016/J.QUAINT.2015.03.044

Steele, T. E. (2004). Variation in mortality profiles of red deer (*Cervus elaphus*) in Middle Palaeolithic assemblages from western Europe. *Int. J. Osteoarchaeol.* 14, 307–320. doi: 10.1002/oa.763

Stiner, M. (2005). *The Faunas of Hayonim Cave, Israel: A 200,000Year Record of Paleolithic Diet, Demography, and Society*. Cambridge: Harvard University Press.

Stiner, M. C. (1990). The use of mortality patterns in archaeological studies of hominid predatory adaptations. *J. Anthropol. Archaeol.* 9, 305–351.

Stiner, M. C. (1994). *Honor among Thieves. A Zooarchaeological Study of Neanderthal Ecology.* Princeton, NJ: Princeton University Press.

Stiner, M. C. (1998). Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *J. Hum. Evol.* 34, 303–326.

Stiner, M. C. (2002). Carnivory, coevolution, and the geographic spread of the genus *Homo*. *J. Archaeol. Res.* 10, 1–63. doi: 10.1023/A:1014588307174

Stiner, M. C. (2004a). Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy. *Rev. Paléobiol. Genève* 23, 771–785.

Stiner, M. C. (2004b). "Small game use and expanding diet breadth in the Eastern Mediterranean Basin during the Palaeolithic," in *Petits Animaux et Sociétiés Humaines, du Complément Alimentaire aux Resources Utilitaires. XXIVe rencontres internationales d'archéologie et d'histoire d'Antibes*, eds. J. Desse, and J.-P. Brugal (Ville d'Antibes: Centre d'études Préhistoire), 499–513.

Stiner, M. C. (2012). Competition theory and the case for Pleistocene Hominin-Carnivore Co-evolution. *J. Taphonomy* 10, 129–145.

Stiner, M. C. (2013). An Unshakable Middle Paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. *Curr. Anthropol.* 54, S288–S304. doi: 10.1086/673285

Stiner, M. C., Gopher, A., and Barkai, R. (2011). Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *J. Hum. Evol.* 60, 213–233. doi: 10.1016/j.jhevol.2010.10.006

Stiner, M. C., Kuhn, S. L., Surovell, T. A., Goldberg, P., Meignen, L., Weiner, S., et al. (2001). Bone preservation in hayonim cave (Israel): a macroscopic and mineralogical study. *J. Archaeol. Sci.* 28, 643—659. doi: 10.1006/jasc.2000.0634

Stiner, M. C., Kuhn, S. L., Weiner, S., and Bar-Yosef, O. (1995). Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* 22, 223–237.

Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E., and Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283, 190–194.

Tagliacozzo, A., Romandini, M., Fiore, I., Gala, M., and Peresani, M. (2013). "Animal exploitation strategies during the Uluzzian at Grotta di Fumane (Verona, Italy)," in *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene*, eds. J. L. Clark, and J. D. Speth (New York, NY: Springer), 129–150.

Théry-Parisot, I., Chabal, L., and Costamagno, S. (2010). Taphonomie de la combustion des résidus organiques et des structures de combustion en context archéologique. *Palethnologie* 2, 1–217. doi: 10.4000/palethnologie.7993

Todd, L. C., and Rapson, D. J. (1988). Long bone fragmentation and interpretation of faunal assemblages: approaches to comparative analysis. *J. Archaeol. Sci.* 15, 307–325. doi: 10.1016/0305

Uzunidis, A. (2020). Large ungulates mobility and Neanderthal subsistence behaviours: a preliminary tooth microwear analysis. *J. Archaeol. Sci. Rep.* 29:102084. doi: 10.1016/j.jasrep.2019.102084

Val, A., Porraz, G., Texier, P.-J., Fisher, J. W., and Parkington, J. (2020). Human exploitation of nocturnal felines at Diepkloof Rock Shelter provides further evidence for symbolic behaviours during the Middle Stone Age. *Sci. Rep.* 10:6424. doi: 10.1038/s41598-020-63250-x

Valensi, P., Aouraghe, H., Bailon, S., Cauche, D., Combier, J., Desclaux, E., et al. (2005). "Les peuplements préhistoriques dans le sud-est de la France à la fin du Pléistocène moyen: 400-120 000 ans. Cadre géochronologique et biostratigraphique, paléoenvironnements et évolution culturelle des derniers anténéandertaliens," in *Peuplements humains et variations environnementales au Quaternaire*, ed. A. Tuffreau (Oxford: BAR International Series 1352), 33–37. Available omline at: https://hal.science/hal-00485334 (accessed January 8, 2025).

Valensi, P., Roussel, A., Visweswara, S. C., Guennouni, K. El, Cauche, D., and Michel, V. (2022). Au temps des derniers acheuléens du sud-est de la France: Nouvelle synthèse sur les faunes de grands mammifères du Pléistocène moyen de la grotte du Lazaret (Nice, France). *Bull. Musée d'Anthropol. Préhist. Monaco* 61, 103–118. Available online at: https://hal.science/hal-04027510 (accessed October 26, 2024).

van Buuren, S., and Groothuis-Oudshoorn, K. (2011). mice: multivariate Imputation by Chained equations in R. *J. Stat. Softw.* 45, 1–67. doi: 10.18637/JSS.V045.I03

van Kolfschoten, T., Buhrs, E., and Verheijen, I. (2015). The larger mammal fauna from the Lower Paleolithic Schöningen Spear site and its contribution to hominin subsistence. *J. Hum. Evol.* 89, 138–153. doi: 10.1016/j.jhevol.2015.09.014

van Kolfschoten, T., Knul, M., Buhrs, E., and Gielen, M. (2018). "Butchered large bovids (Bos primigenius and Bison priscus) from the Palaeolithic throwing spear site Schöningen 13 II-4 (Germany)," in *A Bouquet of Archaeozoological Studie*s, eds. D. C. M. Raemaekers, E. Esser, R. C. G. M. Lauwerier, and J. T. Zeiler (Eelde: Barkhuis), 33–46. doi: 10.2307/j.ctt227285m.6

Verheijen, I., Starkovich, B. M., Serangeli, J., van Kolfschoten, T., and Conard, N. J. (2023). Early evidence for bear exploitation during MIS 9 from the site of Schöningen 12 (Germany). *J. Hum. Evol.* 177:103294. doi: 10.1016/j.jhevol.2022.103294

Vettese, D., Daujeard, C., Blasco, R., Borel, A., Caceres, I., and Moncel, M. H. (2017). Neandertal long bone breakage process: standardized or random patterns? The example of Abri du Maras (Southeastern France, MIS 3). *J. Archaeol. Sci. Rep.* 13, 151–163. doi: 10.1016/j.jasrep.2017.03.029

Vicent, J. (1991). El Neolítico. transformaciones sociales y económicas. *Bol. Antropol. Am.* 24, 31–62.

Villa, P., and Lenoir, M. (2009). "Hunting and hunting weapons of the lower and Middle Paleolithic of Europe," in *Vertebrate Paleobiology and Paleoanthropology*, eds. J. J. Hublin, and M. P. Richards (Cham: Springer), 59–85. doi: 10.1007/978-1-4020-9699-0_5

Villa, P., and Mahieu, E. (1991). Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48. doi: 10.1016/0047-2484(91)90034-s

Wegrzyn, M., and Serwatka, S. (1984). Teeth eruption in the European bison. *Acta. Theriol.* 29, 111–121.

White, M., Pettitt, P., and Schreve, D. (2016). Shoot first, ask questions later: interpretative narratives of Neanderthal hunting. *Quat. Sci. Rev.* 140, 1–20. doi: 10.1016/j.quascirev.2016.03.004

Wißing, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D. G., et al. (2019). Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in Europe. *Sci. Rep.* 9, 1–12. doi: 10.1038/s41598-019-41033-3

Wolverton, S., Dombrosky, J., and Lyman, R. L. (2016). Practical significance: ordinal scale data and effect size in zooarchaeology. *Int. J. Osteoarchaeol.* 26, 255–265. doi: 10.1002/oa.2416

Yravedra, J. (2010). A Taphonomic perspective on the origins of the Faunal Remains from Amalda Cave (Spain). *J. Taphonomy* 8, 301–334.

Yravedra, J., and Cobo-Sánchez, L. (2015). Neanderthal exploitation of ibex and chamois in southwestern Europe. *J. Hum. Evol.* 78, 12–32. doi: 10.1016/j.jhevol.2014.10.002

Yravedra, J., and Uzquiano, P. (2013). Burnt bone assemblages from El Esquilleu cave (Cantabria, Northern Spain): deliberate use for fuel or systematic disposal of organic waste? *Quat. Sci. Rev.* 68, 175–190. doi: 10.1016/j.quascirev.2013.01.019

Yravedra-Sainz de los Terreros, J., Gómez-Castanedo, A., Aramendi-Picado, J., Montes-Barquín, R., and Sanguino-González, J. (2016). Neanderthal and Homo sapiens subsistence strategies in the Cantabrian region of northern Spain. *Archaeol. Anthropol. Sci.* 8, 779–803. doi: 10.1007/s12520-015-0253-4

Zeder, M. A. (2012). The Broad Spectrum Revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. *J. Anthropol. Archaeol.* 31, 241–264. doi: 10.1016/j.jaa.2012.03.003

Zilhão, J., Angelucci, D. E., Igreja, M. A., Arnold, L. J., Badal, E., Callapez, P., et al. (2020). Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* 367:eaaz7943. doi: 10.1126/science.aaz7943

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Ungulates and carnivores from the late MIS-5 Neanderthal occupation of Gruta da Figueira Brava (Portugal)

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This study examines the ungulate and carnivore remains recovered from the Middle Palaeolithic site of Gruta da Figueira Brava, Portugal, to assess Neanderthal subsistence strategies in the region during late Marine Isotope Stage 5 (MIS-5). The site, now facing the Atlantic Ocean, was located up to 2 km inland at the time of occupation, providing access to both terrestrial and coastal environments. Despite extensive fragmentation and carbonate encrustation of the faunal assemblage, zooarchaeological and taphonomic analyses reveal a diversity of prey species, dominated by red deer (*Cervus elaphus*) and ibex (*Capra pyrenaica*), with lesser contributions from aurochs (*Bos primigenius*) and horses (*Equus caballus*). The skeletal element representation, along with cut marks, percussion marks and burning evidence suggest a complex and flexible approach to resource transport, processing and consumption. Neanderthals exploited both high-yield and marginal bone portions, maximising nutritional intake through cooking, defleshing and marrow extraction. The assemblage suggests that whole deer carcasses were occasionally transported to the site, while selective transport strategies were applied to larger taxa. The presence of carnivore remains, including bears (*Ursus arctos*), hyaenas (*Crocuta crocuta*), wolves (*Canis lupus*) and wild cats (*Felis silvestris*), with no evidence of human-carnivore interactions, suggests intermittent use of the cave by non-human predators during periods of human absence (e.g., for cat denning and bear hibernation or as a hyaena latrine).

KEYWORDS

palaeodiet, subsistence strategies, taphonomy, Middle Palaeolithic, Pleistocene

1 Introduction

Neanderthals primarily exploited a variety of ungulate species. In the Iberian Middle Palaeolithic, red deer often predominates in faunal assemblages, while other Cervidae, Caprinae and Equidae are also regularly found; whereas Bovidae, Rhinocerotidae and Suidae remains are less abundant (e.g., Álvarez-Lao and García, 2011a,b; Álvarez-Lao and Méndez, 2016; Marín-Arroyo and Sanz-Royo, 2021; Moclán et al., 2021; Rosell et al., 2012; Sanz et al., 2019; Yravedra and Cobo-Sánchez, 2015). However, the relative abundance of different taxa largely depends on the geographical setting, local environmental conditions and species' seasonal availability (e.g., Salazar-García et al., 2013; Blasco and Fernández Peris, 2012; Blasco et al., 2013; Finlayson et al., 2012). Although less frequent, certain European Middle Palaeolithic contexts present faunal assemblages that indicate

monospecific hunting practices (i.e., when the assemblage is dominated by a single taxon; e.g., Daujeard et al., 2017; Farizy et al., 1994; Gaudzinski and Roebroeks, 2000; Patou-Mathis, 2006). Regardless of whether driven by ecological factors or deliberate human choice, these animals were hunted through ambush and stalking techniques, with different age groups targeted during specific seasons, which demonstrates the adaptability and flexibility of Neanderthal hunting strategies (e.g., Patou-Mathis, 2000; Gaudzinski and Roebroeks, 2000). These cases suggest a well-coordinated predation strategy that involved pre-planned tactics, intensive group collaboration and a deep understanding of the landscape and prey behaviour necessary to effectively intercept herds at water streams or along their migratory routes, and then drive and trap them into natural features like cliffs, gorges, or swamps (e.g., Gaudzinski-Windheuser and Kindler, 2012; Rodríguez-Hidalgo et al., 2017; White et al., 2016).

Consequently, it is not unexpected that several studies analysing Neanderthal skeletal remains have characterised their diet as heavily meat-oriented, with enriched $\delta^{15}N$ isotope values in comparison with other carnivores, such as lions and hyaenas (e.g., Bocherens et al., 2014; Jaouen et al., 2019). However, the consumption of various plant foods has also been demonstrated (e.g., Henry et al., 2014; Zilhão et al., 2020). Several authors have suggested that Neanderthal subsistence strategies varied as a function of the type of ecosystem they lived in—steppe-tundra in the north, variably wooded landscapes in the south, arid steppe in the east (e.g., Carrión et al., 2019; Stewart et al., 2019)—and it has also been recently shown that, when living by the sea, they developed accomplished coastal adaptations (e.g., Stringer et al., 2008; Zilhão et al., 2020). While higher diversity of prey does not necessarily equate to greater adaptability or flexibility *per* se—as it may be dependent on other factors, such as opportunistic catches, the development of new techniques, increased sedentism—, it contributes to the understanding of the complexity of the subsistence strategies used by these hominins. This maturing picture of Neanderthal subsistence patterns draws on several decades of research, which has progressively shifted the perception of Neanderthal behaviour from simplistic to increasingly complex.

However, Neanderthals were not the only predators consuming ungulates, inhabiting or visiting caves; other carnivores, such as bears, hyaenas, wolves, foxes, wild cats, among others, also occupied these spaces (e.g., Cobo-Sánchez et al., 2024; Dusseldorp, 2013; Romandini et al., 2018; Sanchis et al., 2019; Zilhão et al., 2010). As a result, faunal studies of the Palaeolithic period require comprehensive zooarchaeological and taphonomic analyses to distinguish human from non-human contributions to the assemblage. Once human involvement in a faunal accumulation is established, a detailed characterisation of subsistence strategies becomes possible. Given the rarity of direct evidence for hunting techniques in the Middle Palaeolithic, the quantitative and qualitative analysis of ungulate remains, combined with eco-ethological information on game species and their environments, plays a crucial role in reconstructing human subsistence behaviours. These analyses provide insights into acquisition and processing techniques, as well as consumption patterns, offering a better understanding of Neanderthal adaptations and their interaction with the biomes they exploited. The ability to select prey or to opportunistically catch it, to process carcasses efficiently and to respond to ecological variables demonstrates advanced cognitive skills, environmental awareness and strategic decision-making, which are all key indicators of behavioural complexity (e.g., Johansson, 2014; Langley et al., 2008; Rendu, 2022).

In this study, we employ zooarchaeological and taphonomic methods to examine the ungulate and carnivore remains recovered from the Middle Palaeolithic cave site of Gruta da Figueira Brava in central Portugal. Despite the small sample size of identifiable specimens and the presence of dense calcareous coatings on the bones' surfaces, we aim (1) to identify and reconstruct the palaeoecological areas of the surrounding landscape where ungulates were present and available for exploitation, (2) to characterise the agent(s) responsible for the bone accumulation in the cave, (3) to identify the hunting and carcass processing strategies associated with Neanderthal groups that inhabited the site during the later part of Marine Isotope Stage 5 (MIS-5).

2 The site

Gruta da Figueira Brava is located about 30 km (as the crow flies) south of Lisbon (Portugal), on the southern slope of the Arrábida mountain chain (Figure 1A). Currently, the cave features three main entrances but access to the interior is only possible through Entrance 1; the others are blocked by sediment and speleothems (Figures 1B, C). Area C, in the interior part of Entrance 2, was excavated in the 1980s (Antunes, 2000); the recent, 2010–2013 excavations took place in Entrance 3 and the interior area behind (Area F and the SEx trench; Figures 1B–D). Today, Mediterranean vegetation dominated by evergreen trees and shrubs with patches of more forested areas and others of more open terrain covers the limestone slopes rising behind the cave (Ribeiro, 1945). The palaeobotanical evidence indicates that, through the time of the cave's Middle Palaeolithic occupation, the surrounding landscape was much like at present (Zilhão et al., 2020).

The cave opens at the base of a biocalcarenite escarpment and onto an interglacial marine abrasion platform, 5 m above modern sea level. At the time of occupation, estimated distances to the coastline range between 750 m (during occupation phases FB1 and FB2, dated to MIS-5c) and 2,000 m (during occupation phase FB4, dated to MIS-5b) (Zilhão et al., 2020). The site therefore remained within easy reach of the seaside and associated coastal environments (e.g., estuaries, pools, lagoons). The ecotonal environment provided opportunities to exploit a wide range of ecological niches, as evidenced by the inhabitants' diverse diet. This included tortoises, crabs, birds, fish and shellfish (Nabais et al., 2023a,b; Nabais and Zilhão, 2019; Zilhão et al., 2020), as well as marine mammals and very large terrestrial mammals (e.g., rhinoceros), which were identified in the initial excavations conducted at the site during the 1980s (Antunes, 2000).

The coupled dating of sediments (by OSL) and speleothems (by U-series) places the occupation sequence in the ca. 86–106 ka interval. The oldest evidence comes from the SEx trench, where the MIS-5b levels were washed away due to Holocene sea level rise, but brecciated layers dated to MIS-5c could be archaeologically excavated and yielded charcoal, shells, bones and artefacts. The

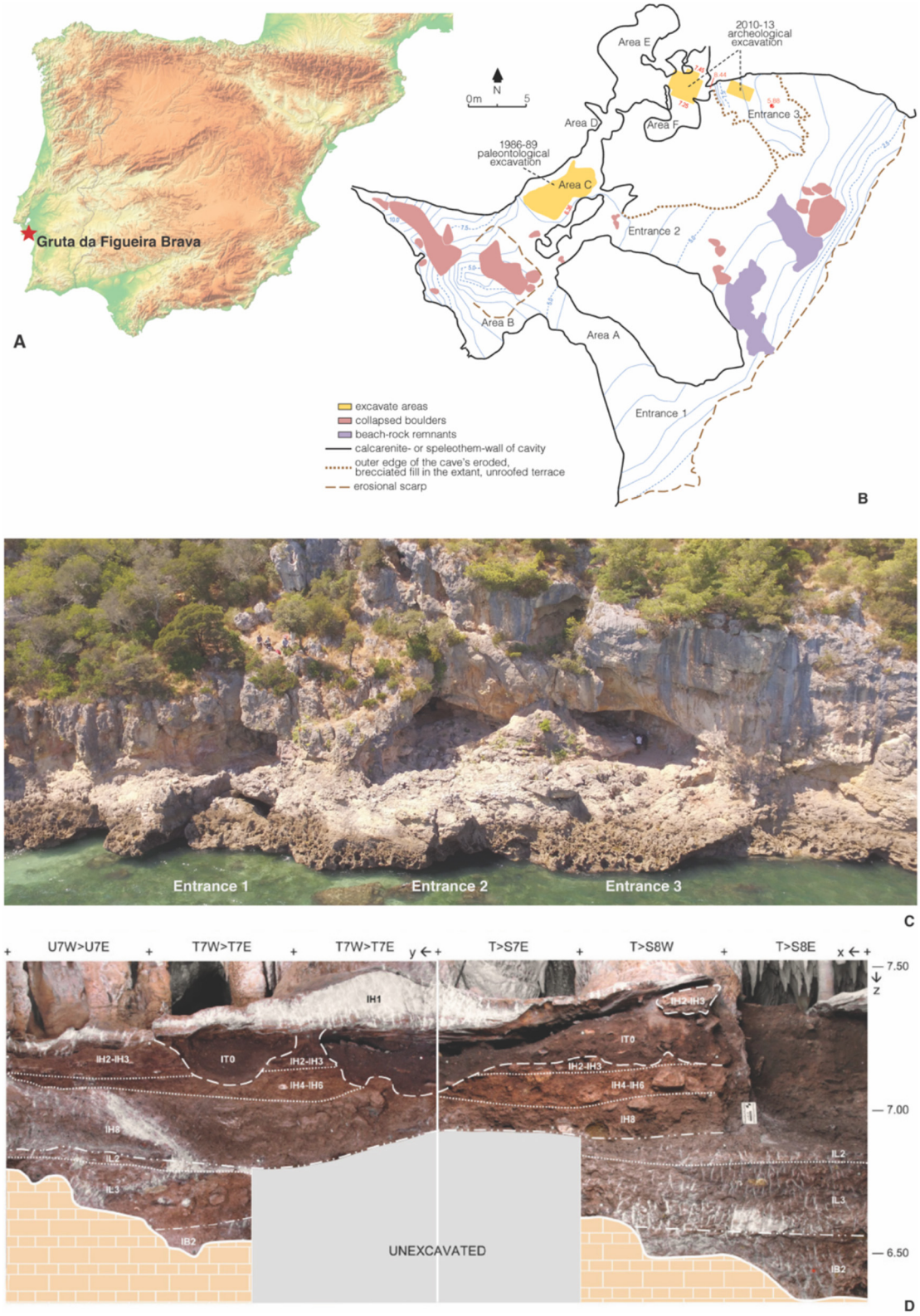

FIGURE 1
The Middle Palaeolithic site Gruta da Figueira Brava, Setúbal, Portugal. **(A)** Site location in the Iberian Peninsula. **(B)** Plan of the cavities—elevations are in metres above sea level. **(C)** The cave seen from the sea; the three different entrances are indicated. **(D)** Stratigraphic profile of Area F; units IL2 and IL3 belong in phase FB3, units IH2-IH3 to IH8 belong in phase FB4; IT0 denotes the reworked deposit. **(A, C)** are reproduced from Nabais et al. (2023a), published under a CC BY license, with permission from Frontiers, original copyright 2023. **(B, D)** are reproduced from Zilhão et al. (2020), published under a CC BY license, with permission from The American Association for the Advancement of Science, original copyright 2020.

remains from the most recent occupation phase come entirely from Area F. Here, the Pleistocene deposit was sealed by flowstone (Figure 1D), but significant small mammal burrowing nonetheless resulted in a network of tunnels and chambers where intrusive Holocene items could be found among the deposit's reworked Pleistocene content. The Holocene intrusions are easy to recognise and, where mammals are concerned, mostly correspond to the bone remains of leporids, rodents and insectivores. The macro-mammal remains found in the reworked levels derive mostly, if not entirely, from sediments laid down during the FB4 occupation phase (Zilhão et al., 2020). However, through abundance of caution, we have counted them separately under the category "Reworked." While these finds will be referenced when pertinent, all relative frequencies and other statistical measures mentioned in the text are calculated exclusively based on the MIS-5 *in situ* material.

3 Materials and methods

All materials recovered were studied and quantifications were done by spit and then agglomerated according to provenience: reworked; and MIS-5 occupation phases FB4, FB3 and FB2. Every bone and tooth fragment was examined, recorded and counted. Every bone fragment, whether it was triangulated on site or not, was assigned a unique database number. Abundance was assessed using the Number of Identified Specimens (NISP), the Minimum Number of Elements (MNE) and the Minimum Number of Individuals (MNI) (Grayson, 1984; Klein and Cruz-Uribe, 1984; Lyman, 1994, 2008; White, 1953). To assess body part representation of the main ungulates in the assemblage, the NISP was chosen over the Minimal Animal Units [MAU, as defined by Binford (1978, 1984)] in the production of Figure 4. This approach is justified by Lyman (2008, p. 248), who states that "NISP is not afflicted by problems of aggregation or definition, so evaluating skeletal completeness can be done with NISP to avoid the problems with the MNE and MAU." Survival percentages of each body part were compared based on Brain's (1969) formula: $\%survival_i = MNE \times 100/\text{number of element}_i$ in the animal skeleton $\times$ MNI (Table 2). This formula is equivalent to Binford's %MAU (Lyman, 2008). The number of elements per animal skeleton followed Lyman (2008: 228).

Mammal identifications were carried out using the osteological reference collection of the Archaeosciences Laboratory (LARC, Lisbon, Portugal) of Património Cultural I.P., the Portuguese government's archaeological heritage management agency (Moreno-García et al., 2003). Mammal identifications were aided by several osteological atlases, like Hillson (2005), Pales and Lambert (1971, 1981), Pérez-Hidalgo and Cobo Rayán (1987), and Schmid (1972). The portion of the skeletal element present was recorded along with the anatomical part identified. Every element was sided (left, right, indeterminate), and ageing was recorded by analysing (1) tooth wear stages and (2) the state of fusion of long bone extremities. The different dentine patterns for Caprinae followed Payne's (1973, 1987) model. Grant's (1982) dentine patterns were used for Suidae and Bovinae. The teeth of Cervidae were described following Brown and Chapman's (1990, 1991) scheme. For age class estimation, long bones were recorded as unfused, fusing or fused (Reitz and Wing, 2008).

Coprolites were tentatively identified to species, or animal group size, based on their shape and size, and through comparison with those published by Sanz et al. (2016). These researchers established three distinct coprolite morphotypes. Morphotype 1, attributed to hyenids, is predominantly globular or spherical, occasionally pointed, and has flat or rounded extremities, a crumbly texture, sparse bone content, a length ranging from 19 to 51 mm and a diameter ranging from 18 to 50 mm. Morphotype 2 is linked to non-hyenid carnivores (such as lynx, fox or wolf), has a cylindrical or tube-like shape with the occasional sharp extremities, a spiral internal structure, several voids, abundant bone inclusions dominated by leporids, and ranges from 20 to 65 mm in length and from 18 to 50 mm in diameter. Finally, Morphotype 3, tentatively associated with larger carnivores (like bears), is larger and crumblier than all other morphotypes, displaying a length ranging from 21 to 87 mm and a diameter between 36 and 57 mm (Sanz et al., 2016).

The relatively large number of unidentified bone fragments could for the most part be assigned to size categories based on shape and thickness of the bone. Seven main animal size categories were created, adapted from the model used by Blasco and Fernández Peris (2012), Bunn (1986) and Díez et al. (1999): (1) Very Large Macrofauna: mammals larger than 1,000 kg (e.g. elephant, rhino); (2) Large Macrofauna: mammals from 300 to 1,000 kg (e.g. horse, aurochs, bear); (3) Medium Macrofauna: mammals from 100 to 300 kg (red deer and generic cervids); (4) Small Macrofauna: mammals from 20 to 100 kg (e.g. chamois, ibex, hyaena, wolf); (5) >Very Small Macrofauna: indeterminate mammal remains impossible to attribute to one of the animal groups but clearly larger than 20 kg; (6) Very Small Macrofauna: animals smaller than 20 kg (e.g. lynx, cat, fox); (7) Indeterminate Macrofauna: indeterminate remains that cannot be attributed to a specific category (mostly composed of heavily fragmented remains).

For a quick assessment of the assemblages' degree of fragmentation every bone (whether complete or fragmented) was assigned to a size interval in centimeters: 0–1, 1–2 cm and so on. Bone breakage was recorded following the criteria defined by Bunn (1983) and Villa and Mahieu (1991), adapted by Blasco and Fernández Peris (2012), and used in the analysis of several Palaeolithic faunal assemblages. Fracture outlines were recorded as transverse, curved/V-shaped, or longitudinal; fracture angles were noted as oblique, right or mixed; surface edges were recorded as jagged or smooth; and the time of fracture was described as old or new, i.e., before or after deposition.

Clear anthropogenic breakage can be assessed through several types of percussion marks, like percussion pits, percussion notches, impact flakes and adhering flakes (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Díez et al., 1999; Pickering and Egeland, 2006; White, 1992). Butchery marks, such as cuts, scrapes and chops were identified according to the criteria defined by Shipman and Rose (1983), Noe-Nygaard (1989) and Fisher (1995). Additional information was recorded, such as the number of striations (0 to *n*), striation distribution (isolated, clustered, crossed), striation orientation (oblique, longitudinal,

TABLE 1 Number of Identified Specimens (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) of ungulate and carnivore remains by the different occupation phases in Gruta da Figueira Brava (2010–2013 excavations).

Taxon	Phase FB4			Phase FB3			Phase FB2			Rworked			Total		
	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI
Large macro-mammals															
Equus caballus	1	2	1	–	–	–	–	–	–	–	–	–	**1**	**2**	**1**
Equus sp.	14	11	4	2	2	2	–	–	–	–	–	–	**16**	**13**	**6**
Bos sp.	6	4	3	–	–	–	–	–	–	1	1	1	**7**	**5**	**4**
Herbivore	6	3	–	5	3	–	2	1	–	1	1	–	**14**	**8**	**–**
Ursus arctos	9	6	2	4	4	2	–	–	–	–	–	–	**13**	**4**	**4**
Indeterminate	36	8	–	19	5	–	–	–	–	1	1	–	**56**	**14**	**–**
Sub-total	72	34	10	30	14	4	2	1	–	3	3	1	**107**	**46**	**15**
Medium macro-mammals															
Cervus elaphus	53	46	7	18	14	2	–	–	–	2	2	1	**73**	**62**	**10**
Cervidae	42	14	4	5	3	2	1	1	1	4	4	2	**52**	**22**	**9**
Herbivore	10	4	–	–	–	–	–	–	–	1	1	–	**11**	**5**	**–**
Indeterminate	81	14	–	8	1	–	4	2	–	2	2	–	**95**	**19**	**–**
Sub-total	186	78	11	31	18	4	5	3	1	9	9	3	**231**	**108**	**19**
Small macro-mammals															
Caprinae	58	42	5	12	9	2	–	–	–	11	8	2	**81**	**59**	**9**
Herbivore	3	2	–	–	–	–	–	–	–	4	2	–	**7**	**4**	**–**
Sus sp.	4	4	2	1	1	1	–	–	–	–	–	–	**5**	**5**	**3**
Hyaenidae	3	3	1	1	1	1	–	–	–	–	–	–	**4**	**4**	**2**
Canis lupus	1	1	1	–	–	–	–	–	–	–	–	–	**1**	**1**	**1**
Martes sp.	–	–	–	–	–	–	–	–	–	1	1	1	**1**	**1**	**1**
Carnivore	33	4	–	3	2	–	–	–	–	1	1	–	**37**	**7**	**–**
Indeterminate	165	16	–	21	4	–	3	2	–	31	6	–	**220**	**28**	**–**
Sub-total	267	72	9	38	17	4	3	2	–	48	18	3	**356**	**109**	**16**
>Very small macro-mammals															
Herbivore	24	5	–	4	3	–	–	–	–	3	1	–	**31**	**9**	**–**
Indeterminate	542	15	–	142	6	–	12	4	–	73	5	–	**769**	**30**	**–**
Sub-total	566	20	–	146	9	–	12	4	–	76	6	–	**800**	**39**	**–**
Very small macro-mammals															
Felis silvestris	7	7	5	1	1	1	–	–	–	2	2	1	**10**	**10**	**7**
Lynx pardinus	1	1	1	–	–	–	–	–	–	–	–	–	**1**	**1**	**1**
Vulpes vulpes	1	1	1	–	–	–	–	–	–	–	–	–	**1**	**1**	**1**
cf. *Vulpes vulpes*	–	–	–	–	–	–	–	–	–	1	1	1	**1**	**1**	**1**
Carnivore	–	–	–	–	–	–	–	–	–	2	1	–	**2**	**1**	**–**
Indeterminate	480	29	–	28	3	–	–	–	–	344	17	–	**852**	49	**–**
Sub-total	489	38	7	29	4	1	–	–	–	349	21	2	**867**	**63**	**10**
Indeterminate macro-mammals															
Indeterminate	1,989	–	–	105	–	–	1	–	–	304	–	–	**2,399**	**–**	**–**
Sub-total	1,989	–	–	105	–	–	1	–	–	304	–	–	**2,399**	**–**	**–**
Total	**3,569**	**245**	**37**	**379**	**62**	**13**	**23**	**10**	**1**	**789**	**57**	**9**	**4,760**	**374**	**59**

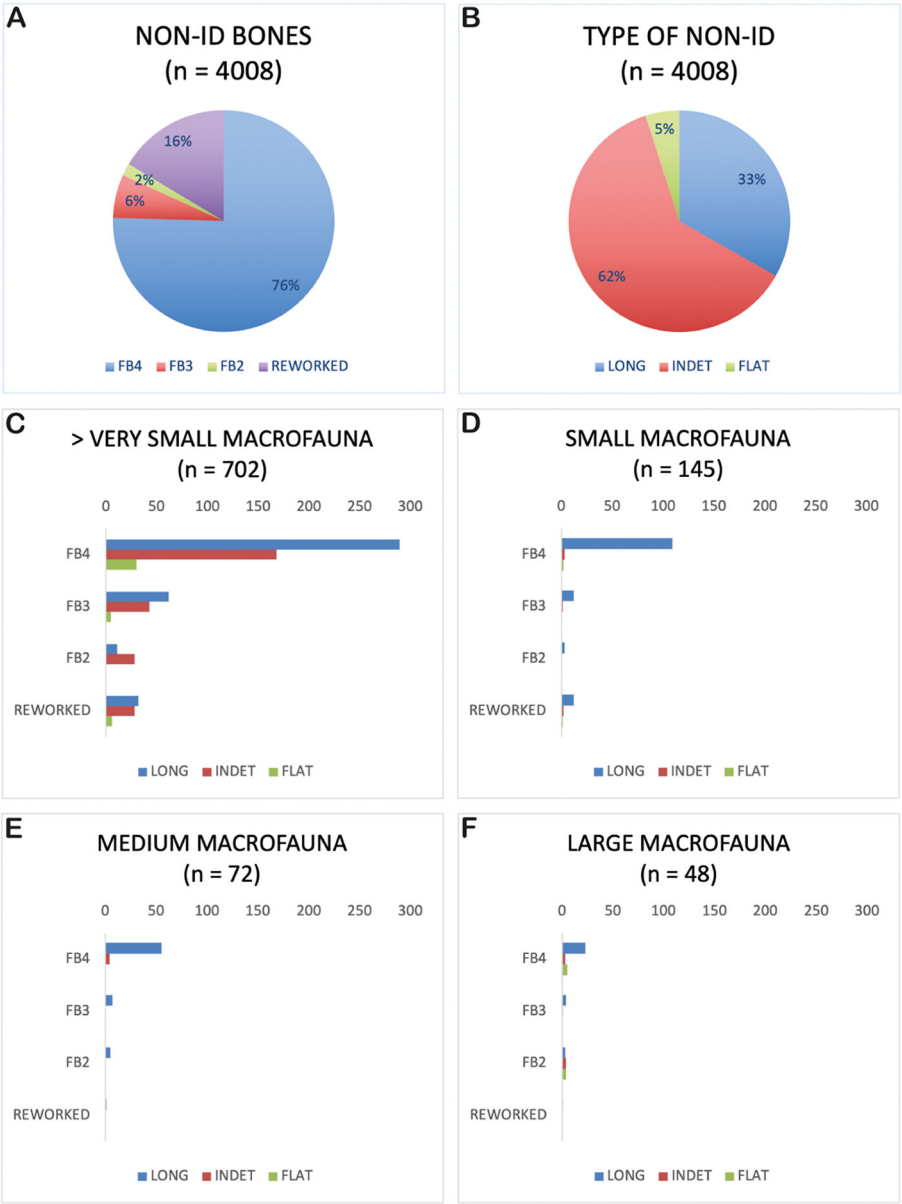

FIGURE 2
Pie charts illustrating the distribution **(A)** and type of fracture **(B)** of non-identified bone fragments across different occupation levels at Gruta da Figueira Brava. The histograms reflect relative abundances of skeletal elements from various ungulate size categories at Gruta da Figueira Brava: >Very Small Macrofauna **(C)**, Small Macrofauna **(D)**, Medium Macrofauna **(E)** and Large Macrofauna **(F)**.

transverse), striation delineation (straight or curved), striation location and side (posterior, anterior, medial, lateral) on the skeletal element. Trampling marks were distinguished from butchery marks following the protocol defined by Domínguez-Rodrigo et al. (2009a). Burning colour observations on bone were based on the schemes of Shipman et al. (1984) and Nicholson (1993), resulting in the creation of five different categories of analysis: (1) Not burnt, (2) Brown, (3) Black, (4) Grey and (5) White. If multiple colours were observed, they were recorded as a combination of categories, such as Brown-Black or Black-White, to accurately reflect the variation.

Carnivore marks were identified according to the categories defined by Binford (1981) and Fisher (1995): punctures, pits, scores, crenulations and digestion marks. The number of marks, their location on the anatomical element and their distribution (isolated, clustered, crossed) were also recorded. The largest width and the largest length of carnivore punctures were registered in millimetres (Andrés et al., 2012). Rodent gnawing was recorded as present or absent, and as to location on the anatomical element. Porcupine gnawing marks, as clearly illustrated by Binford (1984, p. 51), are considered amongst this rodent gnawing category. Other bone

TABLE 2 Number of Identified Specimens (NISP), Minimum Number of Elements (MNE) and percentage of survival (%S) of the MIS-5 main ungulate body parts recovered in Gruta da Figueira Brava (2010–2013 excavations).

Body part	Equidae			Bovidae			Cervidae			Caprinae		
	NISP	MNE	%S	NISP	MNE	%SI	NISP	MNE	%S	NISP	MNE	%S
Cranial												
Antler/horncore	–	–	–	1	1	12.50	9	4	10.53	–	–	–
Skull	–	–	–	–	–	–	–	–	–	–	–	–
Mandible	–	–	–	–	–	–	13	13	34.21	1	1	5.56
Maxilla	–	–	–	–	–	–	3	3	7.89	2	2	11.11
Isolated teeth	13	11	3.93	4	2	1.56	48	28	4.61	62	43	14.93
Axial												
Vertebra	–	–	–	–	–	–	2	2	1.50	–	–	–
Ribs	–	–	–	–	–	–	–	–	–	–	–	–
Front limbs												
Scapula	–	–	–	–	–	–	–	–	–	1	1	5.56
Humerus	–	–	–	–	–	–	1	1	2.63	1	1	5.56
Radius	–	–	–	–	–	–	1	1	2.63	–	–	–
Ulna	–	–	–	–	–	–	–	–	–	–	–	–
Carpals	–	–	–	–	–	–	–	–	–	–	–	–
Metacarpal	1	1	2.38	–	–	–	3	3	7.89	1	1	5.56
Hind limbs												
Pelvis	–	–	–	–	–	–	1	1	2.63	–	–	–
Femur	–	–	–	–	–	–	–	–	–	–	–	–
Tibia	–	–	–	–	–	–	2	2	5.26	–	–	–
Tarsals	1	1	1.19	1	1	2.50	3	3	1.58	1	1	1.11
Metatarsal	2	2	4.76	–	–	–	7	5	13.16	–	–	–
Indet Limbs												
Metapodials	–	–	–	–	–	–	18	6	7.89	–	–	–
Phalanx 1	–	–	–	–	–	–	3	2	1.32	1	1	1.39
Phalanx 2	–	–	–	–	–	–	2	2	1.32	–	–	–
Phalanx 3	–	–	–	–	–	–	2	2	1.32	–	–	–
MNI		**7**			**4**			**19**			**9**	

surface modifications, such as manganese stains, root etching or high concretion-coating, were also recorded.

4 Results

4.1 Taxonomic and body part frequencies

A total of 4,760 macro-mammal remains were analysed. The majority, representing 83.4% of the assemblage, originate from the occupation phases dated to MIS-5b and were recovered from Area F. Specifically, phase FB4 is the most significant contributor, accounting for 75% of the total remains. The remaining correspond to phases FB3 and FB2 (8.4%), and to the reworked assemblage (16.6%; Table 1).

Approximately half of the assemblage (50.4% or $n = 2{,}399$) is indeterminate and cannot be assigned to any animal size categories. Within such categories, 41.9% (or $n = 1{,}992$) remain unidentifiable at family or species level. Consequently, excluding teeth, a considerable part of the faunal collection corresponds to non-identifiable bones ($n = 4{,}008$, or 84.2%). Only 7.8% (or NISP = 369) of the total analysed assemblage provides taxonomic information (Table 1), but the non-taxonomically identifiable portion of the assemblage offers valuable anatomical and taphonomical information, nonetheless.

Amongst the non-identifiable bone fragments, 75.5% (or $n = 3{,}025$) were recovered from phase FB4 levels (Figure 2A). More than half of the non-identifiable bones ($n = 2{,}479$, or 61.9%) cannot be categorised as either long or flat, they have been classified simply as indeterminate (Figure 2B). However, about 33% (or $n = 1{,}331$),

TABLE 3 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of the MIS-5 teeth remains showing age information from ungulates and carnivores recovered in Gruta da Figueira Brava (2010–2013 excavations).

Taxa	Juvenile		Adult		Senile	
	NISP	MNI	NISP	MNI	NISP	MNI
Ungulates						
Equidae	5	2	4	1	–	–
Bovidae	–	–	4	1	–	–
Cervidae	10	3	42	4	1	1
Caprinae	1	1	47	4	–	–
Suidae	1	1	2	1	–	–
Carnivores						
Ursus	–	–	9	2	–	–
Hyaenidae	–	–	–	–	–	–
Canis	–	–	–	–	–	–
Felis	–	–	3	1	–	–
Lynx	–	–	1	1	–	–
Vulpes	–	–	–	–	–	–

TABLE 4 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of the MIS-5 long bone remains showing states of epiphyseal fusion from ungulates and carnivores recovered in Gruta da Figueira Brava (2010–2013 excavations).

Taxa	Unfused		Fused	
	NISP	MNI	NISP	MNI
Ungulates				
Equidae	–	–	4	1
Bovidae	–	–	1	1
Cervidae	6	1	15	1
Caprinae	1	1	3	1
Suidae	–	–	1	1
Carnivores				
Ursus	–	–	3	1
Hyaenidae	–	–	4	2
Canis	–	–	1	1
Felis	–	–	5	2
Lynx	–	–	–	–
Vulpes	–	–	1	1

most from phase FB4, correspond to long bone fragments, from which only 18 correspond to epiphyses. A total of 171 spongy bone fragments were identified within the indeterminate remains. Figures 2C–F presents a closer look at the non-identified bones recovered, in particular among animal size groups corresponding to the ungulates identified at the site, i.e. >Very Small Macrofauna, Small Macrofauna, Medium Macrofauna and Large Macrofauna. Therefore, even though the number of NISP is low, there is a clear presence of long bone remains of the appendicular skeleton, as well as (although in lower frequency) of flat bones of the axial skeleton (Figures 2B–F).

4.1.1 Ungulates

No remains of Very Large Macrofauna were recovered in the 2010–2013 excavations (but note that elephant and rhino are listed among the 1980s Area C finds; Antunes, 2000). The largest species is the aurochs (Table 1), which was identified based on the presence of five tooth fragments (a permanent molar and incisors), a left naviculo-cuboid and a horn core fragment (Figure 4, Tables 2–4). Equids were mainly identified based on tooth remains (NISP = 13, of which five are deciduous; Figure 3F), but there is also one astragalus, two metatarsals and one metacarpal; these bones allow taxonomic attribution to *Equus caballus* (Figure 4; Tables 2–4).

Red deer is the best represented ungulate (Table 1). Identification as *Cervus elaphus* was possible for the majority of the remains, which suggests that most of the fragments assigned to Cervidae probably belong to the species too. Cranial elements—such as mandibles (NISP = 14; Figure 3H), maxillae (NISP = 4) and isolated teeth (NISP = 37)—predominate, but the appendicular skeleton is also represented by phalanges (NISP = 7) as much as hind limbs, tarsals (NISP = 8) and front limbs (NISP = 4; Figure 4; Table 2). The state of long bone fusion and the dental remains indicate that deer of all ages (from juvenile to senile) are represented in the assemblage (Tables 3, 4).

Caprines come close to deer in NISP counts (Table 1). They are mainly represented by isolated teeth (NISP = 69; of which three are deciduous), but there are two adult mandibles and two adult maxillae (Table 3). Front and hind limbs are evenly represented, by three elements each, as well as two first phalanges that could not be assigned to leg (Figure 4; Table 2). All bones are fused, except for a distal humerus (Table 4). Tooth morphology was explored in order to attempt species identification and, based on the LARC reference collection, *Capra pyrenaica* is the best candidate. Finally, boar is the less frequent ungulate; it is represented by two metapodials, two adult mandibular teeth and a juvenile mandible, all from Area F (Tables 1, 3, 4).

As explained before, more of the appendicular and axial skeletons of these taxa are represented amongst the long bone and flat bone fragments of the animal size categories >Very Small Macrofauna, Small Macrofauna, Medium Macrofauna and Large Macrofauna, as shown in Figure 2.

4.1.2 Carnivores

Brown bear (*Ursus arctos*) is the best represented carnivore (Table 1; Figure 3B). The remains include adult teeth (two incisors and seven canines), a nearly complete atlas, one axis, a thoracic vertebra and a left humerus. The vertebral discs are all fused, but the calcareous concretions attached to the humerus do not allow proper observation of the state of long bone fusion (Table 4). Based on Andrews and Turner (1992), canines only erupt at 14 months, suggesting that the two bear individuals minimally represented in the assemblage were more than one year old.

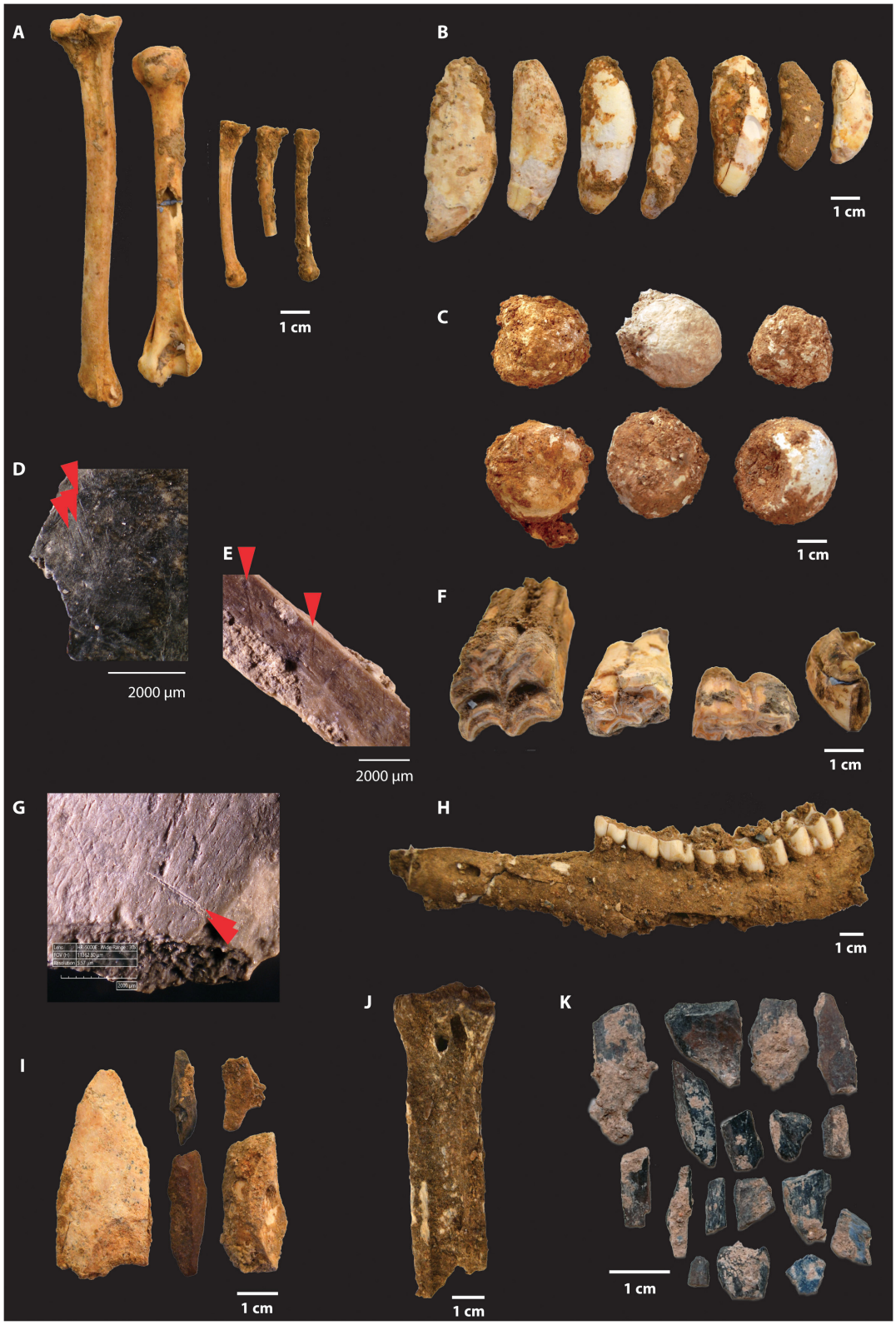

FIGURE 3
Middle Palaeolithic, MIS-5 ungulate and carnivore remains recovered in Area F of Gruta da Figueira Brava. **(A)** *Felis silvestris* (from left to right, tibia, humerus, two metatarsus 3 left and one metatarsus 2). **(B)** *Ursus arctos* canine teeth. **(C)** Hyaena coprolites. **(D)** Cut marks on long bone of >Very Small Macrofauna fragment. **(E)** Cut marks on long bone of >Very Small Macrofauna fragment. **(F)** *Equus caballus* (from left to right, two permanent premolars/molars, one deciduous premolar 4 and one permanent incisor 3). **(G)** Cut marks on long bone of >Very Small Macrofauna fragment. **(H)** *Cervus elaphus* mandible with permanent teeth P2, P3, P4, M1, M2, M3. **(I)** Impact flakes on indeterminate macro-mammal remains. **(J)** *Cervus elaphus* metatarsus with very straight longitudinal fracture. **(K)** Burnt bone fragments of indeterminate macro-mammals.

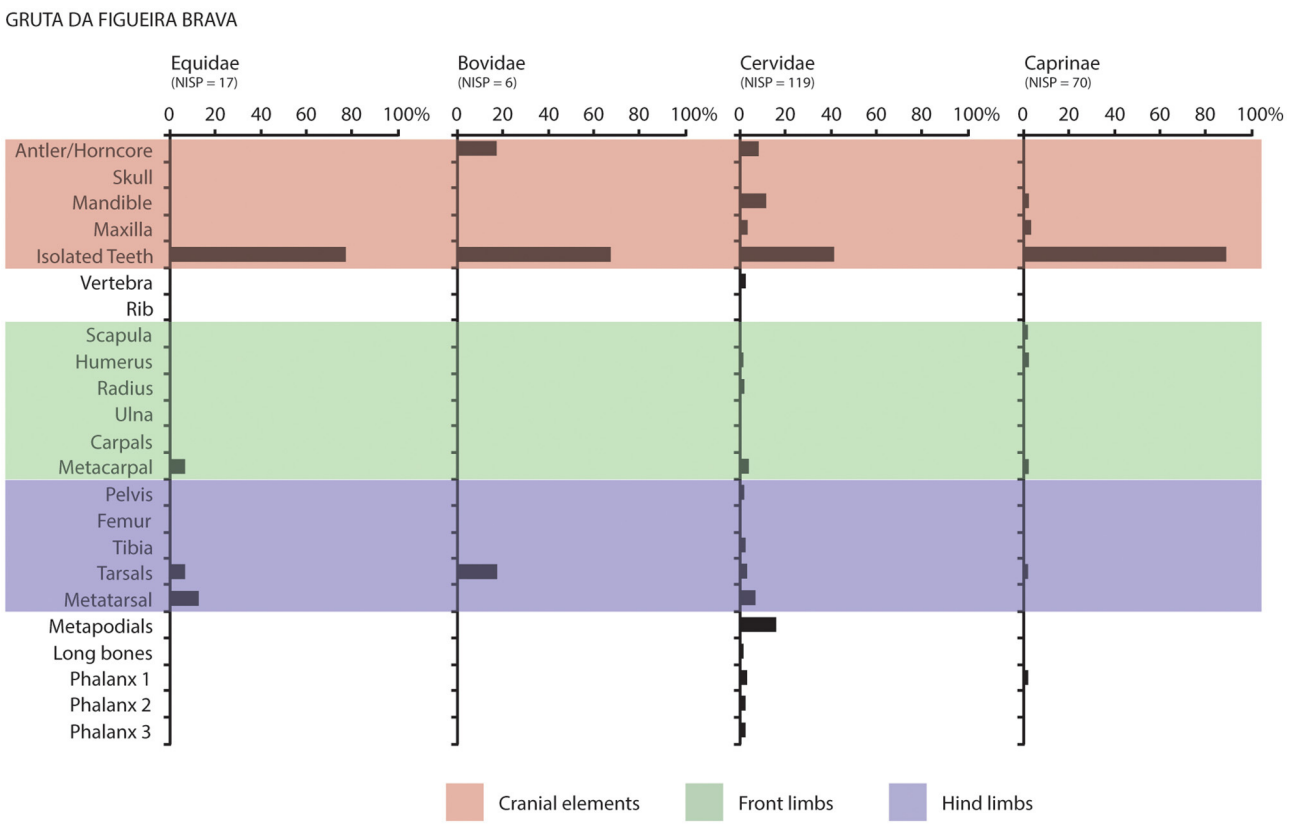

FIGURE 4
Body part representation of the most representative ungulate taxa in the Middle Palaeolithic, MIS-5 macro-mammal assemblage from Gruta da Figueira Brava.

Hyaenas were identified based on two metapodials, a left astragalus and a first phalanx. Most probably, they are of *Crocuta crocuta*, a species commonly found in Europe's Middle and Upper Pleistocene caves (Sanz et al., 2016). Amongst the 37 coprolites recovered, a total of 28 were complete and allowed measurements (Figures 3C, 5; Table 5); most (NISP = 22) cluster with Morphotype 1 and can be attributed to hyaenas, due to their spherical morphology, with flattened or concave ends (Horwitz and Goldberg, 1989; Larkin et al., 2000) and size, which compares well with available data for *Crocuta crocuta*. However, one very large coprolite is close to Morphotype 3 of Furninha and, therefore, is probably of bear. Apart from an outlier of very small size that does not relate to any of the species listed in Table 5 and in Figure 5, all the other non-hyaena coprolites (NISP = 4) cluster in Morphotype 2 and, thus, may belong to wolf (*Canis lupus*). Indeed, the wolf is represented at the site by a complete left calcaneum.

As for the smaller carnivores, the wildcat (*Felis silvestris*; Table 1 and Figure 3A) is represented by fused long bones—three metatarsals, a right humerus, a left tibia—and three maxillary fragments with permanent teeth (Tables 3, 4). A fragment of right maxilla with permanent premolars 2 and 3, and a fused left pelvis were also found in the reworked deposit. Lynx (*Lynx pardinus*) and fox (*Vulpes vulpes*; Tables 1, 3, 4) are represented by a left upper canine and a right fused fifth metacarpus, respectively.

4.2 Fragmentation and type of fracture

The macro-mammal assemblage is heavily fragmented: only 2.47% (or $n = 98$) of the *in situ* remains are complete, corresponding mainly to bones of limb extremities (i.e. metapodials, tarsals, carpals and phalanges) and coprolites; whereas 53.24% (or $n = 2{,}114$) of the fractured bones are smaller than 2 cm. Overall, fractures are preferentially curved/V-shaped (43.72%, or $n = 1{,}736$) and longitudinal (36.94%, or $n = 1{,}467$; Figure 3J); the former with most angles being oblique (56.31%, or $n = 2{,}236$), the latter with most being at right angles (35.81%, or $n = 1{,}422$) and occurring frequently on ungulate metapodials. Smooth edges are the most frequent (86.93%, or $n = 3{,}452$). Such fracture patterns denote bones that were broken when fresh for the curved/V-shaped types, whereas some degree of dry bone fracturing is evidenced by the right angles.

Out of a total of 18 mandibles, longitudinal fractures predominate (66.67%, or $n = 12$), followed by transverse fractures (33.33%, or $n = 6$). Of the 25 vertebrae found, only three are complete: most show fractures along their transversal axis ($n = 18$). Transversal fractures are also the most common among ribs (83.04%, or $n = 93$ from a total of 112 remains). Nearly half of the phalanges are complete ($n = 7$, from a total of 16), and six

TABLE 5 Vertical distribution, per stratigraphic units, of coprolites and their measurements from Gruta da Figueira Brava. Taxon assignation is based on the comparisons provided in Figure 5 using Sanz et al. (2016).

ID	Unit	Phase	Taxon	Length (mm)	Width (mm)	Fragment size (cm)
1	Reworked	–		53.02	33.16	>5
2	Reworked	–		39.24	36.22	3–4
3	IH2-IH3	FB4	–	78.88	–	>5
4	IH2-IH3	FB4	*Canis lupus*	26.47	22.86	2–3
5	IH2-IH3	FB4	*Crocuta crocuta*	36.47	30.21	3–4
6	IH2-IH3	FB4	*Crocuta crocuta*	52.88	41.37	>5
7	IH2-IH3	FB4	–	43.09	–	4–5
8	IH2-IH3	FB4	*Crocuta crocuta*	38.31	37.45	3–4
9	IH4	FB4	*Crocuta crocuta*	35.40	35.31	3–4
10	IH4	FB4	*Crocuta crocuta*	28.12	26.85	2–3
11	IH4	FB4	*Crocuta crocuta*	36.82	33.16	3–4
12	IH4	FB4	*Ursus arctos*	71.18	47.73	>5
13	IH4	FB4	*Canis lupus*	21.65	15.75	2–3
14	IH4	FB4	*Crocuta crocuta*	37.16	28.18	3–4
15	IH6	FB4	*Crocuta crocuta*	48.06	34.30	4–5
16	IH6	FB4	*Crocuta crocuta*	55.06	45.15	>5
17	IH6	FB4	Very small carnivore	13.24	11.05	1–2
18	IH6	FB4	–	20.35	–	2–3
19	IH6	FB4	*Crocuta crocuta*	32.87	31.11	3–4
20	IH6	FB4	–	–	21.80	2–3
21	IH6	FB4	*Crocuta crocuta*	49.97	39.57	4–5
22	IH6	FB4	*Crocuta crocuta*	28.94	27.53	3–4
23	IH6	FB4	*Crocuta crocuta*	54.25	47.38	>5
24	IH6	FB4	*Crocuta crocuta*	38.38	34.13	3–4
25	IH6	FB4	–	31.54	–	3–4
26	IH8	FB4	–	52.81	–	>5
27	IH8	FB4	*Crocuta crocuta*	24.70	25.29	2–3
28	IH8	FB4	*Crocuta crocuta*	45.51	42.92	4–5
29	IH8	FB4	*Canis lupus*	28.90	19.58	2–3
30	IH8	FB4	*Canis lupus*	28.36	23.29	2–3
31	IH8	FB4	*Crocuta crocuta*	28.91	24.79	2–3
32	IH8	FB4	–	39.93	–	3–4
33	IH8	FB4	*Crocuta crocuta*	49.28	35.02	4–5
34	IH8	FB4	–	47.00	–	4–5
35	IH8	FB4	–	50.75	–	>5
36	IL3	FB3	*Crocuta crocuta*	33.43	32.24	3–4
37	IL3	FB3	*Crocuta crocuta*	33.45	30.86	3–4

show transversal fractures. Most limb bones are broken (99.35%, or $n = 1{,}078$ from a total of 1,085), and longitudinal (54.29%, or $n = 589$) and curved/V-shaped (29.12%, or $n = 316$) fractures are predominant. These patterns remain valid if only deer is considered, as one would expect given that it is the most common taxa: out of a total of 33 deer limb bone fragments, 63.64% (or $n = 21$) are longitudinally broken and 24.24% (or $n = 8$) display curved/V-shaped breaks.

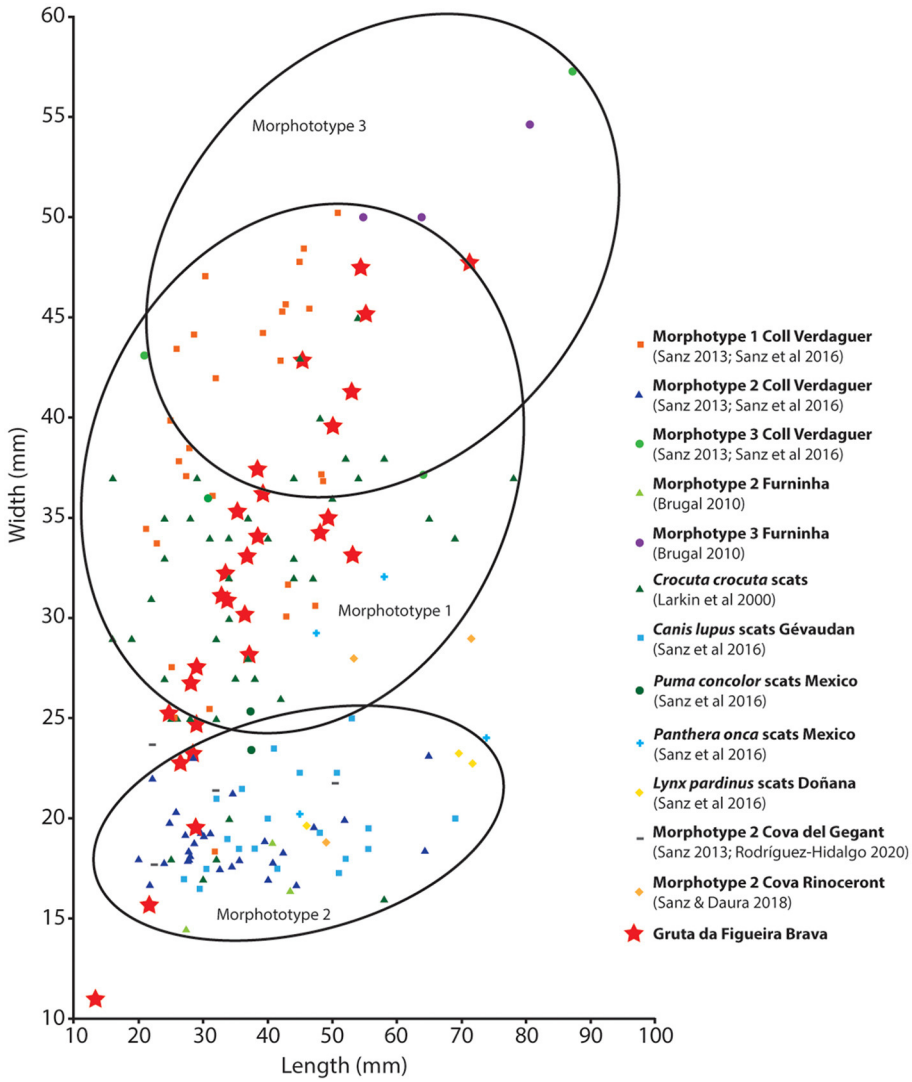

FIGURE 5
Comparative analysis of the coprolites from Gruta da Figueira Brava. The graph is adapted from Sanz et al. (2016). It includes updated information provided by Montserrat Sanz (pers. comm. in October 2020) and data from the 2010–2013 excavations as provided in Table 2.

4.3 Bone surface modifications

The observation of bone surface modifications is hindered by the dense concretion coating covering the bones, which obscures potential marks and greatly reduces the likelihood of detecting additional surface alterations. Percussion marks and impact flakes are less affected by this condition and therefore represent the most frequently observed types of anthropogenic modification (Table 6; Figure 3I). Mostly, they concern unidentifiable fragments but, in a few cases—a distal humerus shaft impacted on the cranial side, two metapodials impacted on the shafts, a metatarsal and a metacarpal impacted on the cranial side of shaft ends—the bones could be determined to deer. Among percussion notches, only two are on identified remains—one on the dorsal side of a proximal shaft of a horse metacarpal, the other on the dorsal side of a proximal shaft of a deer first phalanx. No adhering flakes could be identified to taxon, although they are present on non-identifiable macrofaunal remains. Percussion pits are the least represented anthropogenic mark; in one case, the affected bone could be identified as a deer metatarsal. Cut marks were found on an ibex first phalanx from the reworked deposit; otherwise, all cut marks are on unidentified remains (Figures 3D, E, G). Carnivore marks are scarce and mostly represented by punctures on the root surface of mandibular teeth of caprines and cervids (Table 6).

4.4 Burning

Thermo-alterations were observed in 611, i.e., 15.39% of the *in situ* remains analysed (Table 6; Figure 3K), which for the most part come from the FB4 deposit. Due to the very small size of the fragments (<2 cm) and the lack of diagnostic features, only a few (n = 111, i.e., 18.17%) could be assigned

TABLE 6 Bone surface modifications observed in the macro-mammal assemblage from Gruta da Figueira Brava (2010–2013 excavations).

	Phase FB4	Phase FB3	Phase FB2	Reworked	Total
Burning					
Brown	127	1	–	25	**153**
Black	450	7	3	44	**504**
Grey	16	–	–	–	**16**
White	7	–	–	1	**8**
None	2,969	309	82	719	**4,079**
Total	**3,569**	**317**	**85**	**789**	**4,760**
% Burnt	**16.81**	**2.52**	**3.53**	**8.87**	**14.31**
Butchery					
Chops	2	–	–	9	**11**
Cuts	10	2	–	9	**21**
Scrapes	1	–	–	1	**2**
None	3,556	315	85	770	**4,726**
Total	**3,569**	**317**	**85**	**789**	**4,760**
% Butchery	**0.36**	**0.63**	**0**	**2.41**	**0.71**
Percussion					
Impact flake	143	24	6	51	**224**
Adhering flake	12	–	1	1	**14**
Percussion notch	29	7	2	17	**55**
Percussion pit	6	2	–	4	**12**
None	3,379	284	76	716	**4,455**
Total	**3,569**	**317**	**85**	**789**	**4,760**
% Percussion	**5.32**	**10.41**	**10.59**	**9.25**	**6.41**
Carnivore					
Carnivore pit	–	–	–	1	**1**
Carnivore puncture	14	–	–	3	**17**
Scoring	1	–	–	–	**1**
None	3,554	317	85	785	**4,741**
Total	**3,569**	**317**	**85**	**789**	**4,760**
% Carnivore	**0.38**	**0**	**0**	**0.51**	**0.40**

to species or size category. Black burns predominate, followed by brown burns; grey and white thermo-alterations are rare (Table 6).

In most MIS-5 fragments, burning covers the surfaces of the remains entirely (i.e., is complete), but 41 (or 6.71%) fragments display thermo-alteration only on one side, mostly the exterior part of diaphyseal fragments. In contrast, burning only on the interior surface was observed in four shaft fragments. Shaft fragments are the most represented body part ($n = 585$), but there are also 24 burnt epiphyses and two black burnt tooth fragments. The latter are a maxillary canine fragment of bear from unit IH8 and one mandibular premolar of deer from unit IH4.

5 Discussion

5.1 Local palaeoenvironment

The macro-mammal assemblage from Gruta da Figueira Brava comes from a deposit encompassing the remains of three different human occupation phases (FB4, FB3 and FB2). Due to small sample size, particularly regarding the older occupation phases (refer to Table 1), the following discussion will consider the MIS-5 levels as a whole. This approach is necessary to ensure a comprehensive analysis, mitigating the limitations imposed by the smaller datasets for individual phases.

The ungulates exhibit diverse dietary behaviours, reflective of their ecological adaptability. Aurochs, for instance, likely thrived in dense forested environments, where their diet primarily would have consisted of grasses and graminoids. However, they also must have supplemented their feeding with a variety of forbs, as well as the leaves and branches of bushes and trees, reflecting a degree of dietary flexibility suitable for forested settings (van Vuure, 2005). In contrast, horses are more adapted to open, low-density forests and grassland ecosystems, where their grazing behaviour focuses on a diverse array of grasses (García García et al., 2009). This grazing specialisation is supported by isotopic and morphological evidence that indicates that their diet is dominated by C_3 grasses typical of temperate environments (Schulz and Kaiser, 2012). Such ecological distinctions between these two large size taxa, suggest that the landscape surrounding Gruta da Figueira Brava featured denser, closed-canopy settings (where aurochs thrived), as well as more open, grass-dominated areas (where horses thrived).

Red deer display a mixed feeding strategy that shifts between browsing and grazing according to seasonal variations (e.g., Solounias and Semprebon, 2002). This dietary flexibility enables them to consume a wide variety of resources, including grasses, sedges, foliage of trees and shrubs (Azorit et al., 2012). Such adaptability not only facilitates survival in varied environments but also contributes to their widespread distribution across most of Iberia, where they prosper in heterogenous landscapes comprising forest, grassland and scrubland (Geist, 1998; Clutton-Brock, 1982). These ecological traits highlight the red deer's role as a generalist herbivore, well-suited to dynamic and patchy environments, which must have constituted most of Arrábida's territory, where the cave is located.

Ibex are highly specialised ungulates adapted to mountainous or rocky environments, where their robust limbs are adjusted to move on steep terrain. Despite this specialisation, their habitat can extend to other types of landscape depending on food availability, demonstrating a degree of ecological flexibility. Seasonally, ibex exhibit altitudinal migration patterns, occupying higher elevations during the summer and autumn months when food is abundant in those areas. In contrast, during the winter and spring, they descend to lower elevation open areas where vegetation remains accessible (Granados et al., 2001).

The presence of these taxa through the period of site occupation highlights the sustained presence of a diverse range of ecological niches in the terrestrial surrounding landscape. This mosaic of habitats, ranging from dense forests and open grasslands to mountainous land, provided the Gruta da Figueira Brava's inhabitants with access to a broad spectrum of macro-mammal resources. The variety of species exploited reflects the foraging strategies employed by the human groups, enabling them to capitalise on the seasonal and spatial distribution of fauna. This evidence supports the view that the cave served as a central hub for human activity over time, facilitating the exploitation of different habitats and explaining the resilience of the adaptive system.

5.2 Agents of bone accumulation

Given that no anthropogenic or carnivore-induced marks are to be seen on the bones of carnivores, the parsimonious explanation for their presence is natural demise while taking shelter at the site. The limited number of skeletal elements indicate that episodes of larger carnivore use of the cave were sporadic and primarily took place when humans were not there. This inference is consistent with the stratigraphic distribution of the remains. In the case of hyaenas, for example, they almost entirely (a) date to the three millennia-long hiatus between the end of phase FB3 and the beginning of phase FB4, or (b) post-date the near-complete sedimentary fill-up of Entrance 3 and Area F (Tables 1, 2; Zilhão et al., 2020), which made the site unsuitable for settlement and allowed for the interior to become a hyaena latrine, as revealed by the abundant coprolites and coprolite crumbs seen in the upper reaches of the infilling. Indeed, (a) the scarcity of carnivore skeletal remains, (b) the absence of juveniles, (c) the lack of digested bones, (d) the limited presence of jagged edges on bone fractures and (e) the low frequency of carnivore-induced marks (i.e., carnivore marks account for only 0.38% in phase FB4 and are entirely absent in phases FB3 and FB2, whereas percussion and cut marks show higher frequencies in all phases of occupation; Table 6), collectively exclude the possibility that the site was used as a den where large carnivores engaged in feeding behaviours. While some of these bone surface modifications may be obscured by carbonate concretions, this factor would equally affect evidence of both human and carnivore activity, as well as other potential agents of bone surface modification. Therefore, although the absence of such marks should not be interpreted as definitive evidence of nonexistence, the low carnivore-induce occurrence suggests that carnivores played a minimal role in bone accumulation and bone modification at the site.

Bears and wolves consume their prey at the kill site and are not significant accumulators of faunal remains (Domínguez-Rodrigo, 1993, 1994; Saladié et al., 2013; Sala and Arsuaga, 2013). Whenever wolves transport food back to the den, it tends to be as eaten meat parts that are regurgitated to feed their cubs (Domínguez-Rodrigo, 1994; Castel et al., 2010; Sauqué et al., 2018). However, neither digested bone remains, nor skeletal remains of young wolves were recovered. At archaeological sites, wolves can also be responsible for the modification of previously accumulated bones. The limited number of bite marks found on the root surface of mandibular teeth of deer and ibex can maybe relate to the scavenging of mandibles for marrow (or what was left of it) or as an attempt to extract the tooth pulp (Binford, 1981), either by wolf or one of the other carnivores represented in the cave's faunal assemblage. The involvement of the porcupine, a species represented at the site by a complete mandible (Cardoso et al., 2021), should not be excluded either. Even though, the possibility that these marks resulted from human activity cannot be ruled out, particularly when considering the marrow exploitation activities observed in other parts of the assemblage, as discussed below. If that were to be the case, then it would further support Neanderthal's primary access to these ungulates' carcasses.

The majority of cut marks are observed on non-identifiable diaphyseal remains. Given that most incisions are located on shaft portions, this pattern is indicative of meat removal and filleting, reflecting butchery practices. However, the proportion of faunal remains exhibiting cut marks within this assemblage is comparatively lower than that recorded at other Iberian sites of similar Middle Palaeolithic contexts, e.g., Level IV of Bolomor (7.1%; Blasco and Fernández Peris, 2012) and Level Jb of Abric Romaní (4%; Marín et al., 2017). These assemblages have generally been interpreted as representing occupation sites of varying durations. Nevertheless, it is important to consider once more that the faunal assemblage from Figueira Brava has not been fully released from its concretion coating, which obscures a significant portion of the bones' surface modifications.

Despite the low frequency of cut marks, other lines of evidence indicate hominin involvement in faunal processing. These include the presence of bone fractures and percussion marks consistent with carcass processing activities. A variety of percussion marks, which in this case are the most frequent and the more diagnostic of anthropogenic fracturing, are primarily observed on red deer remains—the most exploited ungulate at the site. The presence of curved/V-shaped fractures with oblique angles, suggests that bones were broken with hammerstones while still fresh, even though different bones from different species can show varying fracture patterns (e.g., Alcántara-García et al., 2006; Coil et al., 2017). Bone fractures and percussion marks are likely related with marrow extraction, and the presence of abundance longitudinal fractures on long bones supports this interpretation (e.g., Stavrova et al., 2019; Vettese et al., 2020).

The presence of right-angled fractures, however, is typically associated with dry bone breakage (e.g. Outram, 2001), suggesting an additional scenario. Since these fractures are predominantly found on long bones, it is plausible that these elements were processed for deferred marrow consumption (e.g., Binford, 1978) or repurposed as raw materials for bone tool production. Notably, ungulate long bones—especially metapodials—have long been known to be preferred for tool manufacture, with a *chaîne opératoire* involving longitudinal fracturing (e.g., Sadek-Kooros, 1972; Yesner and Bonnichsen, 1979). Whether used for consumption, tool production, or both, the observed modifications strongly indicate anthropogenic manipulation of the assemblage.

Moreover, the high incidence of bones exhibiting varying degrees of heat exposure, including those with black colouration associated with burning temperatures linked to cooking activities, aligns with patterns observed at coeval, humanly occupied sites. A notable parallel can be drawn with unit II of Ramandils Cave in France, where similar thermal modifications have been documented (Rusch et al., 2019). However, it is important to note that while some brown-burnt bones were detected at Gruta da Figueira Brava, they cannot be directly attributed to cooking activities. Instead, they may result from bones being buried and subsequently exposed to heat from fire production on the sediment layer above (Téllez et al., 2022). Although these brown burns do not necessarily reflect direct consumption of the affected bones, they provide evidence for repeated fire use within the cave, suggesting a certain intensity of occupation and site reutilisation.

The human consumption of ungulates at Figueira Brava represents a relatively minor component of the diverse array of resources exploited by Neanderthals inhabiting the cave. The presence of other faunal remains of smaller size—such as crabs, birds and tortoises (Nabais et al., 2023a,b; Nabais and Zilhão, 2019)—which have previously been identified as resulting from human accumulation, reinforces this interpretation. Furthermore, all macrofaunal remains were recovered from stratigraphic levels containing abundant lithic artefacts attributable to the Mousterian tradition (Zilhão et al., 2020). Collectively, and despite the limitations imposed on analysis by the bones' concretion-coated surface and the relatively small excavated area, these indicators suggest that the role of primary accumulator and primary modifiers of the site's faunal remains was played by humans.

Given the evidence for anthropogenic modification—including burning, intentional breakage and butchery, to be discussed in detail below—the ungulate bones at the site reflect human subsistence behaviour. This interpretation is further supported by the taxonomic composition of the assemblage (ibex, red deer, horse, aurochs), the age profiles of the animals (predominantly adults, with some juvenile remains) and the skeletal part representation (primarily long bones and heads). These characteristics suggest primary access to the carcasses, consistent with previous studies (e.g., Domínguez-Rodrigo, 1999; Gaudzinski and Roebroeks, 2000).

5.3 Ungulate hunting and processing

The transport of animal carcasses to archaeological sites is influenced by multiple factors, including the proximity to the kill site, the value placed on different parts of the carcass and the energetic cost associated with transport, but the prevailing view is that animals hunted near the site are more likely to be skeletally complete upon deposition, as shorter transport distances reduce the likelihood of carcass part attrition during transportation [see a good summary by Reitz and Wing (2008) and references therein; and also a recent example from Bertacchi et al. (2025)]. Skeletal part frequencies can therefore provide insight into hunting practices and the distance from the kill site to the habitation area. Less desirable portions of a carcass are often left at the kill site—normally body parts with lower nutritional yield—, while higher-value parts are transported to residential areas (e.g., Marín et al., 2017). However, these decisions are shaped by multiple factors including weather conditions, topography, the number of individuals participating in the hunt, the energy costs associated with carcass transportation and processing, prey body size and competition with other carnivores (e.g., Bunn et al., 1988; Monahan, 1998; Schoville and Otárola-Castillo, 2014). It should also be considered that the identification of "valuable" or "prestigious" elements is context-dependent, influenced by personal and cultural preferences, specific subsistence needs and environmental conditions (O'Connell et al., 1990). For example, cranial elements may be transported despite their weight and bulk, at a great energetic expense, driven by symbolic behaviour or the value of the brain and other soft tissues for nutritional or other purposes (e.g., Stiner, 1994; Baquedano et al., 2023).

Despite the limitations of the assemblage, Gruta da Figueira Brava's skeletal remains reveal distinct patterns of carcass transport, suggesting a range of exploitation strategies. Although utility indices—such as Binford's (1978) MUI, MI GUI and MGUI, or Metcalfe and Jones's (1988) FUI—are challenging to apply due to the limited sample size, some fundamental principles can still be considered in the analysis and interpretation of our assemblage. According to these researchers, the likelihood of a body part being transported increases with its nutritional value, while less valuable parts are more likely to be discarded. Consequently, if a specific body part with a given nutritional value is removed from the kill-site, body parts with lower nutritional value are also expected to be transported (Binford, 1978; Metcalfe and Jones, 1988).

Applying these principles to our assemblage, it is evident that high-meat-bearing elements, such as the humerus and scapula of ibex, were transported to the site, showing significant survival rates (Figure 4; Table 2). Similarly, high-utility elements such as the humerus, radius, pelvis and tibia of deer were also brought in (Figure 4; Table 2). Following the basic principles outlined earlier, this suggests that all other limb bones were transported as well. Given the well-documented practice of marrow extraction, which results in extensive bone breakage, most evidence of long bones is archaeologically represented by taxonomically indeterminate long bone fragments within the >Very Small, Small and Medium Macrofauna size categories. However, the relatively higher presence of deer and ibex distal limb bones (i.e. metapodials, carpals, tarsals and phalanges) indicates that entire limbs were transported to the site. This pattern aligns with meat-utility predictions, which suggest that if high-utility elements—such as the humerus or a tibia—were transported, then all associated lower-nutritional-value bones—like the metapodials, carpals/tarsals and phalanges—would also have been brought in.

The axial skeleton, primarily represented by ribs and vertebrae, is highly non-diagnostic. Additionally, ribs are prone to breakage, often resulting in their classification within the generic flat bone group. From the axial skeleton, only two deer vertebrae were identified; however, given the substantial number of flat bone fragments categorised within the >Very Small, Small and Medium Macrofauna size classes recovered from the site (Figures 2C–F), it is likely that additional axial elements are present but not easily identifiable. Conversely, cranial elements are well represented for both deer and ibex, exhibiting the highest skeletal survival rates (Figure 4; Table 2). This evidence is strongly indicative that complete carcasses of both deer and ibex were transported to the cave, where they were subsequently processed and consumed.

In contrast, the skeletal remains of aurochs and horses at Gruta da Figueira Brava primarily consist of cranial fragments and limb extremities. The traditional interpretation of this "head and foot pattern" suggests that the abundance of skulls, hands and feet, alongside the absence of meat-rich bones, is indicative of scavenging activities (Binford, 1984). However, the taxonomic and anatomical characterisation of the overall bone assemblage of Figueira Brava does not align with a scavenging scenario. Alternative explanations have been proposed for this distinctive skeletal representation.

Amongst the Hadza, hunters try to transport as much food as possible, while reducing the weight they are transporting back to the base camp. Thus, they discard bones that are easy to process, such as ribs and long bones (Monahan, 1998). At several archaeological sites, cranial elements are disproportionately represented in horse remains, suggesting a deliberate transport strategy. For example, in level Pa and Pb of Abric Romaní (in Spain), horses exhibit a higher presence of cranial elements (Marín et al., 2019). Similarly, at the Chinese Palaeolithic site of Lingjing, horse skulls and mandibles are the most frequently identified skeletal parts (Zhang et al., 2012). This pattern aligns with observations from modern hunter-gatherer societies, where equid meat and milk are considered valuable due to their higher essential fatty acid (EFA) content (Levine, 1998). Experimental studies further demonstrate that equid bones retain significant muscle attachments and nutritional content even after processing. As a result, humans could have prioritised transporting these nutrient-rich skeletal elements to base camps, where they had the necessary time and resources to extract all available nutrients—a strategy that remains relevant among contemporary hunter-gatherers (Lupo, 2006).

There are examples from Qesem and Tabun caves, in Israel (Blasco et al., 2024; Kuhn and Stiner, 2019) showing habitation sites where some carcasses were initially processed at kill sites and then transported to the cave for further butchering. This suggests a selective transport strategy, where only the most nutritionally valuable portions of the skeleton were brought back to the residential site, consistent with the observations of Lupo (2006). In France, at Pech de l'Azé IV, Niven (2013) documented a high representation of reindeer skulls, which she linked to the presence of fire within the site. This association suggests that controlled use of fire facilitated the efficient processing of cranial remains, allowing for their regular transport. This explanation could also account for the strong presence of large ungulate skulls at other sites. Experimental work on cow heads processing further supports this hypothesis, as percussion-based removal of cranial parts has been shown to result in the detachment of multiple teeth, thus increasing the number of cranial elements identified in an assemblage (Baquedano et al., 2023). A recent case study comes from the Epigravettian horse-killing site at Stránská skála IV in the Czech Republic, where animals were extensively dismembered and processed on-site, while the heads were likely transported to the base camp (Svoboda et al., 2020). However, no alternative explanations have been proposed beyond the hypothesis that these heads were used primarily for their fat content. These finds collectively suggest that the transport and processing of large ungulates followed a structured strategy influenced by nutritional optimisation, technological capabilities and environmental factors rather than simple scavenging behaviours.

This ungulate skeletal representation and transport strategy based on size-weight found in Gruta da Figueira Brava—where deer and ibex were transported whole while only selected parts of aurochs and horse were brought back to the base camp—is similar to one found in other Middle Palaeolithic sites, such as Abric Romaní (see Marín et al., 2017 and references therein). However, it should be highlighted that this variation in different-size-ungulate transport strategies appears to be influenced not only by species-specific factors but also by a combination of ecological, logistical and social variables. As well summarised by Faith et al. (2009) the

proximity of the kill site to the habitation area likely played a role, as short distances would have facilitated the transport of entire carcasses, whereas longer distances may have necessitated selective transport of body parts. Additionally, the physical condition of the prey at the time of capture, such as its age, health and weight, could have influenced decisions about which parts to transport. The size and composition of the hunting group may have impacted transport strategies, as larger groups would have had greater capacity for carrying whole carcasses, while smaller groups might have prioritised the most nutritionally valuable portions. The presence of potential threats from competing predators could have further shaped these decisions, with hunters needing to balance efficiency with risk minimisation (Faith et al., 2009).

Carcass transport decisions may also reflect the potential for grease and marrow extraction. Assemblages indicative of bone grease exploitation are typically characterised by a marked underrepresentation of epiphyses, basipodials and acropodials (e.g., carpals, tarsals, phalanges), and spongy bone fragments, coupled with an overrepresentation of long bone diaphysis (e.g., Blasco et al., 2024; Crezzini et al., 2023). These patterns suggest deliberate selection and intensive processing of cancellous-rich skeletal parts for the purpose of fat extraction. High levels of fragmentation, the prevalence of small-sized shaft fragments, the presence of percussion marks are also consistent with grease rendering practices (Outram, 2001; Morin, 2007). The highly fragmented faunal assemblage from Gruta da Figueira Brava exhibits a notably low representation of indeterminate epiphyses, a pattern that could maybe reflect intensive processing activities possibly related to grease exploitation.

Even though utility indices are challenging to apply due to the limited size of the sample, the abundance of long bone fragments suggests the introduction of elements rich in medullary cavities filled with marrow (Binford, 1978; Thomas and Mayer, 1983). Among ungulates, such as red deer, exploitation for marrow is demonstrated by breakage patterns, particularly limb bones and metapodials. Marrow extraction is a vital dietary strategy, providing a rich source of animal fat with higher caloric value than carbohydrates and protein (Mead et al., 1986; Outram, 2001). Bone marrow, notably richer in essential fatty acids, represents a high-quality resource (Brink, 1997). Marrow extraction is a low-cost activity, requiring minimal time and effort, particularly for defleshed bones like mandibles and metapodials (e.g. Blasco et al., 2019; Marean and Cleghorn, 2003; Outram, 2001). At Gruta da Figueira Brava, percussion marks are frequently observed on shaft fragments of ungulate long bones, with the most compelling evidence found on red deer remains. Additionally, a percussion notch has been identified on a horse metacarpal. While similar patterns could not be confirmed for other ungulates, primarily due to the extensive fragmentation of long bones, that same high degree of fragmentation itself suggests intensive percussion activity, likely aimed at marrow extraction.

Before marrow extraction, bones must first be skinned, separated from the carcass and defleshed. It was not possible to determine whether incisions were present on articular areas of long bones—features typically associated with dismemberment—, which is likely due to the highly fragmentary state of the assemblage and the presence of calcareous concretions that complicate cut mark identification. However, the presence of incisions on an ibex phalanx at Gruta da Figueira Brava likely reflects skinning, an initial stage in carcass processing. Skinning typically involves making precise cuts around the extremities, particularly on the phalanges, to facilitate the removal of the hide. This practice is crucial not only for obtaining the skin, which may have been used for clothing or other functional purposes, but also as a preparatory step for butchery and further processing of the carcass. The location of the cut marks on the phalanx aligns with previously documented patterns of skinning in archaeological assemblages, where incisions on extremities are commonly associated with this activity (Binford, 1981; Campana and Crabtree, 2019; Faith et al., 2009; Shipman and Rose, 1983; Soulier and Costamagno, 2017).

Among the observable cut marks in Gruta da Figueira Brava, the majority are concentrated on long bone shafts. This distribution of cut marks and their longitudinal orientation indicates a strong focus on the processing of long bone diaphyses, which are normally associated with meat-bearing elements. Such patterns have been generally interpreted as evidence of subsistence strategies associated with filleting (e.g., Domínguez-Rodrigo et al., 2009a,b; Galán and Domínguez-Rodrigo, 2013; Livraghi et al., 2020; Soulier and Costamagno, 2017), which reflect primary access to carcasses, wherein early-stage butchery activities were conducted to remove muscle tissue (e.g., Noe-Nygaard, 1989; Marean, 1998). The location of these marks thus suggests that Neanderthals at the site were engaging in butchering techniques, emphasising meat extraction rather than secondary scavenging. Additionally, the anatomical placement of the cut marks provides insight into the butchery techniques employed. The concentration on the midshaft region of long bones suggests the use of cutting motions to detach muscle fibres efficiently (Galán and Domínguez-Rodrigo, 2013). Taken together, this evidence points to an organised and deliberate approach to ungulate carcass processing, demonstrating the economic use of these faunal resources within Neanderthal subsistence behaviours.

The burning patterns observed at the site further elucidate on subsistence practices. Although burnt bones are relatively low in number, the predominance of black burns suggests exposure to moderate temperatures, typically reaching up to 400°C (Nicholson, 1993). This temperature range is consistent with controlled fire use, such as roasting, rather than accidental burning from open flames or natural wildfires. The presence of partially burnt elements further supports this interpretation, as these are often associated with cooking activities where bones are exposed to heat for a limited duration rather than being completely incinerated (Gifford-Gonzalez, 1993; Pearce and Luff, 1994; Montón-Subías, 2002).

Additionally, certain burnt remains, such as bear canines and other elements not typically associated with human consumption, indicate secondary burning events rather than intentional roasting or food processing. These elements were likely affected by hearth fires ignited above previously deposited skeletal remains, suggesting repeated occupation phases where discarded bones were later exposed to combustion (e.g. Téllez et al., 2022). This pattern aligns with finds from other Palaeolithic sites, where fire use not only served subsistence purposes but also played a role in site maintenance and waste disposal (e.g., Pietraszek et al., 2022; Starkovich et al., 2020). These burning patterns

reinforce the evidence for deliberate fire use and structured food processing strategies.

In sum, Gruta da Figueira Brava's faunal assemblage reveals how, during late MIS-5 times, local Neanderthal populations exploited the ungulate resources made available by the surrounding environment. Such resources, though, constituted but one component of a broader and diverse dietary spectrum that also included small prey and aquatic resources, as previously described. The transport and processing of entire deer and ibex carcasses, along with the selective transport of high-value body parts of aurochs and horse, demonstrate a strategic approach to resource exploitation and energy efficiency. Additionally, practices such as marrow extraction, defleshing and cooking highlight the cave inhabitants' capacity to maximise the nutritional potential of various food sources, contributing to a diversified and well-rounded diet.

6 Conclusion

The macro-mammal assemblage from Gruta da Figueira Brava offers compelling insights into the complex and diverse subsistence strategies employed by Neanderthal populations during MIS-5. The taxonomic composition and skeletal part representation indicate a well-structured approach to hunting, carcass transport and resource processing. The transport of complete ibex and red deer carcasses, alongside the selective transport of high-value elements from larger ungulates, such as aurochs and horses, suggests an adaptive strategy influenced by ecological conditions, prey size and transport logistics.

Further evidence of butchery activities, including cut marks on long bone shafts reflecting defleshing activities, incisions on phalanges suggesting skinning, percussion marks indicative of marrow extraction and the burning of skeletal elements, highlights the comprehensive use of ungulate resources. The presence of structured burning patterns, particularly black burns associated with controlled fire use, suggests that cooking played an integral role in Neanderthal dietary practices. Moreover, the identification of bones affected by secondary burning events implies long-term site occupation and repeated use of hearths.

While carnivore activity was present, the absence of digested bone and the lack of carnivore juvenile remains, is inconsistent with denning. The hyaena coprolites, nonetheless, indicate their intermittent use of the interior of the cave as a latrine when humans were absent. However, the low frequency of carnivore-induced modifications coupled with the stratigraphic context of their remains, indicates that human activity was the dominant factor in bone accumulation. The presence of anthropogenic modifications further reinforces this interpretation. The site's faunal assemblage also aligns with broader Middle Palaeolithic trends observed at other Neanderthal occupation sites, where ungulate exploitation following intentional carcass processing and selective transport depending on weight-size were central components of subsistence behaviour.

The diversity of ungulate prey reflects the exploitation of a range of ecological niches within the surrounding landscape, including patches of forest, grassland and shrubland. This further highlights the adaptability and efficiency of the region's Neanderthal subsistence strategies. Ultimately, the integration of ungulate hunting with the exploitation of small prey and aquatic resources reflects a diversified subsistence system that maximised food availability across different ecological zones and different times of the year, which accentuates the versatility of Neanderthal diets and behaviour in coastal Atlantic occupations. This adaptive flexibility underscores Neanderthals' capacity to respond to environmental variability and resource distribution, reinforcing their role as skilled hunters and efficient resource managers within the Middle Palaeolithic landscape.

Data availability statement

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

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because these are archaeological materials, no animals were harmed at any point of this research.

Author contributions

MN: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. JZ: Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, 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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References

Alcántara-García, V., Barba Egido, R., Barral del Pino, J. M., Crespo Ruiz, A. B., Eiriz Vidal, A. I., Falquina Aparicio, Á., et al. (2006). Determinación de procesos de fractura sobre huesos frescos: un sistema de análisis de los ángulos de los planos de fracturación como discriminador de agentes bióticos. *Trabajos Prehist.* 61, 25–38. doi: 10.3989/tp.2006.v63.i1.3

Álvarez-Lao, D., and Méndez, M. (2016). Latitudinal gradientes and indicator species in ungulate paleoassemblages during the MIS 3 in W Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 449, 455–462. doi: 10.1016/j.palaeo.2016.02.050

Álvarez-Lao, D. J., and García, N. (2011a). Geographical distribution of Pleistocene cold adapted large mammal faunas in the Iberian Peninsula. *Quat. Int.* 233, 159–170. doi: 10.1016/j.quaint.2010.04.017

Álvarez-Lao, D. J., and García, N. (2011b). Southern dispersal and palaeoecological implications of woolly rhinoceros (*Coelodonta antiquitatis*): review of the Iberian occurrences. *Quat. Sci. Rev.* 30, 2002–2017. doi: 10.1016/j.quascirev.2011.05.005

Andrés, M., Gidna, A., Yravedra, J., and Domínguez-Rodrigo, M. (2012). A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeol. Antropol. Sci.* 4, 209–219. doi: 10.1007/s12520-012-0093-4

Andrews, P., and Turner, A. (1992). Life and death of the Westbury bears. *Ann. Zool. Fennici* 28, 139–149.

Antunes, M. (2000). *Last Neanderthals in Portugal. Odontologic and Other Evidence. Classe das Ciências. Tomo XXXVIII.* Lisboa: Academia das Ciências de Lisboa.

Azorit, C., Tellado, S., Oya, A., and Moro, J. (2012). Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. *Anim. Prod. Sci.* 52:720. doi: 10.1071/AN12016

Baquedano, E., Arsuaga, J. L., Pérez-González, A., Laplana, C., Márquez, B., Huguet, R., et al. (2023). A symbolic Neanderthal accumulation of large herbivore crania. *Nat. Hum. Behav.* 7, 342–352. doi: 10.1038/s41562-022-01503-7

Bertacchi, A., Kaliba, P., and Thompson, J. (2025). Short-distance hunting strategies of Late Quaternary foragers in the miombo woodlands of Malawi. *J. Anthropol. Archaeol.* 77:101656. doi: 10.1016/j.jaa.2025.101656

Binford, L. (1978). *Nunamiut Ethnoarchaeology*. New York, NY: Academic Press.

Binford, L. (1981). *Bones: Ancient Men and Modern Myths*. New York, NY: Academic Press.

Binford, L. (1984). *Faunal Remains from Klasies River Mouth*. New York, NY: Academic Press.

Blasco, R., and Fernández Peris, J. (2012). Small and large game: human use of diverse faunal resources at Level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus Palevol* 11, 265–282. doi: 10.1016/j.crpv.2012.01.003

Blasco, R., Rosell, J., Arilla, M., Margalida, A., Villalba, D., Gopher, A., et al. (2019). Bone marrow storage and delayed consumption at Middle Pleistocene Qesem Cave, Israel (420 to 200 ka). *Sci. Adv.* 5:eaav9822. doi: 10.1126/sciadv.aav9822

Blasco, R., Rosell, J., Assaf, E., Barkai, R., and Gopher, A. (2024). Exploring the lack of articular ends at the Middle Pleistocene site of Qesem Cave, Israel. *J. Hum. Evol.* 189:103509. doi: 10.1016/j.jhevol.2024.103509

Blasco, R., Rosell, J., Fernández-Peris, J., Arsuaga, J. L., Bermúdez Castro, J. M., Carbonell, E., et al. (2013). Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quat. Sci. Rev.* 70, 124–144. doi: 10.1016/j.quascirev.2013.03.008

Blumenschine, R., and Selvaggio, M. (1988). Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 333, 763–765. doi: 10.1038/333763a0

Bocherens, H., Drucker, D. G., and Madelaine, S. (2014). Evidence for a ^{15}N positive excursion in terrestrial foodwebs at the Middle to Upper Palaeolithic transition in south-western France: implications for early modern human palaeodiet and palaeoenvironment. *J. Hum. Evol.* 69, 31–43. doi: 10.1016/j.jhevol.2013.12.015

Brain, C. K. (1969). The contribution of Namib desert Desert Hottentots to the understanding of Australopithecine bone accumulations. *Sci. Papers Namib Desert Res. Station* 39, 13–22.

Brink, J. W. (1997). Fat content in leg bones of *Bison bison*, and applications to archaeology. *J. Archaeol. Res.* 24, 259–274. doi: 10.1006/jasc.1996.0109

Brown, W., and Chapman, G. (1990). The dentition of fallow deer (*Dama dama*): a scoring scheme to assess age from wear of the permanent molariform teeth. *J. Zool.* 221, 659–682. doi: 10.1111/j.1469-7998.1990.tb04023.x

Brown, W., and Chapman, G. (1991). The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. *J. Zool.* 224, 519–536. doi: 10.1111/j.1469-7998.1991.tb03783.x

Bunn, H. T. (1983). "Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and Olduvai Gorge, Tanzania," in *Animals and Archaeology*. International Series 163, eds. J. Clutton-Brock, and C. Grigson (Oxford: British Archaeological Reports), 21–30.

Bunn, H. T. (1986). Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690. doi: 10.1016/S0047-2484(86)80004-5

Bunn, H. T., Bartram, L. E., and Kroll, E. M. (1988). Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. *J. Antrhopol. Archaeol.* 7, 412–457. doi: 10.1016/0278-4165(88)90004-9

Campana, D. V., and Crabtree, P. (2019). Evidence for skinning and craft activities from the Middle Palaeolithic Shanidar Cave, Iraq. *J. Archaeol. Sci. Rep.* 25, 7–14. doi: 10.1016/j.jasrep.2019.03.024

Capaldo, S., and Blumenschine, R. (1994). A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* 59, 724–748. doi: 10.2307/282345

Cardoso, J. L., Detry, C., and Zilhão, J. (2021). The first appearance of *Hystrix* (rodentia, mammalia) in Portugal, Last Interglacial, Gruta da Figueira Brava (Setúbal). *Quaternaire* 32, 173–182. doi: 10.4000/quaternaire.18541

Carrión, J. S., Lalueza, C., and Stewart, J. (2019). Neanderthals: ecology and evolution. *Quat. Sci. Rev.* 217, 1–6. doi: 10.1016/j.quascirev.2019.05.008

Castel, J. C., Coumont, M. P., Boudadi-Maligne, M., and Prucca, A. (2010). Rôle et origine des grans carnivores dans les accumulations naturelles. Les cas des loups (*Canis lupus*) de l'Igue du Gral (Sauliac-sur-Célé, Lot, France). *Rev. Paléobiol.* 29, 411–425.

Clutton-Brock, T. H. (1982). *Red Deer: Behavior and Ecology of the Two Sexes.* Chicago, IL: University of Chicago Press.

Cobo-Sánchez, L., Rufà, A., and Cascalheira, J. (2024). Alternating carnivore and Neanderthal activities at Escoural Cave: insights from the taphonomic and machine learning analysis of leporid remains. *Front. Environ. Archaeol.* 3:1473266. doi: 10.3389/fearc.2024.1473266

Coil, R., Tappen, M., and Yezzi-Woodley, K. (2017). New analytical methods for comparing bone fracture angles: a controlled study of hammerstone and hyena (*Crocuta crocuta*) long bone breakage. *Archaeometry* 59, 900–917. doi: 10.1111/arcm.12285

Crezzini, J., Boscato, P., Ronchitelli, A., and Boschin, F. (2023). *A* peculiar exploitation of ungulates at Grotta di Santa Croce: bone grease rendering and nutritional patterns among Neanderthals in southern Italy. *Hist. Biol.* 36, 2133–2145. doi: 10.1080/08912963.2023.2242630

Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., et al. (2017). Neanderthal selective hunting of reindeer? The case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011. doi: 10.1007/s12520-017-0580-8

Díez, J., Fernández-Jalvo, Y., Rosell, J., and Cáceres, I. (1999). Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). *J. Hum. Evol.* 37, 623–652. doi: 10.1006/jhev.1999.0346

Domínguez-Rodrigo, M. (1993). La formación de las acumulaciones óseas de macrofauna: revisión de los criterios de discernimiento de los agentes biológicos no antrópicos desde un enfoque ecológico. *Zephyrus* 46, 103–122.

Domínguez-Rodrigo, M. (1994). Las razones adaptativas del comportamiento subsistencial de los animales carnívoros y sus estrategias iniciales de consumo de presas: relevancia en el proceder tafonómico. *Cuad. Prehist. Arqueol. Castellon* 16, 9–17.

Domínguez-Rodrigo, M. (1999). Distinguishing between apple and oranges: the application of modern cut mark studies to the Plio-Pleistocene (a reply to Monahan). *J. Hum. Evol.* 33, 793–800. doi: 10.1006/jhev.1999.0358

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B., and Rodríguez, M. (2009a). A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654. doi: 10.1016/j.jas.2009.07.017

Domínguez-Rodrigo, M., Mabulla, A., Bunn, H. T., Barba, R., Diez-Martín, F., Egeland, C. P., et al. (2009b). Unraveling hominin behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. *J. Hum. Evol.* 57, 260–283. doi: 10.1016/j.jhevol.2009.04.006

Dusseldorp, G. L. (2013). "Neanderthals and cave hyenas: co-existence, competition or conflict?" in *Zooarchaeology and Modern Human Origins. Vertebrate Paleobiology and Paleoanthropology*, eds. J. Clark, and J. Speth (Dordrecht: Springer), 191–208. doi: 10.1007/978-94-007-6766-9_12

Faith, J. T., Domínguez-Rodrigo, M., and Gordon, A. D. (2009). Long-distance carcass transport at Olduvai Gorge? A quantitative examination of Bed I skeletal element abundances. *J. Hum. Evol.* 56, 247–256. doi: 10.1016/j.jhevol.2008.12.008

Farizy, D., David, F., and Jaubert, J. (1994). *Hommes et Bisons du Paléolithique Moyen à Mauran (Haute-Garonne)*. Gallia Préhistoire, XXXe Suppléments. Paris: CNRS éditions.

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., Bortolotti, G. R., et al. (2012). Birds of a feather: Neanderthal exploitation of raptors and corvids. *PLoS ONE* 7:e45927. doi: 10.1371/annotation/5160ffc6-ec2d-49e6-a05b-25b41391c3d1

Fisher, J. (1995). Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory*, 2, 7–68. doi: 10.1007/BF02228434

Galán, A. B., and Domínguez-Rodrigo, M. (2013). An experimental study of the anatomical distribution of cut marks created by filleting and disarticulation on long bone ends. *Archaeometry* 55, 1132–1149. doi: 10.1111/j.1475-4754.2012.00730.x

García García, N., Feranec, R. S., Arsuaga, J. L., Bermúdez de Castro, J. M., and Carbonell, E. (2009). Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleitocene deposits of Sierra de Atapuerca, northern Spain. *J. Archaeol. Sci.* 36, 1142–1151. doi: 10.1016/j.jas.2008.12.018

Gaudzinski, S., and Roebroeks, W. (2000). Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, Northern Germany. *J. Hum. Evol.* 38, 497–521. doi: 10.1006/jhev.1999.0359

Gaudzinski-Windheuser, S., and Kindler, L. (2012). Research perspectives for the study of Neanderthal subsistence strategies based on the analysis of archaeozoological assemblages. *Quat. Int.* 247, 59–68. doi: 10.1016/j.quaint.2010.11.029

Geist, V. (1998). *Deer of the World. Their Evolution, Behavior, and Ecology*. Pennsylvania, PA: Stackpole Books, Mechanicsburg.

Gifford-Gonzalez, D. (1993). "Gaps in zooarchaeological analyses of butchery: is gender an issue?" in *From Bones to Behaviour. Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains,* ed. J. Hudson (Carbondale: Center for Archaeological Investigations, Southern Illinois University), 181–199.

Granados, J. E., Pérez, J. M., Márquez, F. J., Serrano, E., Soriguer, R. C., Fandos, P., et al. (2001). La cabra montés (*Capra pyrenaica*, SCHINZ 1838). *Galemys* 13, 3–37.

Grant, A. (1982). "The use of tooth wear as a guide to the age of domestic ungulates," in *Ageing and Sexing Animal Bones from Archaeological Sites*. BAR British Series 109, eds. B. Wilson, C. Grigson, and S. Payne (Oxford: Archaeopress), 91–108.

Grayson, D. K. (1984). *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Orlando: Academic Press.

Henry, A., Brooks, A., and Piperno, D. (2014). Plant foods and the dietary ecology of Neanderthals and early modern humans. *J. Hum. Evol.* 69, 44–54. doi: 10.1016/j.jhevol.2013.12.014

Hillson, S. (2005). *Teeth,* 2nd Edn. Cambridge: Cambridge University Press.

Horwitz, L. K., and Goldberg, P. (1989). A study of Pleistocene and Holocene hyaena coprolites. *J. Archaeol. Sci.* 16, 71–94. doi: 10.1016/0305-4403(89)90057-5

Jaouen, K., Richards, M. P., Le Cabec, A., Welker, F., Rendu, W., Hublin, J. J., et al. (2019). Exceptionally high δ^{15}N values in collagen single amino acids confirm Neandertals as high-trophic level carnivores. *Proc. Natl Acad. Sci.* 116, 4928–4933. doi: 10.1073/pnas.1814087116

Johansson, S. (2014). The thinking Neanderthals: what do we know about Neanderthal cognition? *Wiley Interdiscip. Rev. Cogn. Sci.* 5, 613–620. doi: 10.1002/wcs.1317

Klein, R., and Cruz-Uribe, G. (1984). *The Analysis of Animal Bones from Archaeological Sites*. Chicago, IL: University of Chicago Press.

Kuhn, S., and Stiner, M. (2019). Hearth and home in the Middle Pleistocene. *J.. Anthropol. Res.* 75. doi: 10.1086/704145

Langley, M., Clarkson, C., and Ulm, S. (2008). Behavioural complexity in Eurasian Neanderthal populations: a chronological examination of the archaeological evidence. *Cambridge Archaeol. J.* 18, 289–307. doi: 10.1017/S0959774308000371

Larkin, N. R., Alexander, J., and Lewis, M. D. (2000). Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, UK. *J. Archaeol. Sci.* 27, 19–31. doi: 10.1006/jasc.1999.0437

Levine, M. A. (1998). Eating horses: the evolutionary significance of Hippophagy. *Antiquity* 72, 90–100. doi: 10.1017/S0003598X00086300

Livraghi, A., Fanfarillo, G., Dal Colle, M., Romandini, M., and Peresani, M. (2020). Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: a study on De Nadale cave, Italy. *Quat. Int.* 586, 24–41. doi: 10.1016/j.quaint.2019.11.024

Lupo, K. D. (2006). What explains the carcass field processing and transport decisions of contemporary hunter-gatherers? Measures of economic anatomy and zooarchaeological skeletal part representation. *J. Archaeol. Method Theory* 13, 9–66. doi: 10.1007/s10816-006-9000-6

Lyman, R. L. (1994a). Quantitative units and terminology in zooarchaeology. *Am. Antiq.* 59, 36–71. doi: 10.2307/3085500

Lyman, R. L. (2008). *Quatitative Paleozoology*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511813863

Marean, C. (1998). A critique of the evidence for scavenging by Neandertals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 Layer 10 (South Africa). *J. Hum. Evol.* 35, 111–136. doi: 10.1006/jhev.1998.0224

Marean, C. W., and Cleghorn, N. (2003). Large mammal skeletal element transport: applying foraging theory in a complex taphonomy system. *J. Taphonomy* 1, 15–42.

Marín, J., Rodríguez-Hidalgo, A., Vallverdú, J., Gómez de Soler, B., Rivals, F., Rabuñal, J. R., et al. (2019). Neanderthal logistic mobility during MIS3: zooarchaeological perspective of Abric Romaní level P (Spain). *Quat. Sci. Rev.* 225:106033. doi: 10.1016/j.quascirev.2019.106033

Marín, J., Saladié, P., Rodríguez-Hidalgo, A., and Carbonell, E. (2017). Ungulate carcass transport strategies at the Middle Palaeolithic site of Abric Romaní (Capellades, Spain). *Comptes Rendus Palevol* 16, 103–121. doi: 10.1016/j.crpv.2015.11.006

Marín-Arroyo, A. B., and Sanz-Royo, A. (2021). What Neanderthals and AMH ate: reassessment of the subsistence across the Middle-Upper Palaeolithic transition in the Vasco-Cantabrian region of SW Europe. *J. Quat. Sci.* 37, 320–334. doi: 10.1002/jqs.3291

Mead, J. F., Alfin-Slater, R. B., Howton, D. R., and Popják, G. (1986). *Lipids: Chemistry, Biochemistry, and Nutrition*. New York, NY: Plenum Press. doi: 10.1007/978-1-4613-2107-1

Metcalfe, D., and Jones, K. T. (1988). A reconsideration of animal body-part utility indices. *Am. Antiq.* 53, 486–504. doi: 10.2307/281213

Moclán, A., Huguet, R., Márquez, B., Laplana, C., Galindo-Pellicena, M., García, N., et al. (2021). A Neanderthal hunting camp in the central system of the Iberian Peninsula: a zooarchaeological and taphonomic analysis of the Navalmaíllo Rock Shelter (Pinilla del Valle, Spain). *Quat. Sci. Rev.* 269:107142. doi: 10.1016/j.quascirev.2021.107142

Monahan, C. M. (1998). The Hadza Carcass transport debate revisited and its Archaeological Implications. *J. Archaeol. Sci.* 25, 405–424. doi: 10.1006/jasc.1997.0241

Montón-Subías, S. (2002). "Cooking in zooarchaeology: is this issue still raw?" in *Consuming Passions and Patterns of Consumption*, eds. P. Miracle, and N. Milner (Cambridge: McDonald Institute of Archaeological Research), 7–15.

Moreno-García, M., Pimenta, C., Davis, S., and Gabriel, S. (2003). "A osteoteca: uma ferramenta de trabalho," in *Paleoecologia Humana e Arqueociências. Um programa Multidisciplinar Para a Arqueologia sob a Tutela da Cultura.* Trabalhos de Arqueologia 29, eds. M. Moreno-García, and J. Mateus(Lisboa: Instituto Português de Arqueologia), 235–262.

Morin, E. (2007). Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. *J. Archaeol. Sci.* 34, 69–82. doi: 10.1016/j.jas.2006.03.015

Nabais, M., Dupont, C., and Zilhão, J. (2023a). The exploitation of crabs by Last Interglacial Iberian Neanderthals: the evidence from Gruta da Figueira Brava (Portugal). *Front. Environ. Archaeol.* 2:1097815. doi: 10.3389/fearc.2023.1097815

Nabais, M., Pimenta, C., and Zilhão, J. (2023b). Human-bird interaction in Last Interglacial Iberia: a combined approach using skeletal part analysis, bone surface modification, bird ethology and ethnography. *J. Archaeol. Sci. Rep.* 49:104023. doi: 10.1016/j.jasrep.2023.104023

Nabais, M., and Zilhão, J. (2019). The consumption of tortoise among Last Interglacial Iberian Neanderthals. *Quat. Sci. Rev.* 217, 225–246. doi: 10.1016/j.quascirev.2019.03.024

Nicholson, R. (1993). A morphological investigation of burnt animal bone and an evaluation of its utility in archaeology. *J. Archaeol. Sci.* 20, 411–428. doi: 10.1006/jasc.1993.1025

Niven, L. (2013). "A diachronic evaluation of neanderthal cervid exploitation and site use at Pech de l'Aze IV, France," in *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene,* eds. J. L. Clark, and J. D. Speth (Dordrecht: Springer Netherlands), 151–161. doi: 10.1007/978-94-007-6766-9_9

Noe-Nygaard, N. (1989). Man-made trace fossils on bones. *Hum. Evol.* 4, 461–491. doi: 10.1007/BF02436295

O'Connell, J., Hawkes, K., and Blurton-Jones, N. (1990). Reanalysis of large mammal body part transport among the Hadza. *J. Archaeol. Sci.* 17, 301–316. doi: 10.1016/0305-4403(90)90025-Z

Outram, A. K. (2001). A new approach to identifying bone marrow and grease exploitation: why the "Indeterminate" fragments should not be ignored. *J. Archaeol. Sci.* 28, 401–410. doi: 10.1006/jasc.2000.0619

Pales, L., and Lambert, C. (1971). *Atlas Ostéologique pour server à l'identification des mammifères du Quaternaire. I. Les membres.* Paris: Éditions du Centre National de la Recherche Scientifique.

Pales, L., and Lambert, C. (1981). *Atlas Ostéologique pour server à l'identification des mammifères du Quaternaire. II. Tête – Rachis Ceintures scapulaire et pelvienne*. Paris: Éditions du Centre National de la Recherche Scientifique.

Patou-Mathis, M. (2000). Neanderthal subsistence behaviours in Europe. *Int. J. Osteoarchaeol.* 10, 379–395. doi: 10.1002/1099-1212(200009/10)10:5<379::AID-OA558>3.0.CO;2-4

Patou-Mathis, M. (2006). "Comportements de subsistence des Néandertaliens d'Europe," in *Neanderthals in Europe. Proceedings of the International Conference held in the Gallo-Roman Museum in Tougereu (September 17-19th 2004), vol. 117*, eds. B. Demansin, and M. Otte (Liège: Eraul), 67–76.

Payne, S. (1973). Kill-off patterns in sheep and goats: the mandibles from Asuan Kale. *Anatol. Stud.* 23, 281–303. doi: 10.2307/3642547

Payne, S. (1987). Reference codes for wear states in the mandibular cheek teeth of sheep and goats. *J. Archaeol. Sci.* 14, 609–614. doi: 10.1016/0305-4403(87)90079-3

Pearce, J., and Luff, R. (1994). "The taphonomy of cooked bone," in *Whither Environmental Archaeology?* eds. R. Luff, and P. Rowley-Conwy (Oxford: Oxbow Books), 51–56.

Pérez-Hidalgo, T., and Cobo Rayán, R. (1987). *Atlas Anatomico de Ursidos del Pleistoceno Holoceno de la Peninsula Iberica*. Madrid: Federación Madrileña de Espeleología.

Pickering, T., and Egeland, C. (2006). Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33, 459–469. doi: 10.1016/j.jas.2005.09.001

Pietraszek, A., Zaidner, Y., and Shahack-Gross, R. (2022). The distribution and treatment of fire remains across Unit V of the Middle Paleolithic open-air site of Nesher Ramla, Israel. *Quat. Int.* 624, 107–116. doi: 10.1016/j.quaint.2021.03.027

Reitz, E., and Wing, E. (2008). *Zooarchaeology*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511841354

Rendu, W. (2022). "Selection versus opportunism: a view from Neanderthal subsistence strategies," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (London: Academic Press), 109–122. doi: 10.1016/B978-0-12-821428-2.00013-5

Ribeiro, O. (1945). *Portugal. O Mediterrâneo e o Atlântico.* Lisboa: Livraria Sá da Costa Editora.

Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Arsuaga, J. L., Bermúdez de Castro, J. M., and Carbonell, E. (2017). Human predatory behavior and the social implications of comunal hunting based on evidence from the TD10.2 bison boné bed at TGran Dolina (Atapuerca, Spain). *J. Hum. Evol.* 105, 89–122. doi: 10.1016/j.jhevol.2017.01.007

Romandini, M., Terlato, G., Nannini, N., Tagliacozzo, A., Benazzi, S., Peresani, M., et al. (2018). Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *J. Archaeol. Sci.* 90, 71–91. doi: 10.1016/j.jas.2017.12.004

Rosell, J., Cáceres, I., Blasco, R., Bennàsar, M., Bravo, P., Campeny, G., et al. (2012). A zooarchaeological contribution to establish occupational patterns at level J of Abric Romaní (Barcelona, Spain). *Quat. Int.* 247, 69–84. doi: 10.1016/j.quaint.2011.01.020

Rusch, L., Gregoire, S., Pois, V., and Moigne, A. M. (2019). Neanderthal and carnivore occupations in unit II form the Upper Pleistocene site of Ramandils Cave (Port-la-Nouvelle, Aude, France). *J. Archaeol. Sci. Rep.* 28:102038. doi: 10.1016/j.jasrep.2019.102038

Sadek-Kooros, H. (1972). Primitive bone fracturing: a method of research. *Am. Antiq.* 37, 369–382. doi: 10.2307/278436

Sala, N., and Arsuaga, J. L. (2013). Taphonomic studies with wild brown bears (*Ursus arctos*) in the mountains of northern Spain. *J. Archaeol. Sci.* 40, 1389–1396. doi: 10.1016/j.jas.2012.10.018

Saladié, P., Huguet, R., Díez, J. C., Rodríguez-Hidalgo, A., and Carbonell, E. (2013). Taphonomic modifications produced by modern brown bears (*Ursus arctos*). *Int. J. Osteoarchaeol.* 23, 13–33. doi: 10.1002/oa.1237

Salazar-García, D., Power, R., Sanchis Serra, A., Villaverde, V., Walker, M., Henry, A., et al. (2013). Neanderthal diets in central and southeastern Mediterranean Iberia. *Quat. Int.* 318, 3–18. doi: 10.1016/j.quaint.2013.06.007

Sanchis, A., Real, C., Sauqué, V., Núñez-Lahuerta, C., Égüez, N., Tormo, C., et al. (2019). Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: Faunal study of Mousterian levels (MIS 3). *Comptes Rendus Palevol* 18, 113–141. doi: 10.1016/j.crpv.2018.06.001

Sanz, M., Daura, J., Éguez, N., and Brugal, J. P. (2016). Not only hyenids: a multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 443, 249–262. doi: 10.1016/j.palaeo.2015.11.047

Sanz, M., Rivals, F., García, D., and Zilhão, J. (2019). Hunting strategy and seasonality in the last interglacial occupation of Cueva Antón (Murcia, Spain). *Archaeol. Anthropol. Sci.* 11, 3577–3594. doi: 10.1007/s12520-018-0768-6

Sauqué, V., Sanchis, A., and Madurell-Malapeira, J. (2018). Late Pleistocene leopards as a bone accumulator: taphonomic results from S'Espasa cave and other Iberian key sites. *Hist. Biol.* 30, 821–834. doi: 10.1080/08912963.2017.1343313

Schmid, E. (1972). *Atlas of Animal Bones*. Amsterdam: Elsevier.

Schoville, B. J., and Otárola-Castillo, E. (2014). A model of hunter-gatherer skeletal element transport: the effect of prey body size, carrier, and distance. *J. Hum. Evol.* 73, 1–14. doi: 10.1016/j.jhevol.2014.06.004

Schulz, E., and Kaiser, T. M. (2012). Historical distribution, habitat requirements and feeding ecology of the genus *Equus* (Perissodactyla). *Mamm. Rev.* 43, 111–123. doi: 10.1111/j.1365-2907.2012.00210.x

Shipman, P., Foster, G., and Schoeninger, M. (1984). Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. *J. Archaeol. Sci.* 11, 307–325. doi: 10.1016/0305-4403(84)90013-X

Shipman, P., and Rose, J. (1983). Early hominid hunting, butchering and carcass processing behaviors: approaches to the fossil record. *J. Anthropol. Archaeol.* 2, 57–98. doi: 10.1016/0278-4165(83)90008-9

Solounias, N., and Semprebon, G. M. (2002). Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49. doi: 10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2

Soulier, M. C., and Costamagno, S. (2017). Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. *J. Archaeol. Sci. Rep.* 11, 782–802. doi: 10.1016/j.jasrep.2016.12.033

Starkovich, B., Elefanti, P., Karkanas, P., and Panagopoulou, E. (2020). Site use and maintenance in the middle Palaeolithic at Lakonis I (Peloponnese, Greece). *J. Paleolithic Archaeol.* 3, 157–186. doi: 10.1007/s41982-018-0006-x

Stavrova, T., Borel, A., Daujeard, C., and Vettese, D. (2019). A GIS based approach to long bone breakage patterns derived from marrow extraction. *PLoS ONE* 14:e0216733. doi: 10.1371/journal.pone.0216733

Stewart, J. R., García-Rodríguez, O., Knul, M. V., Sewell, L., Montgomery, H., Thomas, M. G., et al. (2019). Palaeoecological and genetic evidence for Neanderthal power locomotion as an adaptation to a Woodland environment. *Quat. Sci. Rev.* 217, 310–315. doi: 10.1016/j.quascirev.2018.12.023

Stiner, M. (1994). *Honor Among Thieves: A zooarchaeological study of Neanderthal ecology*. Princeton, NJ: Princeton University Press.

Stringer, C. B., Finlayson, J. C., Barton, R. N. E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R. C., et al. (2008). Neanderthal exploitation of marine mammals in Gibraltar. *Proc. Natl. Acad. Sci. USA* 105, 14319–14324. doi: 10.1073/pnas.0805474105

Svoboda, J., Borinová, S., Lengyel, G., Pokorny, P., Prichystal, A., Sázelová, S., et al. (2020). Last Glacial Maximum landscape and Epigravettian horse hunting stretgy in Central Europe: the case of Stránská skála IV. *Prehled Výzkumu* 61, 59–70. doi: 10.47382/pv0611-06

Téllez, E., Saladié, P., Pineda, A., Marín, J., Vallverdú, J., Chacón, M. G., et al. (2022). Incidental burning on bones by Neanderthals: the role of fire in the Qa level of Abric Romaní rock-shelter (Spain). *Archaeol. Anthropol. Sci.* 14:119. doi: 10.1007/s12520-022-01577-4

Thomas, D. H., and Mayer, D. (1983). "Behavioral faunal analysis of selected horizons," in *The Archaeology of Monitor Valley, Vol. 2: Gatecliff Shelter*, ed. D. H. Thomas (New York, NY: Anthropological Papers of the American Museum of Natural History), 353–391.

van Vuure, C. T. (2005). *Retracing the Aurochs: History, Morphology and Ecology of an Extinct Wild Ox*. Sofia, Moscow: Pensoft Publishers.

Vettese, D., Blasco, R., Cáceres, I., Gaudzinski-Windheuser, S., Moncel, M. H., Hohenstein, U., et al. (2020). Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeol. Anthropol. Sci.* 12:48. doi: 10.1007/s12520-019-00972-8

Villa, P., and Mahieu, E. (1991). Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48. doi: 10.1016/0047-2484(91)90034-S

White, M., Pettitt, P., and Schreve, D. (2016). Shoot first, ask questions later: Interpretative narratives of Neanderthal hunting. *Quat. Sci. Rev.* 140, 1–20. doi: 10.1016/j.quascirev.2016.03.004

White, T. (1953). A method of calculating the dietary percentage of various food animals utilized by aboriginal peoples. *Am. Antiq.* 18, 396–398. doi: 10.2307/277116

White, T. (1992). *Prehistoric Cannibalism at Mancos 5MTURM-2346*. Princeton, NJ: Princeton University Press. doi: 10.1515/9781400852925

Yesner, D., and Bonnichsen, R. (1979). Caribou metapodial shaft splinter technology. *J. Archaeol. Sci.* 6, 303–308. doi: 10.1016/0305-4403(79)90015-3

Yravedra, J., and Cobo-Sánchez, L. (2015). Neanderthal exploitation of ibex and chamois in southwestern Europe. *J. Hum. Evol.* 78, 12–32. doi: 10.1016/j.jhevol.2014.10.002

Zhang, S., Li, Z., Zhang, Y., and Gao, X. (2012). Skeletal element distributions of the large herbivores from the Lingjing site, Henan Province, China. *Sci. China Earth Sci.* 55, 246–253. doi: 10.1007/s11430-011-4279-x

Zilhão, J., Angelucci, D., Araújo, M., Arnold, L., Badal, E., Callapez, P., et al. (2020). Last interglacial Iberian Neandertals as Fisher-Hunter-Gatherers. *Science* 367:eaaz7943. doi: 10.1126/science.aaz7943

Zilhão, J., Angelucci, D. E., Argant, J., Brugal, J. P., Carrión, J. S., Carvalho, R., et al. (2010). "Humans and hyenas in the Middle Palaeolithic of Gruta da Oliveira (Almonda karstic system, Torres Novas, Portugal)," in *Actas de la 1ª Reunion de Científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos de la Península Ibérica,* eds. E. Baquedano, and J. Rosell (Madrid: Museo Arqueológico Regional), 299–308.

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Neanderthal had a "crush" on fats. Macronutrient estimation in Middle Paleolithic (Late Mousterian) hunter-gatherers of southern Italy

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During the Late Mousterian period Apulia (southeastern Italy) was characterized by frequent and prolonged aridity that could have caused the scarcity of vegetable foods and, consequently, a lack of important nutritional compounds. Zooarchaeological studies from several Mousterian contexts show that Apulian Neanderthals may have responded to this crisis by increasing the exploitation of ungulates. In particular, bone grease rendering was likely one of the dominant activities conducted on-site. Anthropologists and nutritionists have long recognized that the diets of modern-day hunter-gatherers may represent a reference standard for human nutrition in the past and a model for their adaptation to specific environmental conditions. In addition, evaluating of certain qualitative and quantitative aspects of the animal/plant nutrient intake and absorption may provide important information regarding the nutritional needs and the physiology of these human groups. In this analysis, we combine ethnographic data related to animal economic subsistence patterns of hunter-gatherers, zooarchaeological data from Late Mousterian assemblages located in Apulia, the physiology of medium-large ungulates, as well as new paleo genomic analyses of Neanderthals and modern humans. Analyzing and displaying multiple sources of information allowed us to quantify a low daily energy intake from carbohydrates for Late Mousterian populations in southern Italy, in contrast to a surplus of animal protein and fats, obtained from the specific treatment of carcasses inferred from the zooarchaeological data.

KEYWORDS

Neanderthal diet, late Mousterian, southern Italy, genome analysis, zooarchaeology, macronutrient compositions

1 Introduction

Climate and environmental constraints have strongly influenced human behaviors and cultures forcing past communities to develop peculiar settlement techniques to overcome these limits (Agustí et al., 2009; Timmermann et al., 2022).

Several archaeological records provide evidence that Neanderthals were able to adapt to harsh environments through their hunting capabilities focused upon specific animal

species (Gaudzinski, 1995, 1996; Jaubert et al., 1990; Farizy et al., 1994; Brugal et al., 1996; Airvaux, 2004), as well as exploiting wider spectrum of different resources (Blasco et al., 2022 and references therein, Hardy, 2019).

Banks et al. (2021) demonstrated that between MIS 5a and MIS 4, Western European Neanderthals developed highly adaptive cultural innovations to continue exploiting habitual environments affected by pronounced climate change. This coincided with the appearance of the Quina lithic production system during MIS 4 in some areas of Europe (Banks et al., 2021).

Analyzing occlusal molar microwear texture in Western Eurasian Paleolithic hominins, El Zaatari et al. (2016) demonstrated behavioral differences that distinguish modern humans from Neanderthals, in relation to fluctuations in climatic conditions of the Pleistocene. They evidenced that Neanderthals altered their diets in response to changing palaeoecological conditions, in contrast to *Homo sapiens*, who seem to have been less affected by slight changes in vegetation/climatic conditions, modifying their technological complexes accordingly.

Unquestionably, diet represents the functional link through which climatic and environmental factors can cause strong evolutionary pressures, leading to different patterns in resources use. In this regard, analysis of the nutritional qualities and energetic costs of acquiring and processing of foods can help identify the nutritional needs of the Paleolithic hunter-gatherers. Eaton et al. (1997) and Eaton and Konner (1985) reconstructed a Paleolithic diet and their model was revisited by Cordain et al. (2000, 2001). All these authors suggested lower consumption of carbohydrates and higher intakes of protein and polyunsaturated fatty acid (Eaton et al., 1998; Cordain et al., 2001).

When the environmental constraints are extended for a long time, even genomic mutations can occur (Ameur et al., 2012). Although an ever-increasing number of works in recent years have focused on understanding in greater depth the Neanderthal genome (Cerqueira Caio et al., 2012; Weasel, 2022; McArthur et al., 2021), little effort has been made to investigate the possible physiological characteristics that can be inferred from the expression of the identified genes in these human groups. Southern Italy offers us the opportunity to study the adaptations and responses of Neanderthals to climate changes and to different environmental conditions in depth, at a regional scale and over a long period, due to its richness in Middle Paleolithic sites with well dated long-term stratigraphies spanning from MIS 5 to MIS 3 (Boscato and Crezzini, 2012a,b; Boschin et al., 2021). In the last 20 years detailed zooarchaeological analyses on faunal assemblages from different sites in southern Italy referable to both Mousterian and Upper Paleolithic technocomplexes (MIS 4-3), give us the possibility of identifying differences in animal exploitation between Neanderthals and modern humans. It was possible to highlight a particular treatment of carcasses during the Mousterian, not recorded in Upper Paleolithic samples (Crezzini et al., 2023; Boscato et al., 2006; Boscato and Crezzini, 2012a,b).

In this work, considering the ethnographic data related to the economic subsistence patterns of hunter-gatherers, we merged zooarchaeological and palaeoecological data with the nutritional value of the anatomical parts in medium-large ungulate carcasses. Additionally, a paleo genome- analysis was carried out to investigate possible genetic bases of the differences in fat metabolism between Neanderthals and modern humans.

The aim of this work was to investigate the likely quality and quantity of the dietary macronutrients comprised in the Last Mousterian diet through peculiar zooarchaeological data from southern Italy.

2 Materials and methods

The zooarchaeological data considered in this study is related to Late Mousterian ungulate assemblage from Grotta di Santa Croce (SUs 525-535-539) dated to the end of MIS 4/beginning of MIS 3 (Boscato and Crezzini, 2006; Ciullo, 2016; Boscato, 2017; Crezzini et al., 2023) (Supplementary Figure 1B, see also text in Supplementary material). The faunal composition is dominated by only two species: the horse and the aurochs, while a third *taxon*, the red deer, is represented by a femur fragment (Supplementary Tables 1, 2).

The assemblage is characterized by strong fragmentation, and it mainly comprise 3–6 cm size class remains. This likely increased the high identification of isolated teeth compared to postcranial elements. Among the latter, carpal and tarsal bones, as well as phalanges and sesamoids are scarce or absent and long bones are mainly represented by diaphyseal fractions rather than epiphyseal portions (Supplementary Tables 2–4) (Crezzini et al., 2023). In addition, a high ratio of diaphysis/epiphysis fragments and a low quantity of spongy bone remains are recorded in the taxonomically unidentified sample (Boscato and Crezzini, 2012a,b).

The bone sample does not show alterations from carnivore activities or post-depositional processes. The relationship between aurochs and horse skeletal elements and bone density indicated that the BMD does not fully explain the peculiar skeletal frequencies of these *taxa* (Crezzini et al., 2023). Analysis of tooth eruption and wear points to the exploitation of adult individuals, rather than juveniles and sub-adults (Crezzini et al., 2023).

The ungulate assemblage composition from two other important Mousterian assemblages from Apulia, Grotta del Cavallo – SU F (Nardò – province of Lecce) and Riparo l'Oscurusciuto – SUs 2, 4, and 9 (Ginosa – province of Taranto) show strong similarities with that of Grotta di Santa Croce (Boscato et al., 2006, 2010; Boscato and Crezzini, 2006, 2012a,b; Boscato, 2017; Crezzini et al., 2023).

These samples (where the aurochs is the most common ungulate, followed by horse and/or red deer) are all dated to MIS 3 and the sites are close to each other (about 120 km as the crow flies, Supplementary Figure 1A) It is important to keep in mind that investigations carried out in these three sites are different depositional contexts: a rockshelter (Riparo l'Oscurusciuto), a cave (Grotta del Cavallo) and a *talus* (Grotta di Santa Croce). This reduces the possibility that similarities between samples are biased by similar post-depositional factors. No evidence of the systematic use of bones as fuel was recorded (Spagnolo et al., 2016): the lack or scarcity of spongy elements in Apulian assemblages, together with the evidence of fresh-bone breakage, it was interpreted as an intense exploitation of bone marrow and grease by Neanderthals (Crezzini et al., 2023).

TABLE 1 Bone grease grams and energy yield of the bison carcass products (Emerson, 1990).

	Gr	Kcal	KJ
Skull	-	-	-
Scapula	8.8	79.2	331.4
Proximal humerus	73.6	662.4	2,771.5
Distal humerus	25.2	226.8	948.9
Proximal radius	9.9	89.1	372.8
Distal radius	27.4	246.6	1,031.8
Carpal	5.4	48.6	203.3
Prossimal metacarpal	1.7	15.3	64
Distal metacarpal	9.6	86.4	361.5
Proximal femur	49.9	449.1	1,879
Distal femur	78.2	703.8	2,944.7
Proximal tibia	39.3	353.7	1,479.9
Distal tibia	14	126	527.2
Tarsal	25.6	230.4	964
Proximal metatarsal	2.2	19.8	82.8
Distal metatarsal	16	144	602.5
Phalanges	11	99	414.2

TABLE 2 Protein grams and energy yield of the bison carcass products (Emerson, 1990).

	Gr	Kcal	KJ
Skull	464.7	1,858.8	7,777.2
Scapula	1,905.7	7,622.8	31,893.8
Proximal Humerus	943.9	3,775.8	15,797.9
Distal Humerus	943.9	3775.8	15,797.9
Proximal Radius	311.9	1,247.6	5,219.9
Distal Radius	311.9	1,247.6	5,219.9
Carpal	-	-	-
Prossimal Metacarpal	-	-	-
Distal Metacarpal	-	-	-
Proximal Femur	3,399.5	13,598.2	56,894.8
Distal Femur	3,399.5	13,598.2	56,894.8
Proximal Tibia	433.1	1,732.6	7,249.2
Distal Tibia	433.1	1,732.6	7,249.2
Tarsal	-	-	-
Proximal Metatarsal	1.55	6.2	25.9
Distal Metatarsal	1.55	6.2	25.9
Phalanges	-	-	-

An assessment of the presence of aurochs skeletal parts from Grotta di Santa Croce as a function of their economic significance, such as modified total products, skeletal fat utility, protein and white grease fat content was carried out by Crezzini et al. (2023), using the economic anatomy of nowadays bison examined by Emerson (1990, see data relate to the individual of bison indicate by Emerson with the name *SAM*). In our work, we enlarged this analysis by investigating the skeletal frequencies of *Bos primigenius* as a function of their caloric and energetic values, in order to investigate the possible energetic contribution provided by animal food in Neanderthal diet.

The calorie yield of the carcass products indicated by Emerson (1990) are reported in Tables 1, 2. In addition, we added in each of the tables two new columns.

In Table 1 the new columns contain the bone grease grams and the relative energy yield (KJ) of carcass products, while in Table 2 the new columns contain protein grams and the relative energy yield (KJ) of carcass products. We calculated these values as follows:

$$KJ\ energy\ yield = Kcal\ energy\ yield \times 4.184$$

$$Bone\ grease\ grams = \frac{Bone\ grease\ calorie\ yield}{9\ Kcal/gr}$$

$$Protein\ grams = \frac{Protein\ calorie\ yield}{4\ Kcal/gr}$$

The bone grease and the protein grams were calculated using the reverse process followed by Emerson to calculate the respective of calorie yield values (see Emerson, 1990, p. 888). To estimate the possible energetic contribution provided by plant food in Neanderthal diet, we considered the macronutrient composition and energy value of plants suggested by Eaton et al. (1998). Finally, we assumed a daily energy intake of 12,500 KJ, as suggested by Kuipers et al. (2010) for the Palaeolithic hunter-gatherers, and we used the equation suggested by Eaton and Konner (1985) for the determination of the projected macronutrient composition of pre-agricultural diets:

$$A\,(Ca\ \times x) + B\,(Cp \times x) = daily\ energy\ intake$$

where Ca and Cp are the assumed proportions of animal and plant foods consumed, A is the mean energy content (KJ/gr) of animal foods and B is the mean energy content (KJ/gr) of plant foods. Considering a database of 21 wild animal foods and 44 plant foods, Eaton and Konner (1985) suggested the following values: A = 5.90 KJ/gr (or 1.41 Kcal/gr) and B = 5.40 KJ/gr (or 1.29 Kcal/gr). The variable x represents the total number of grams required to provide any given amount of food energy. For genomic investigations, among all the published human ancient genomes, we selected individuals present complete (or almost complete) genome with at least 2× coverage and with available alignment files (in BAM format) mapped on *Homo sapiens* reference genome assembly GRCh37/hg19. Finally, 14 archaic human genomes were obtained (Table 3).

Moreover, we included 2 unpublished ancient individuals processed in the Laboratory of Anthropology (University of Florence) for other research projects. The haplotype analysis was based on the 28 SNP positions, previously found to distinguish haplotypes A and D (Ameur et al., 2012), spanning a 38.9 kb region that includes the promoter regions of FADS1 and FADS2. The variants were called using bcftools (RRID: SCR_005227, v1.16) (Li

TABLE 3 Estimated haplotype of the FAD genes in ancient individuals.

Upper Palaeolithic - *Homo sapiens*					Mesolithic - *Homo sapiens*		Neolithic - *Homo sapiens*				Copper age - *Homo sapiens*	Roman - *Homo sapiens*
Ust-Ishim	Peştera Muierii	Mura	ST2	Bichon	Loschbour	SF12	WC1	NE1	NE5	Mota	Oetzi	Roman individual
AA	AA	AA	AA	AA	AA	CA	CA	CA	CC	CC	CA	CC
GG	GG	-	GG	GG	GG	CG	CG	CG	CC	CC	CG	CC
TT	CT	TT	TT	TT	TT	CT	CT	CT	CC	CC	CT	CC
CC	CT	CC	CC	CC	CC	TC	TC	TC	TT	TT	TC	TT
GG	CG	GG	GG	GG	GG	CG	CG	CG	CG	CG	CG	CC
AA	GA	AA	AA	AA	AA	GA	GA	GA	GG	GG	GA	GG
CC	CC	CC	CC	CC	CC	TC	TC	TC	TT	TT	TC	TT
-	CC	-	-	-	-	TC	TT	-	-	-	-	-
GG	GG	GG	GG	GG	GG	AG	AG	AG	AA	AG	AG	AA
GG	AG	GG	-	GG	GG	AG	AG	AG	AA	AA	AG	AG
CC	TC	CC	CC	CC	CC	TC	TC	TC	TT	TT	TC	TT
TT	CT	TT	TT	TT	TT	CT	CT	CT	CC	CC	CT	CC
CC	CC	CC	CC	CC	CC	TC	TC	TC	TC	CC	TC	TT
CC	TC	CC	CC	CC	CC	TC	TC	TC	TT	TT	TC	TT
GG	GG	GG	GG	GG	GG	AG	AG	AG	AA	AA	AG	AA
GG	GG	GG	GG	GG	GG	AG	AG	AG	AA	GG	AG	AA
GG	AG	-	GG	GG	GG	AG	AG	N	GG	GG	GG	AA
GG	GG	GG	GG	GG	GG	AG	AG	AG	AG	GG	AG	AA
GG	GG	GG	GG	GG	GG	AG	AG	AG	AA	GG	AG	AA
TT	TT	TT	TT	TT	TT	CT	CC	CT	CC	CC	CT	CC
TT	TT	TT	TT	TT	TT	CT	CT	CT	CT	TT	CT	CC
GG	GG	GG	GG	GG	GG	AG	AA	AG	AA	AA	AG	AA
AA	AA	AA	AA	AA	AA	AC	AC	AC	AC	AA	AC	CC
AA	AA	AA	AA	AA	AA	CA	CA	CA	CA	AA	CA	CC
AA	CA	AA	AA	AA	AA	CA	CA	CA	CA	AA	CA	CC

(Continued)

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TABLE 3 (Continued)

Upper Palaeolithic - *Homo sapiens*					Mesolithic - *Homo sapiens*		Neolithic - *Homo sapiens*				Copper age - *Homo sapiens*	Roman - *Homo sapiens*
Ust-Ishim	Peștera Muierii	Mura	ST2	Bichon	Loschbour	SF12	WC1	NE1	NE5	Mota	Oetzi	Roman individual
AA	AA	AA	AA	AA	AA	TA	TA	TA	TA	AA	TA	TT
GG	AG	GG	GG	GG	GG	AG	AG	AG	AG	GG	AG	AA
AA	GA	AA	AA	AA	AA	GA	GA	GA	GA	AA	GA	GG
Haplotype A	Haplotype A	Haplotype A	Haplotype A	Haplotype A	Haplotype A	Haplotype A	Haplotype D	Haplotype D	Haplotype D	Haplotype A-D	Haplotype D	Haplotype D

Homo neanderthalensis: Chagyrskaya 8 (Russia) - 80,000 B.P.; Vindija 33.19 (Croatia) - 45,500 B.P.; Denisova 5 (Russia) 100,000 B.P.; Upper Palaeolithic *Homo sapiens*: Ust-Ishim (Russia) - 45,000 B.P.; Peștera Muierii (Romania) – 35,000 cal. B.P.; Mura (Italy) - 17,000 B.P.; ST2 (San Teodoro 2) (Italy) - 13,462-13,347 cal. B.P.; Bichon (Switzerland)–13,000 B.P.; Mesolithic *Homo sapiens*: Loschbour (Luxembourg) - 8,000 B.P.; SF12 (Scandinavia) - 9,033-8,757 cal. B.P.; Neolithic *Homo sapiens*: WC1 (Iran) - 7,455-7,082 cal. B.C.E.; NE1 (Hungary) - 5,310–5,070 cal. B.P.; NE5 (Hungary) - 5,210-4,990-cal. B.P.; Mota (Ethiopia) – 4,500 B.P.; Copper age *Homo sapiens*: Oetzi (Italy) - 3,350–3,120 cal. B.C.E.; Roman *Homo sapiens*: Roman individual (Italy) - 1st century D.C. (see references in the text).

et al., 2009). Only the reads with a minimum mapping quality of 30 were used to call confident bases.

3 Results

3.1 Dietary macronutrient composition of the Apulian Neanderthals

During the Late Mousterian period Apulia was characterized by frequent and prolonged drought climate conditions.

Speleothem data (covariation of δ18O and δ13C) recorded on stalagmite PC from Pozzo Cucù Cave (Apulia, 40.90° N, 17.16° E), indicated two periods of extremely dry conditions: from 66.7+0.9/−1.2 to 65.6+1.1/−1.3 ka during MIS 4, and from 55.3+1.1/−2.5 to 54.9+1.1/−2.7 ka during MIS 3. The occurrence of these events fit with speleothem, lacustrine and marine records from the Mediterranean region. These periods are considered as the driest and probably coldest of the entire MIS 5–3-time span, at least in southern Italy, and the event at ∼55 ka was certainly the driest of the entire record (Columbu et al., 2020 and references therein).

These climate conditions could have caused the scarcity of vegetable foods for Apulian Neanderthals (Boscato and Crezzini, 2012a; Boschin et al., 2021).

Consequently, in this analysis we use a P: A energy subsistence ratio of 15:85, considering mean subsistence economies by primary living environment in hunter-gatherer societies (Cordain et al., 2000, 2002; Speth, 2010). A significant value of plant contribution was assumed due to the archaeological evidence of plant use/collection from some Neanderthal sites (Henry et al., 2011; Hardy et al., 2012; Salazar-García et al., 2013; Power et al., 2018; Mariotti Lippi et al., 2023). Thus, through the equation suggested by Eaton and Konner (1985), the total number of grams required to provide the necessary amount of food energy in our model is:

$$x = \frac{12,500}{5.9 \times 0.85 + 5.4 \times 0.15} = 2,146\ gr$$

Under these idealized and probably intermittent isocaloric conditions, the total daily food intake of 2,146 gr would have been provided by 1,824.1 gr of animal food (85%) and 321.9 gr of vegetable food (15%).

The daily energy intake derived from the consumption of these food quantities, respectively is (Supplementary Table 5):

$$\begin{aligned} \textit{daily energy intake from game} &= 5.9\,(0.85 \times 2,146) \\ &= 10,762\ KJ\ (or\ 2,572.2\ Kcal) \\ \textit{daily energy intake from plant} &= 5.4\,(0.15 \times 2,146) \\ &= 1,738\ KJ\ (or\ 415.4\ Kcal) \end{aligned}$$

3.1.1 The aurochs consumption

In the Grotta di Santa Croce assemblage, no remains of birds, fish and mollusk were recorded. Aurochs and horses (more rarely red deer) were hunted by Neanderthals (Supplementary Tables 1, 2) (Boscato et al., 2010; Crezzini et al., 2023). In the estimation of the macronutrients of these human groups we decided to consider only

the exploitation of aurochs as animal food. Our decision was based on three different reasons: the need to simplify calculations in the construction of a food model for Neanderthals of Grotta di Santa Croce, the high presence of *Bos primigenius* in the Apulian Middle Palaeolithic zooarchaeological assemblages, indicating this species as one of the most widespread and exploited prey by humans in this area (Boscato et al., 2006, 2010; Boscato and Crezzini, 2006, 2012a,b; Boscato, 2017), and the availability of a detailed macronutrient quantitative and qualitative distributions in bovid carcass reported by Emerson in her study on the economic anatomy of nowadays adult bison (Emerson, 1990).

Emerson reported that the carcass weight of the examined individual was 640 Kg (Emerson, 1990, Table 2.4, p. 32). Levine et al. (1973) suggest that in ungulates in which the hooves, antlers, hide, and internal gastrointestinal contents were discarded, the remaining carcass represented 72% of the live weight. Therefore, we consider an edible carcass weighing 460.8 Kg. Pitts and Bullard (1968) demonstrated that the percentage body fat of a mammalian species can be estimated from its relative size via a formula:

$$Percentage\ body\ fat = 1.5 \times FFM^{0.20}$$

Where FFM is the fat-free mass expressed in grams. For the bison examined by Emerson (1990) this value is 116.9 Kg (Emerson, 1990, note a, Table 6.7, p. 456, individual *SAM*), that give a percentage body fat of 19.5. This represents the x parameter included in the equation from Cordain et al. (2000 – Figure 3; p. 687):

$$y = 3.21 - (7.92 \times x) + \left(0.403\ \times x^2\right) - \left(0.009\ \times x^3\right)$$

useful to determine the relative contribution of fat energy from game food. Thus, an animal with 19.5% body fat would derive 71% of its energy as fat that, in our case, correspond to 7,641.02 KJ (10,762 KJ × 0.71) or to 1,826.24 Kcal (Supplementary Table 5). The relative contribution of protein energy from hunted animal food was also determined by using the equation proposed by Cordain et al. (2000 – Figure 3, p. 687):

$$y = 96.79 - (7.92 \times x) + \left(0.403\ \times x^2\right) - \left(0.009\ \times x^3\right)$$

We found that an animal with 19.5% body fat would derive 29% of its energy as protein, which corresponds to 3,120.98 KJ (10,762 KJ × 0.29) or to 745.93 Kcal (Supplementary Table 5).

3.1.2 The vegetal consumption

For the macronutrient composition and energy value of plant foods we considered the following distribution: 19 en% of fat, 13 en% of protein and 68 en% of carbohydrate (Eaton et al., 1998). This allowed us to determine, for an assumed P: A subsistence ratio of 15:85 and an energy intake of 12,500 KJ, the contribution of 243.75 KJ (0.13 × 0.15 × 12,500 KJ) or 58.25 Kcal from plant protein; the contribution of 356.25 KJ (0.19 × 0.15 × 12,500 KJ) or 85.14 Kcal, from plant fat; and a contribution of 1,275 KJ (0.68 × 0.15 × 12,500 KJ) or 304.73 Kcal from plant carbohydrates (Supplementary Table 5).

3.2 The intake and the metabolism of different macronutrients

In the previous paragraph we calculated the grams of animal and plant food that would have had to be consumed by Apulian Neanderthals on a P: A = 15%:85% diet and the energy contribution provided by different macronutrients.

Regarding animal food, we do not know which parts of the bovid carcass would have been preferably meet Neanderthal daily energy requirements. By comparing the macronutrients/energy data calculated in the previous paragraph and the economic values of bison parts reported by Emerson (1990) with the skeletal frequencies recorded at Grotta di Santa Croce (Supplementary Tables 2–4) (Crezzini et al., 2023), we aim to investigate some peculiar aspects of aurochs' exploitation by southern Italy Neanderthals, likely related to their nutritional needs.

In addition, the section on carbohydrates includes speculations on the possible contributions provided with plant food. Finally, we describe the results of our preliminary research on the fat metabolism related to characteristic mutations of FADS1 and FADS2 genes.

3.2.1 Lipids

Examining the energy intake (KJ) related to the different anatomical parts of bison published by Emerson (1990) it is noteworthy that the rare or absent aurochs skeletal elements at Grotta di Santa Croce are characterized by the highest values of bone grease (carpal and tarsal bones, proximal and distal femur, proximal humerus, distal radius, distal metapodials, phalanges) (Table 1; Supplementary Tables 2–4).

Exploitation of skeletal fat only from these bones could provide about 11,172 KJ (2,670 Kcal), a higher amount of energy than the total provided by animal food calculated in this paper (about 10,762 KJ or 2,572.2 Kcal, Supplementary Table 5), for an assumed P:A subsistence ratio of 15:85. Such amounts of energy from these skeletal elements can be obtained through only 296.7 gr of bone grease intake, a small amount in respect to the total grams of animal food that probably must have been included in the Neanderthal diet hypothesized in this study (1,824.1 gr). A low quantity of bone grease rendering (about 100 gr) from specific skeletal portions such as distal radius, carpals, distal tibia, tarsals, distal metapodial and phalanges (the rarest aurochs bones recorded in the Grotta di Santa Croce assemblage) provides about 4,104.5 KJ, more than half the energy from animal fat calculated in our model (7,641.02 KJ, Supplementary Table 5).

3.2.2 Protein

According to the hypothesized diet in this paper, Apulian Neanderthals should have obtained about 3,120.98 KJ (or 745.93 Kcal) from animal protein (Supplementary Table 5). At Grotta di Santa Croce the aurochs body parts are positively correlated with their protein quantity ($p = 0.27$, Crezzini et al., 2023, Figure 6, p. 8).

This correlation is not significant, but the highest MAU (Minimal Animal Units) values are related to the medial

portions of humerus, tibia and femur (Supplementary Table 3). Excluding the scapula (which still present), these skeletal portions provide the largest amounts of energy from protein (Table 2). Archaeological records indicate that European Neanderthals and quasi-contemporary modern humans of the mid-Upper Paleolithic may have had to rely repeatedly on diets characterized by large (excessive) amounts of animal protein. This evidence comes from isotope studies of the fossil human remains: the collagen of these Late Pleistocene humans is more enriched in 15N than that of contemporary carnivores (Lee-Thorp and Sponheimer, 2006; Robbins et al., 2005). However, it is noted that the maximum amount of lean meat that a forager can safely consume is finite. This is due to the limit of the liver that can no longer effectively deaminate the amino acids to avoid a hazardous build-up of ammonia (hyperammonemia) and excess amino acids (hyperaminoacidemia) in the blood (Dimski, 1994; Husson et al., 2003; Powers-Lee and Meister, 1988).

If protein averages about 16% nitrogen, a widely used value to estimate total or "crude" protein that an 80 kg (176 lb) adult can consume is about 261 gr per day (range 221–305 g) (Cordain et al., 2000; Mann, 2000).

If we consider the meat nutritional value of the proximal humerus of bison reported by Emerson (1990) (Table 2), we can calculate the energy provided by the consumption of 200 gr of meat recovered from this anatomical part:

$$943.95gr \ : \ 15,797.94KJ = 200gr : x$$
$$x = 3,347.2KJ$$

This suggests that Neanderthal (an 80 kg adult) could probably obtain the entire quantity of energy from animal protein (3,120.98 KJ) assumed in our model by consuming a "safe" amount of bovid protein.

3.2.3 Carbohydrates

In our hypothesized diet, the proportion of plants consumed is low. The amount that would have been consumed slightly exceeds 320 gr. The energy from fat and protein (356.25 and 243.75 KJ respectively, Supplementary Table 5) probably could be easily offset by the high availability of animal resources. On the other hand, plant carbohydrates would contribute the highest value: 1,275 KJ (Supplementary Table 5). This daily energy contribution from plant carbohydrates appears to be quite high if we consider the quality and quantity of plant resources recoverable in a prairie-steppe environment such as that hypothesized for the Late Mousterian in Apulia (Columbu et al., 2020; Boschin et al., 2021). Studies conducted to investigate biochemical characteristics of common steppe species indicate a low caloric content of their seeds (generally the plant structure with the higher nutritional value). Examining the seeds of *Oryzopsis hymenoides* (*Poaceae*), Kelrick and MacMahon (1985) determined a value of 4,058 calories per gram (Table 2, p. 67). This value corresponds to 16,9 KJ. The (soluble and structural) carbohydrates represent 49.1% of the total seed weight (Kelrick and MacMahon, 1985, Table 3, p. 68). Therefore, to reach the daily amount of carbohydrate energy from plants assumed in our model, Neanderthal would have had to consume daily about 75.4 gr of these seeds.

3.2.4 The paleogenome analysis

If the zooarchaeological data from the investigated Late Mousterian contexts of southern Italy indicated an intense exploitation of fats by Neanderthals, analogous analyses on faunal assemblages from different sites in southern Italy referable to Upper Palaeolithic, don't evidence this settlement pattern in modern humans, although the preys remained the same (Boscato and Crezzini, 2012b). To find a possible genetic basis for these resource needs by Neanderthal, we analyzed FADS1 and FADS2 genes for Neanderthals and modern human.

These genes, located in chromosome 11, encoding two key enzymes for the long-chain polyunsaturated fatty acids (LC-PUFAs) biosynthesis (Nakamura and Nara, 2004), the omega-3 docosahexaenoic (DHA) acid and the omega-6 arachidonic acid (AA). LC-PUFAs are essential to maintain the function of human brain and central nervous system and they can be supplied through dietary intake as DHA and AA directly or as their 18-carbon precursors. DHA is mainly found in fish, AA is also present in eggs, land-animal fats, and liver while the precursors are found in high quantities in some vegetable oils (Ratnayake and Galli, 2009). The conversion of the 18-carbon precursors to LC-PUFAs is done through a series of elongations and desaturations of the fatty-acid molecules and the efficiency of this process is strongly correlated with enzymes encoded by FADS1 and FADS2 (Schaeffer et al., 2006; Bokor et al., 2010). In extant human populations, two FAD haplotypes (A and D) were identified – defined by 28 closely linked SNPs – that differ in their ability for synthesizing LC-PUFAs (Ameur et al., 2012). Haplotype D, is characterized as an enzymatically efficient gene signature, showing significantly increased desaturase activity. It is nearly fixed in African populations, while in Europe and the Middle East shows a frequency of 75%. Haplotype A is associated with a reduction in the enzymatic efficiently and its frequency is close to 100% in American populations. Recent data suggests that the functionality of diverse fatty acid desaturase enzymes found in humans today have been shaped over the course of evolution by environmental, dietary, and nutritional selective pressures in combination with genetic events, such as duplications, losses, and mutations (Castro et al., 2012; Vicedomini et al., 2021). Moreover, Ameur et al. (2012) observed that primates and archaic humans, notably the Neanderthals and the Denisovans, have haplotypes that are very similar to haplotype A, suggesting that haplotype D likely appeared in modern human lineage after the split from the common ancestor with Neanderthals. According to this observation, we investigated the possible interaction between genetic variants of FAD genes and regional exclusive dietary in Neanderthals and ancient modern humans. With this aim, we analyzed genomic data of 16 ancient individuals from different regions and cultures, which include 3 high coverage genomes of Neanderthal (Prüfer et al., 2014, 2017; Mafessoni et al., 2020), 7 Upper Paleolithic and Mesolithic hunter-gatherers (Fu et al., 2014; Svensson et al., 2021; Higgins et al., 2024; Posth et al., 2023; Jones et al., 2015; Lazaridis et al., 2014; Günther et al., 2018), 5 Neolithic farmers (Lazaridis et al., 2014; Broushaki et al., 2016; Gamba et al., 2014; Gallego Llorente et al., 2015; Wang et al., 2023) and one individual from Roman age (Table 3), focusing on the 28 SNPs that distinguish haplotypes A and D.

Our analysis showed that all Neanderthals have nucleotide variants found on both human haplotypes but with high

similarity with haplotype A, confirming previous results based on incomplete sequence of Neanderthal genome (Ameur et al., 2012). Interestingly, Chagyrskaya 8 and Vindija 33.19, who are more closely related to each other than to the Neanderthal from Denisova Cave (Mafessoni et al., 2020), share seven deletions absent in Denisova 5 (Table 3).

Regarding the Upper Paleolithic hunter-gatherers, all the specimens analyzed were homozygous for haplotype A, except for Peştera Muierii, an Early Upper Paleolithic woman from Romania (Svensson et al., 2021) which displays a higher genetic variability with 12 heterozygous variants. The ancestral haplotype A is also recovered in Mesolithic individuals from Luxembourg (Lazaridis et al., 2014) and from Scandinavia (Günther et al., 2018).

Starting from the Neolithic period, we observed the first evidence of the derived haplogroup D. Among the early farmers, Mota, a 4,500-year-old individual from Ethiopia (Gallego Llorente et al., 2015), carry mixed FADS haplotype consistent with a progressive reduction of haplotype A by recombination with haplotype D in African populations. Additionally, our results indicate that Neolithic individuals from Europe and the Near East were characterized by a high genetic variability in FAD genes as suggested by the observed heterozygosity which is not found in the Paleolithic specimens. In our ancient dataset, the first occurrence of homozygous haplotype D was detected in a historical individual from Roman period.

4 Discussion

4.1 Lipids

At Grotta Santa Croce aurochs body parts are positively and significantly correlated with Unsaturated Marrow Index ($p = 0.006$; Crezzini et al., 2023). Binford (1978) mentions that marrow with high oleic acid content being more desirable in Nunamiut people due to its taste. However, mere flavor can't represent the only reason when considering an adaptation for exploiting the marrow from specific ungulate body parts (Binford, 1978).

Besides a specific taste, differences in fat chemistry cause different consistency, appearances and melting points that may be useful both to obtain satiety, delay postprandial appetite sensations, increase energy intake, and for daily activities, like waterproofing clothes, heat production, mechanical buffering and lubrication (Hadley, 1985; Klaus, 2001).

In recent medical literature there is a lack of consensus regarding whether changes in the saturation profile of a high-fat meal can affect post-ingestion satiety and energy intake (Burton-Freeman, 2005; Kamphuis et al., 2001; Strik et al., 2010).

On the other hand, it is possible that the Palaeolithic hunter-gatherers were "aware" that the consumption of resources characterized by specific fat chemistry could have a long-term effect on their health (Outram, 1998).

Oleic acid, together with other18-C FA compounds, is an important precursor for the *de novo* biosynthesis of pivotal substances like LC-PUFA (DHA and AA) through elongations and desaturase activity by enzymes encoded by specific genes including FADS1 and FADS2.

The marrow and the bone grease of the distal limb bones, the most represented ungulate parts, together with the skull, in Palaeolithic contexts, are characterized by the higher percentage of oleic acid and other 18-carbon unsaturated fatty acids like ALA and LA (Morin, 2007).

The presence in both Neanderthal and modern humans of the ancestral FAD haplotypes (A), characterized as an enzymatically less efficient gene signatures could explain the significant exploitation of these parts of the ungulate carcasses to ensure the biosynthesis of a sufficient amount of LC-PUFA, achievable only through the intake of high quantity of their precursors.

Focusing on our Mousterian faunal assemblage, these dietary habits could have been particularly crucial for Apulian Neanderthal due to specific environment constraints. During the frequent and prolonged drought climate conditions that characterized the Late Mousterian period in this region (Columbu et al., 2020), the availability of 18-C FA compounds, contained in high quantities in vegetable food could have been very scarce.

Examining the percentages of oleic acid in caribou anatomical parts published by Binford (1978), it's possible to note that the most exploited skeletal elements at Grotta di Santa Croce contain higher amounts of oleic acid in skeletal grease than in marrow (Supplementary Table 3).

The specific exploitation of bone grease by Apulian Neanderthal could be related to the necessity of increasing the intake/absorption of 18-carbon precursors to LC-PUFAs from animal resources, through intense bone fragmentation/destruction of the limb bone epiphyses, the carpals, the tarsals, and the phalanges.

4.2 Proteins

Despite the large number of studies, the amount of protein that one can safely consume on a long-term basis is a topic in need of much more research, and different amounts are suggested according to different human groups (past and present) (Speth, 2010). The human body can adapt to changes in consumption by regulating the enzymes involved in protein metabolism and urea synthesis. This process of adaptation may take a few days to complete, a period longer than the duration of many of the nutritional studies designed to explore the effects of high-protein intakes (Institute of Medicine, 2005).

It is noted that arctic people present genome mutation that allows them avoid toxicity with ingestion of high amounts of meat (Clemente et al., 2014), through a diet with a P:A ratio very unbalanced toward animal resources (Binford, 1978; Sinclair, 1953).

If as calculated in our work, already low amounts of protein could meet the animal protein energy requirements of Apulian Mousterians, what advantage could a probable excess of protein intake (probably above the safe limit of 261 g for an adult weighing 80 kg) have? This issue is addressed in the next paragraph.

4.3 Carbohydrates

The gathering pattern of plant food in Palaeolithic can be predicted by the "optimal foraging theory" (Hawkes et al., 1982; Simms, 1987). Studies of hunter-gatherers have shown that the

plants were collected with a general prioritization that maximizes the rate of energy capture relative to energy expenditure. More than 100 plant species can be used, but only a small fraction of these were regularly consumed and providing the greatest ratio of energy capture to energy expenditure (Simms, 1987; O'Connell and Hawkes, 1981).

This optimal foraging has been complex to implement in a prairie-steppe environment like that probably present in Apulia during the Late Mousterian. Zimov et al. (2012) indicate that typical steppe which developed during the Late Pleistocene in Europe is understood to have comprised primarily plant *taxa* as *Cyperaceae*, *Artemisia*, and *Gramineae*. Many species of *Cyperaceae* store carbohydrates in their underground systems, but not all are edible, and some require processing to access the nutrients (Zhang et al., 2024). *Artemisia* is a genus of bitter-tasting aromatic herbs and shrubs with strong chemical constituents that can be poisonous (Bora and Sharma, 2011). *Gramineae* (*Poaceae*) is a family of grasses widely spread in different vegetal ecosystems. Despite this, it includes *taxa* that store their energy as carbohydrates largely in its rhizomes and so it must be dug out (Hardy et al., 2022).

Other *Gramineae* species produce small edible seeds are characterized by low rates of energy. This is the case of *Oryzopsis hymenoides* (*Eriocoma hymenoides*) described in the previous paragraph: in respect to the amount admitted in our Neanderthal model, a low return of carbohydrate energy from this type of plant could be obtained, with high energy expenditure due to the collection of large quantity of their small seeds. The carbohydrate intake in these human groups could thus have been low.

As suggested by Hardy et al. (2022), although individual and short-term survival is possible on a relatively low-carbohydrate diet, Neanderthals had large, energy-expensive brains and led physically active lifestyles, suggesting that for optimal health they would have required a high intake of carbohydrates, in particular glucose. The European Food Information Council (EUFIC) indicates that a modern normal weight adult requires 200 gr of glucose per day, two-thirds of which (about 130 grams) is specifically needed by the brain to cover its glucose needs (Howarth et al., 2012). Despite the brain accounts for ∼2% of the body weight, it consumes ∼20% of glucose-derived energy (Institute of Medicine, 2005; Sweeting et al., 2021).

One hypothesis is that to meet this need, high-performance physiological processes capable of regulating blood glucose might have been present in Neanderthals. Among these processes, gluconeogenesis that needs to be given the most consideration (Hardy et al., 2022).

Gluconeogenesis (i.e., *de novo* synthesis of glucose) occurs in the liver and kidneys, it is stimulated by the diabetogenic hormones (glucagon, growth hormone, epinephrine, and cortisol). It is a metabolic pathway that results in the biosynthesis of glucose from certain non-carbohydrate carbon substrates like glycerol (derived from fat breakdown), lactate (derived from muscles), propionate and certain specific amino acids obtained from the breakdown of proteins (for example, alanine). These amino acids are converted into urea through the urea cycle, whereas their carbon skeletons are transformed into other intermediates, mostly glucose.

Gluconeogenesis becomes vital during periods of metabolic stress, such as starvation (Acheson et al., 1984). It is interesting to note that Veldhorst et al. (2009) investigated gluconeogenesis and energy expenditure after a high-protein, carbohydrate-free diet and they demonstrated that forty-two percent of the increase in energy expenditure after this diet was related to an increase in gluconeogenesis. The cost of gluconeogenesis was 33% of the energy content of the produced glucose (Veldhorst et al., 2009).

Our hypothesis is that the Neanderthal very-high-protein diet could have stimulated the process of gluconeogenesis. A probable excess of protein intake could have furnished a high quantity of amino-acids. The bio synthesis of glucose from these compounds may have compensated for the carbohydrate requirement deficit in Neanderthal due to low plant consumption.

5 Conclusions

The estimation of the dietary macronutrient ratio performed in this paper has permitted to better understand of the specific treatments of ungulate carcasses by Neanderthals, evidenced through the zooarchaeological studies carried out in southern Italy.

The scarcity/lack of epiphyses and spongy bones of ungulates recorded in assemblages can be explained by the intensive exploitation of these parts, characterized by a high fat energy yield. Paleogenomic data from the analysis of FADS1 and FADS2 genes underlined the importance for Apulian Neanderthals of 18-carbon unsaturated fatty acid intake from animal resources, to address the low availability of these compounds from plant resources. A high consumption of animal protein for the human groups investigated in this study was also determined. This could have meant a surplus of these substances in respect to the daily protein energy needs, providing high quantities of amino acids, important non-carbohydrate precursors for the gluconeogenesis. The gluconeogenesis products could have compensated for the low carbohydrate intake from plant consumption.

Our results stimulate investigating the possible presence of enzymatically related gene signatures for high-performance gluconeogenesis in Neanderthals. Obtaining data on this biochemical process in the context of Neanderthal physiology could be important to highlight new differences between these human groups compared with modern humans.

Like all metabolic processes, gluconeogenesis is characterized by different phases and dynamics that may characterize the metabolic structure of the species and express its specific nutritional requirements and chronic diseases.

Probably the most important aspect of this process for the topics discussed in this paper, is the hepatic insulin signaling that regulates gluconeogenetic activity (Onyango, 2022). In modern populations, if insulin target cells of the liver become less responsive to insulin, the hepatic insulin resistance (HIR) occurs, which, promoting excessive gluconeogenesis, contributes to the development of (pre)diabetes (Basu et al., 2013).

Paradoxically, HIR also promotes *de novo* lipid synthesis (Smith et al., 2020), leading to excessive deposition of fat in the liver (hepatic steatosis) and secretion of very low-density lipoproteins (VLDL) into the blood (Meshkani and Khosrow, 2009; Cook et al., 2015). These metabolic dysregulations cause dyslipidemia, cardiovascular disease and atherosclerosis (Meshkani and Khosrow, 2009; Berndt et al., 2021), which can progress to cirrhosis and hepatocellular carcinoma (Lu et al., 2021).

Specific metabolic mechanisms in the absorption and production of fats may have preserved Neanderthals from these diseases are related to gluconeogenic overactivity.

Finally, it's important to note that the breakdown of the proteins and the turn them into amino acids, pivotal substrates for gluconeogenesis, can also be obtained by chemical reactions that occur in specific food processing. This is the case of the external fermentation. Besides amino acids, the fermentation of lipids also produces long chain fatty acids (LCFAs) and glycerol, other important substrates for gluconeogenesis.

The external fermentation is hypothesized as an activity conducted by the Mousterian hunter gatherers at Grotta di Santa Croce (Crezzini et al., 2023).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

JC: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. AM: Conceptualization, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CC: Conceptualization, Methodology, Software, Writing – review & editing. DC: Funding acquisition, Methodology, Resources, Validation, Writing – review & editing. AR: Writing – review & editing. PB: Writing – review & editing. AM: Writing – review & editing. FB: Formal analysis, Funding acquisition, Resources, Supervision, Visualization, Writing – review & editing, Writing – original draft.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2025.1558698/full#supplementary-material

References

Acheson, K. J., Schutz, Y., Bessard, T., Ravussin, E., Jequier, E., Flatt, J. P., et al. (1984). Nutritional influences on lipogenesis and thermogenesis after a carbohydrate meal. *Am. J. Physiol.* 246, 62–70. doi: 10.1152/ajpendo.1984.246.1.E62

Agustí, J., Blain, H. A., Cuenca-Bescós, G., and Bailon, S. (2009). Climate forcing of first hominid dispersal in Western Europe. *J. Hum. Evol.* 57, 815–821. doi: 10.1016/j.jhevol.2009.06.005

Airvaux, J. (2004). "Le site paléolithique de chez-Pinaud à Jonzac, Charente-Maritime," in *Prehistoire du Sud-Ouest, Vol. 8*, 108.

Ameur, A., Enroth, S., Johansson, A., Zaboli, G., Igl, W., Johansson, A. C., et al. (2012). Genetic adaptation of fatty-acid metabolism: a human-specific haplotype increasing the biosynthesis of long-chain omega-3 and omega-6 fatty acids. *Am. J. Hum. Genet.* 90, 809–820. doi: 10.1016/j.ajhg.2012.03.014

Arrighi, S., Freguglia, M., Ranaldo, F., and Ronchitelli, A. (2009). Production and use in the lithic industry of the Mousterian in Santa Croce (Bisceglie, Italy). *Humna E*24, 91–106.

Banks, W. E., Moncel, M. H., Raynal, J. P., Cobos, M. E., Romero-Alvarez, D., Woillez, M. N., et al. (2021). An ecological niche shift for Neanderthal populations in Western Europe 70,000 years ago. *Sci. Rep.* 11:5346. doi: 10.1038/s41598-021-84805-6

Basu, R., Barosa, C., Jones, J., Dube, S., Carter, R., Basu, A., et al. (2013). Pathogenesis of prediabetes: role of the liver in isolated fasting hyperglycemia and combined fasting and postprandial hyperglycemia. *J Clin Endocrinol Metab.* 98, E409–E417. doi: 10.1210/jc.2012-3056

Berndt, N., Kolbe, E., Gajowski, R., Eckstein, J., Ott, F., Meierhofer, D., et al. Matz-Soja, M. (2021). Functional consequences of metabolic zonation in murine livers: insights for an old story. *Hepatology* 73, 795–810. doi: 10.1002/hep.31274

Binford, L. R. (1978). Dimensional analysis of behavior and site structure: learning from an Eskimo hunting stand. *Am. Antiq.* 43, 330–361. doi: 10.2307/279390

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (London: Academic Press), 123–143. doi: 10.1016/B978-0-12-821428-2.00010-X

Bokor, S., Dumont, J., Spinneker, A., Gonzalez-Gross, M., Nova, E., Widhalm, K., et al. (2010). HELENA Study Group Single nucleotide polymorphisms in the FADS gene cluster are associated with delta-5 and delta-6 desaturase activities estimated by serum fatty acid ratios. *J. Lipid Res.* 51, 2325–2333. doi: 10.1194/jlr.M006205

Bora, K. S., and Sharma, A. (2011). The genus Artemisia: a comprehensive review. *Pharm. Biol.* 49, 101–109. doi: 10.3109/13880209.2010.497815

Boscato, P. (2017). Ambienti e economia nel Paleolitico medio della Puglia: lo studio delle faune. *Studi di Preistoria e Protostoria*. 4, 119–124.

Boscato, P., and Crezzini, J. (2006). The exploitation of ungulate bones in Homo neanderthalensis and Homo sapiens. *Hum. Evol. E*21, 311–320. doi: 10.1007/s11598-006-9031-8

Boscato, P., and Crezzini, J. (2012a). "Il deposito musteriano del Riparo l'Oscurusciuto (Ginosa - TA): la fauna a grandi mammiferi delle UUSS 1÷9," in *Proceedings of the 6° Convegno Nazionale di Archeozoologia*, eds. J. De Grossi Mazzorin, D. Saccà, and C. Tozzi May 21–24, 2009; Orecchiella (IT). 25–32.

Boscato, P., and Crezzini, J. (2012b). Middle-upper palaeolithic transition in Southern Italy: Uluzzian macromammals from Grotta del Cavallo (Apulia). *Quat. Int.* 252, 90–98. doi: 10.1016/j.quaint.2011.03.028

Boscato, P., Crezzini, J., Freguglia, M., Gambassini, P., Ranaldo, F., and Ronchitelli, A. (2010). "Activités de subsistance et exploitation des ressources de l'environnement à S. Croce (Bisceglie - Bari - Italie du Sud): les unités stratigraphiques 546 et 535 du Paléolithique moyen", in *Settlement dynamics of the middle paleolithic and middle stone age*, eds. N. J. Conard and A. Delagnes (Vol. III. Kerns Verlag: Tübingen), 265–282.

Boscato, P., Crezzini, J., and Pellegrini, A. (2006). "Le parti mancanti: faune del Paleolitico medio nel deposito esterno della U," in *Archaeozoological studies in honour of Alfredo Riedel*, ed. B. Sala (Bolzano: Ufficio Beni Archeologici), 39–50.

Boschin, F., Columbu, A., Spagnolo, V., Crezzini, J., Bahain, J. J., Falguères, C., et al. (2021). Human occupation continuity in southern Italy towards the end of the Middle Palaeolithic: a palaeoenvironmental perspective from Apulia. *J. Q. Sci.* 37, 204–216. doi: 10.1002/jqs.3319

Broushaki, F., Thomas, M. G., Link, V., López, S., van Dorp, L., Kirsanow, K., et al. (2016). Early neolithic genomes from the eastern fertile crescent. *Science*, 353, 499–503. doi: 10.1126/science.aaf7943

Brugal, J-. P., Costamagno, S., Jaubert, J., and Mourre, V. (1996). "Les gisements paléolithiques de Coudoulous (Tour de Faure, Lot, France)," in *Proceeding of the XIII International Congress of Prehistoric and Protohistoric Sciences; September 8–14; Forlì* (Italy).

Burton-Freeman, B. (2005). Sex and cognitive dietary restraint influence cholecystokinin release and satiety in response to preloads varying in fatty acid composition and content. *J. Nutr.* 135, 1407–1414. doi: 10.1093/jn/135.6.1407

Cardini, L. (1954). Scoperte e scavi paletnologici in Italia 1954: Bisceglie, Bari. *Rivista Scienze Preistoriche* IX:128.

Castro, L. F., Monroig, Ó., Leaver, M. J., Wilson, J., Cunha, I., Tocher, D. R., et al. (2012). Functional desaturase Fads1 (Δ5) and Fads2 (Δ6) orthologues evolved before the origin of jawed vertebrates. *PLoS ONE.* 7:31950. doi: 10.1371/journal.pone.0031950

Cerqueira Caio, C. S., Paixão-Côrtes, V. R., Zambra, F. M. B., Salzano, F. M., Hünemeier, T., Bortolini, M. C., et al. (2012). Predicting Homo pigmentation phenotype through genomic data: from Neanderthal to James Watson. *Am. J. Hum. Biol.* 24, 705–709. doi: 10.1002/ajhb.22263

Ciullo, S. (2016). *Archeozoologia nella Grotta di Santa Croce (Bisceglie - BT). Le unità stratigrafiche* (bachelor thesis). University of Siena, Siena, Italy. 538–549.

Clemente, F. J., Cardona, A., Inchley, C. E., Peter, B. M., Jacobs, G., Pagani, L., et al. (2014). A selective sweep on a deleterious mutation in CPT1A in Arctic populations. *Am. J. Hum. Genet.* 95, 584–589. doi: 10.1016/j.ajhg.2014.09.016

Columbu, A., Chiarini, V., Spötl, C., Benazzi, S., Hellstrom, J., Cheng, H., et al. (2020). Speleothem record attests to stable environmental conditions during Neanderthal-modern human turnover in southern Italy. *Nat. Ecol. Evol.* 4, 1188–1195. doi: 10.1038/s41559-020-1243-1

Cook, J. R., Langlet, F., Kido, Y., and Accili, D. (2015). Pathogenesis of selective insulin resistance in isolated hepatocytes. *J. Biol. Chem.* 290, 13972–13980. doi: 10.1074/jbc.M115.638197

Cordain, L., Eaton, S. B., Miller, J. B., Mann, N., and Hill, K. (2002). The paradoxical nature of hunter-gatherer diets: meat-based, yet non-atherogenic. *Eur. J. Clin. Nutr.* 56, S42–S52. doi: 10.1038/sj.ejcn.1601353

Cordain, L., Miller, J. B., Eaton, S. B., Mann, N., Holt, S. H., Speth, J. D., et al. (2000). Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *Am. J. Clin. Nutr.* 71, 682–692. doi: 10.1093/ajcn/71.3.682

Cordain, L., Watkins, B. A., and Mann, N. J. (2001). Fatty acid composition and energy density of foods available to African hominids. Evolutionary implications for human brain development. *World Rev. Nutr. Diet* 90, 144–161. doi: 10.1159/000059813

Crezzini, J., Boscato, P., Ronchitelli, A., and Boschin, F. (2023). A peculiar exploitation of ungulates at Grotta di Santa Croce: bone grease rendering and nutritional patterns among Neanderthals in southern Italy. *Hist. Biol.* 36, 2133–2145. doi: 10.1080/08912963.2023.2242630

Dimski, D. S. (1994). Ammonia metabolism and the urea cycle: function and clinical implications. *J. Vet. Intern. Med.* 8, 73–78. doi: 10.1111/j.1939-1676.1994.tb03201.x

Eaton, S. B., Eaton, S. B., III, and Konner, M. J. (1997). Paleolithic nutrition revisited: a twelve-year retrospective on its nature and implications. *Eur. J. Clin. Nutr.* 51, 207–216. doi: 10.1038/sj.ejcn.1600389

Eaton, S. B., Eaton, S. B., III, Sinclair, A. J., Cordain, L., and Mann, N. J. (1998). Dietary intake of long-chain polyunsaturated fatty acids during the paleolithic. *World Rev. Nutr. Diet* 83, 12–23. doi: 10.1159/000059672

Eaton, S. B., and Konner, M. (1985). Paleolithic nutrition. A consideration of its nature and current implications. *N. Engl. J. Med.* 312, 283–289. doi: 10.1056/NEJM198501313120505

El Zaatari, S., Grine, F. E., Ungar, P. S., and Hublin, J-. J. (2016). Neandertal versus modern human dietary responses to climatic fluctuations. *PLoS ONE* 11:e0153277. doi: 10.1371/journal.pone.0153277

Emerson, A. M. (1990). *Archaeological Implications of Variability in the Economic Anatomy of Bison* (dissertation). Washington State University, United States.

Farizy, C., David, F., and Jaubert, J. (1994). *Hommes et Bisons du Palèolithique moyen a Mauran (Haute Garonne)*. Paris: ed. CNRS.

Fu, Q., Li, H., Moorjani, P., Jay, F., Slepchenko, S. M., Bondarev, A. A. et al. (2014). Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514, 445–449. doi: 10.1038/nature13810

Gallego Llorente, M., Jones, E. R., Eriksson, A., Siska, V., Arthur, K. W., Arthur, J. W., et al. (2015). Ancient Ethiopian genome reveals extensive Eurasian admixture throughout the African continent. *Science* 350, 820–822. doi: 10.1126/science.aad2879

Gamba, C., Jones, E. R., Teasdale, M. D., McLaughlin, R. L., Gonzalez-Fortes, G., Mattiangeli, V., et al. (2014). Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* 5:5257. doi: 10.1038/ncomms6257

Gaudzinski, S. (1995). Wallertheim revisited: a re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhessen/Germany). *J Archaeol Sci.* 22, 51–66. doi: 10.1016/S0305-4403(95)80162-6

Gaudzinski, S. (1996). On bovid assemblages and their consequences for the knowledge of subsistence patterns in the Middle Palaeolithic. *Proceedings of the Prehistoric Society*, 62, 19–39. doi: 10.1017/S0079497X00002723

Günther, T., Malmström, H., Svensson, E. M., Omrak, A., Sánchez-Quinto, F., Kilinç, G. M. et al. (2018). Population genomics of Mesolithic Scandinavia: investigating early postglacial migration routes and high-latitude adaptation. *PLoS Biol.* 16:e2003703. doi: 10.1371/journal.pbio.2003703

Hadley, N. F. (1985). *The Adaptive Role of Lipids in Biological Systems*. Hoboken: John Wiley and Sons.

Hardy, K. (2019). Paleomedicine and the use of plant secondary compounds in the Paleolithic and Early Neolithic. *Evol Anthropol.* 28, 60–71. doi: 10.1002/evan.21763

Hardy, K., Bocherens, H., Miller, J. B., and Copeland, L. (2022). Reconstructing Neanderthal diet: the case for carbohydrates. *J. Hum. E*162:103105. doi: 10.1016/j.jhevol.2021.103105

Hardy, K., Buckley, S., Collins, M. J., Estalrrich, A., Brothwell, D., Copeland, L., et al. (2012). Neanderthal medics? Evidence for food, cooking and medicinal plants entrapped in dental calculus. *Naturwissenschaften* 99, 617–626. doi: 10.1007/s00114-012-0942-0

Hawkes, K., Hill, K., and O'Connell, J. F. (1982). Why hunters gather: optimal foraging and the Ache of eastern Paraguay. *Am. Ethnol.* 9, 379–398. doi: 10.1525/ae.1982.9.2.02a00100

Henry, A. G., Brooks, A. S., and Piperno, D. R. (2011). Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc. Natl. Acad. Sci. U. S. A.* 108:486e491. doi: 10.1073/pnas.1016868108

Higgins, O. A., Modi, A., Cannariato, C., Diroma, M. A., Lugli, F., Ricci, S., et al. (2024). Life history and ancestry of the late Upper Palaeolithic infant from Grotta delle Mura, Italy. *Nat. Commun.* 15:8248. doi: 10.1038/s41467-024-51150-x

Howarth, C., Gleeson, P., Attwell, D. (2012). Updated energy budgets for neural computation in the neocortex and cerebellum. *J. Cereb. Blood Flow. Metab.* 32, 1222–1232. doi: 10.1038/jcbfm.2012.35

Husson, A., Brasse-Lagnel, C., Fairand, A., Renouf, S., and Lavoinne, A. (2003). Argininosuccinate synthetase from the urea cycle to the citrulline-NO cycle. *Eur. J. Biochem.* 270, 1887–1899. doi: 10.1046/j.1432-1033.2003.03559.x

Institute of Medicine. (2005). *Dietary Reference Intakes for Energy, Carbohydrate, Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids (Macronutrients). Institute of Medicine, Panel on Macronutrients, Standing Committee on the Scientific Evaluation of Dietary Reference Intakes*. Washington, DC: National Academies Press.

Jaubert, J., Lorblanchet, M., Laville, H., Slot-Moller, R., Turq, A., Brugal, J-. P., et al. (1990). *Les Chasseurs d'Auroch de La Borde*. Paris, ed. de la Maison des Sciences del'Homme. doi: 10.4000/books.editionsmsh.36013

Jones, E., Gonzalez-Fortes, G., Connell, S., Siska, V., Eriksson, A., Martiniano, R., et al. (2015). Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat. Commun.* 6:8912. doi: 10.1038/ncomms9912

Kamphuis, M. M., Westerterp-Plantenga, M. S., and Saris, W. H. (2001). Fat-specific satiety in humans for fat high in linoleic acid vs fat high in oleic acid. *Eur. J. ClinNutr.* 55, 499–508. doi: 10.1038/sj.ejcn.1601222

Kelrick, M. I., and MacMahon, J. A. (1985). Nutritional and physical attributes of seeds of some common sagebrush-steppe plants: Some implications for ecological theory and management. *J. Range Manage.* 38, 65–69. doi: 10.2307/3899336

Klaus, S. (2001). *Adipose Tissues*. Georgetown: Eurekah.com/Landes Bioscience. doi: 10.1201/9781498712644

Kuipers, R. S., Luxwolda, M. F., Janneke Dijck-Brouwer, D. A., Eaton, S. B., Crawford, M. A., Cordain, L., et al. (2010). Estimated macronutrient and fatty

acid intakes from an East African Paleolithic diet. *Brit. J. Nutr.* 104, 1666–1687. doi: 10.1017/S0007114510002679

Lazaridis, I., Patterson, N., Mittnik, A., Renaud, G., Mallick, S., et al. (2014). Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* 513, 409–413. doi: 10.1038/nature13673

Lee-Thorp, J., and Sponheimer, M. (2006). Contributions of biogeochemistry to understanding hominin dietary ecology. *Yearb. Phys. Anthropol.* 49, 131–148. doi: 10.1002/ajpa.20519

Levine, E., Collins, V., Varner, S., Williams, G., and Hardenbrook, H. J. (1973). Dietary protein for man and animal. *Ill Vet* 16, 10–14.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., et al. (2009). The sequence alignment/map format and SAMtools. *Bioinforma. Oxf. Engl.* 25, 2078–2079. doi: 10.1093/bioinformatics/btp352

Lu, Q., Tian, X., Wu, H., Huang, J., Li, M., Mei, Z., et al. (2021). Metabolic changes of hepatocytes in NAFLD. *Front. Physiol.* 12:710420. doi: 10.3389/fphys.2021.710420

Mafessoni, F., Grote, S., de Filippo, C., Slon, V., Kolobova, K. A., Viola, B., et al. (2020). A high-coverage neandertal genome from Chagyrskaya Cave. *PNAS* 117, 15132–15136. doi: 10.1073/pnas.2004944117

Mallegni, F., Piperno, M., and Segre, A. (1987). Human remains of Homo sapiens neanderthalensis from the pleistocene deposit of Sants Croce Cave, Bisceglie(Apulia), Italy. *Am. J. Phys. Anthropol.* 72, 421–429. doi: 10.1002/ajpa.1330720402

Mann, N. (2000). Dietary lean red meat and human evolution. *Eur. J. Nutr.* 39, 71–79. doi: 10.1007/s003940050005

Mariotti Lippi, M., Aranguren, B., Arrighi, S., Attolini, D., Benazzi, S., Boschin, F., et al. (2023). New evidence of plant food processing in Italy before 40ka. *Quat. Sci. Rev.* 312:108161. doi: 10.1016/j.quascirev.2023.108161

McArthur, E., Rinker, D. C., and Capra, J. A. (2021). Quantifying the contribution of Neanderthal introgression to the heritability of complex traits. *Nat. Commun.* 12:4481. doi: 10.1038/s41467-021-24582-y

Meshkani, R., and Khosrow, A. (2009). Hepatic insulin resistance, metabolic syndrome and cardiovascular disease. *Clin. Biochem.* 42, 1331–1346. doi: 10.1016/j.clinbiochem.2009.05.018

Morin, E. (2007). Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. *J. Archaeol Sci.* 34, 69–82. doi: 10.1016/j.jas.2006.03.015

Nakamura, M. T., and Nara, T. Y. (2004). Structure, function, and dietary regulation of delta6, delta5, and delta9 desaturases. *Annu. Rev. Nutr.* 24, 345–376. doi: 10.1146/annurev.nutr.24.121803.063211

O'Connell, J. F., and Hawkes, K. (1981). "Alyawara plant use and optimal foraging theory," in *Hunter-Gatherer Foraging Strategies*, eds. B. Winterhalder and E. A. Smith (Chicago: University of Chicago), 99–125.

Onyango, A. N. (2022). Excessive gluconeogenesis causes the hepatic insulin resistance paradox and its sequelae. *Heliyon* 8, 8–12. doi: 10.1016/j.heliyon.2022.e12294

Outram, A. K. (1998). *The identification and palaeoeconomic context of prehistoric bone marrow and grease exploitation* (dissertation). University of Dhuram, Durham, United Kingdom.

Pitts, G. C., and Bullard, T. R. (1968). "Some interspecific aspects of body composition in mammals," in *Body Composition in Animals and Man*. Washington, DC: National Academy of Sciences, 45–70.

Posth, C., Yu, H., Ghalichi, A., Rougier, H., Crevecoeur, I., Huang, Y., et al. (2023). Palaeogenomics of upper palaeolithic to neolithic European hunter-gatherers. *Nature* 615, 117–126. doi: 10.1038/s41586-023-05726-0

Power, R. C., Salazar-García, D. C., Rubini, M., Darlas, A., Harvati, K., Walker, M., et al. (2018). Dental calculus indicates widespread plant use within the stable Neanderthal dietary niche. *J. Hum.* E119, 27e—41. doi: 10.1016/j.jhevol.2018.02.009

Powers-Lee, S. G., and Meister, A. (1988). "Urea synthesis and ammonia metabolism," in *The Liver: Biology and Pathobiology2 2nd Edn*, eds. I. M. Arias, W. B. Jakoby, H. Popper, D. Schachter, D. A. Shafritz (New York, NY: Raven Press), 317–329.

Prüfer, K., de Filippo, C., Grote, S., Mafessoni, F., Korlević, P., Hajdinjak, M., et al. (2017). A high-coverage Neandertal genome from Vindija Cave in Croatia. *Science* 358, 655–658. doi: 10.1126/science.aao1887

Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., et al. (2014). The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* 505, 43–49. doi: 10.1038/nature12886

Ranaldo, F., Arrighi, S., Freguglia, M., Boscato, P., and Ronchitelli, A. (2017). La variabilitàtecnica del Musteriano della Grotta di Santa Croce (Bisceglie - BT). *Studi diPreistoria e Protostoria* 4, 153–158.

Ratnayake, W. M., and Galli, C. (2009). Fat and fatty acid terminology, methods of analysis and fat digestion and metabolism: a background review paper. *Ann. Nutr. Metab.* 55, 8–43. doi: 10.1159/000228994

Robbins, C. T., Felicetti, L. A., and Sponheimer, M. (2005). The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* 144, 534–540. doi: 10.1007/s00442-005-0021-8

Salazar-García, D. C., Power, R. C., Serra, A. S., Villaverde, V., Walker, M. J., Henry, A. G., et al. (2013). Neanderthal diets in central and southeastern Mediterranean Iberia. *Quat. Int.* 318, 3–18. doi: 10.1016/j.quaint.2013.06.007

Schaeffer, L., Gohlke, H., Müller, M., Heid, I. M., Palmer, L. J., Kompauer, I., et al. (2006). Common genetic variants of the FADS1 FADS2 gene cluster and their reconstructed haplotypes are associated with the fatty acid composition in phospholipids. *Hum. Mol. Genet.* 15, 1745–1756. doi: 10.1093/hmg/ddl117

Segre, A. G., and Cassoli, P. F. (1987). "Giacimento preistorico del Pleistocene medio e superiore della grotta di S. Croce, Bisceglie (Bari)," *Proceedings ofthe XXV Riunione Scientifica I.I.P.P. Monopoli*, 111–118.

Simms, S. R. (1987). *Behavioral Ecology and Hunter-Gatherer Foraging*. Oxford, United Kingdom: BAR International Series. 381, 1–157. doi: 10.30861/9780860544937

Sinclair, H. M. (1953). The diet of Canadian Indians and Eskimos. *Proc. Nutr. Soc.* 12, 69–82. doi: 10.1079/PNS19530016

Smith, G., Shankaran, I., Yoshino, M., Schweitzer, M., Chondronikola, G. G., Beals, M., et al. (2020). Insulin resistance drives hepatic de novo lipogenesis in nonalcoholic fatty liver disease. *J. Clin. Investig.* 130, 1453–1460. doi: 10.1172/JCI134165

Spagnolo, V., Marciani, G., Aureli, D., Berna, F., Boscato, P., Ranaldo, F., et al. (2016). Between hearths and volcanic ash: the SU 13 palimpsest of theOscurusciuto rock shelter (Ginosa - Southern Italy): analytical and inter-pretative questions. *Quat. Int.* 417, 105–121. doi: 10.1016/j.quaint.2015.11.046

Speth, J. D. (2010). *The Paleoanthropology and Archaeology of Big-Game Hunting*. New York: Springer. doi: 10.1007/978-1-4419-6733-6

Strik, C. M., Lithander, F. E., McGill, A. T., MacGibbon, A. K., McArdle, B. H., Poppitt, S. D., et al. (2010). No evidence of differential effects of SFA, MUFA or PUFA on post-ingestive satiety and energy intake: a randomised trial of fatty acid saturation. *Nutr. J.* 9:24. doi: 10.1186/1475-2891-9-24

Svensson, E., Günther, T., Hoischen, A., Hervella, M., Munters, A. R., et al. (2021). Genome of Peştera Muierii skull shows high diversity and low mutational load in pre-glacial Europe. *Curr. Biol.* 31, 2973–2983.e9. doi: 10.1016/j.cub.2021.04.045

Sweeting, A., Mijatovic, J., Brinkworth, G. D., Markovic, T. P., Ross, G. P., Brand-Miller, J., et al. (2021). The carbohydrate threshold in pregnancy and gestational diabetes: how low can we go? *Nutrients* 13:2599. doi: 10.3390/nu13082599

Timmermann, A., Yun, K-. S., Raia, P., Ruan, J., Mondanaro, A., Zeller, E., et al. (2022). Climate effects on archaic human habitats and species successions. *Nature* 604, 495–501. doi: 10.1038/s41586-022-04600-9

Veldhorst, M. A., Westerterp-Plantenga, M. S., and Westerterp, K. R. (2009). Gluconeogenesis and energy expenditure after a high-protein, carbohydrate-free diet. *Am. J. Clin. Nutr.* 90, 519–526. doi: 10.3945/ajcn.2009.27834

Vicedomini, R., Righetti, N., Polit, L., Condemi, S., Longo, L., Carbone, A., et al. (2021). Genetic dietary adaptation in Neandertal, Denisovan and Sapiens revealed by gene copy number variation. *bioRxiv [Preprint]*. doi: 10.1101/2021.10.30.466563

Wang, K., Prüfer, K., Krause-Kyora, B., Childebayeva, A., Schuenemann, V. J., Coia, V., et al. (2023). High-coverage genome of the Tyrolean Iceman reveals unusually high Anatolian farmer ancestry. *Cell Genom.* 3:100377. doi: 10.1016/j.xgen.2023.100377

Weasel, L. (2022). How Neanderthals became white: the introgression of race into contemporary human evolutionary genetics. *Am. Nat.* 200, 129–139. doi: 10.1086/720130

Zhang, H., Zhu, Z., Di, Y., Luo, J., Su, X., Shen, Y., et al. (2024). Understanding the triacylglycerol-based carbon anabolic differentiation in *Cyperus esculentus* and *Cyperus rotundus* developing tubers via transcriptomic and metabolomic approaches. *BMC Plant Biol.* 24:1269. doi: 10.1186/s12870-024-05999-1

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., and Chapin, F. S. (2012). Mammoth steppe: a high-productivity phenomenon. *Quat. Sci. Rev.* 57:26e45. doi: 10.1016/j.quascirev.2012.10.005

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Late Neanderthal subsistence and foraging mobility at Lapa do Picareiro: a zooarchaeological and taphonomic analysis of Level JJ

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Recent revisions of Neanderthal behavioral models call into question the notion of inflexible subsistence strategies. Here, we present new zooarchaeological and taphonomic data from Level JJ at Lapa do Picareiro (Portuguese Estremadura), dating to ~51.5–42.5 ka cal BP, to evaluate Neanderthal prey selection, mobility, and adaptive responses to climatic fluctuations during MIS 3. Our zooarchaeological and taphonomic analysis of macro-mammalian faunal assemblages—divided into three stratigraphic subunits—reveals a consistent emphasis on red deer exploitation, supplemented by occasional hunting of ibex, chamois, aurochs, and horse. Despite paleoenvironmental disturbances associated with Heinrich Stadial (HS) 5, the stable abundance and processing of red deer indicate that these key resources remained reliable, supporting a localized foraging territory estimated at 225–400 km². In contrast, the lithic record shows a shift in raw material procurement before and after the climatic event, suggesting adaptive technological responses. Overall, our findings imply that Neanderthals at Picareiro employed brief, intermittent site occupations while maintaining resilient, regionally adapted subsistence and mobility strategies in the face of environmental variability.

KEYWORDS

Neanderthals, taphonomy, zooarchaeology, Iberia, Paleolithic

1 Introduction

Neanderthal behavioral models, particularly in the realm of subsistence, have undergone considerable revision in the last few decades (e.g., Blasco et al., 2022). Earlier views that Neanderthal subsistence was inflexible and narrow in diet breadth (e.g., Straus, 1992; Richards et al., 2000; Grayson and Delpech, 2002; Patou-Mathis, 2000) and that this may have contributed to their demise (e.g., Fa et al., 2013) have been challenged by emerging zooarchaeological evidence at numerous sites tri-peninsular southern Europe (e.g., Blasco and Peris, 2012; Blasco et al., 2016a; Carvalho et al., 2018; Blasco et al., 2022; Finlayson et al., 2012; Peresani et al., 2011; Nabais and Zilhão, 2019; Boneta Jiménez et al., 2025; Cortés-Sánchez et al., 2011; Villa et al., 2020; Nabais et al., 2023; Livraghi et al., 2021; Rendu et al., 2023; Terlato et al., 2019), France (e.g., Hardy and Moncel, 2011; Cochard et al., 2012; Morin and Laroulandie, 2012; Hardy et al., 2013; Pelletier et al., 2019; Daujeard et al., 2017; Marin et al., 2020), the Levant (e.g., Stiner, 1994; Blasco et al., 2016b, 2019; Orbach and Yeshurun, 2021; Yaroshevich et al., 2023;) and elsewhere

in Eurasia (e.g., Evins, 1982; Gaudzinski-Windheuser and Niven, 2009; Van Neer and Wouters, 2009; Darlas and Psathi, 2016; Stepanchuk et al., 2017; Goffette et al., 2024) of a wide array of foraging behaviors and adaptive strategies, from exploiting small game, and marine resources to targeting one or two larger ungulates. This dietary diversity suggests that Neanderthals displayed flexibility in foraging tactics and expertly exploited their surrounding environments, contradicting the idea that limited prey selection had a role in their demise.

In Iberia, where the timing of the last Neanderthal occupations is contentious (e.g., Wood et al., 2013; Higham et al., 2014), prey selection behaviors among Middle and Upper Paleolithic human populations were similar (Altuna, 1992; Straus, 2013; Yravedra, 2013; Marín-Arroyo and Sanz-Royo, 2021) and may have been driven by bioclimatic region (Jones and Carvalho, 2023) and biomass availability (Vidal-Cordasco et al., 2022). Differences in land use and mobility, rather than prey selection, may have been a key behavioral separation between Middle and Upper Paleolithic humans. Perhaps unsurprisingly, scales of analysis influence the patterns observed. Based on cluster and nonmetric multidimensional scaling analyses of anthropogenic faunal assemblages dated 60–30 kya from all over Iberia, Neanderthals and modern human prey selection was similar and influenced by the availability of mammalian taxa in different bioclimatic regions on a peninsular scale (Jones and Carvalho, 2023). Differences in prey selection between the two human populations were hypothesized by the authors to be driven by mobility patterns, wherein Neanderthals had high foraging mobility and shorter site occupation while Upper Paleolithic peoples exploited more localized hunting patches and occupied sites more intensely, for longer durations (Jones and Carvalho, 2023). At the regional scale, however, evidence varies. A converse pattern has been observed in northern Spain (Marín-Arroyo and Sanz-Royo, 2021), with early modern humans highly mobile on the landscape with short occupations at sites while Neanderthals remained at sites for longer durations. In the Iberian Mediterranean basin, however, evidence points to highly mobile Neanderthal populations who left behind accumulations of materials at sites indicative of short duration occupations (Martínez-Moreno et al., 2004; Real et al., 2018; Rosell et al., 2017; Vallverdú et al., 2005; Zilhão and Villaverde, 2008). As in Iberia, variation in Neanderthal foraging mobility throughout Eurasia seems to be shaped by regional environmental and potentially cultural factors (see Marin et al., 2020 and references therein) and fits into two categories proposed by Stiner (2013): high mobility and short-term site occupations or lower mobility and more intensive site occupations. The potential for local adaptations to climate and resource fluctuations suggest detailed, multi-layered site-based analyses could reveal nuances in Neanderthal subsistence, mobility and landscape use not visible at broader geographic scales.

Prey choice offers a valuable lens for reconstructing Neanderthal mobility and land use. The species composition of a faunal assemblage can reflect the habitats Neanderthals exploited for food procurement and has been widely used to infer land use and mobility strategies (e.g., Villaverde et al., 1996; Daujeard et al., 2017; Marín et al., 2019). Investigating the ecological requirements of the taxa selected by Neanderthals allows for the identification of potential habitats in which Neanderthals could find specific prey items. Calculating the distance between the site and the nearest habitat in which a taxon can be encountered results in a minimum subsistence mobility radius that Neanderthals frequented. For example, the presence of ibex (*Capra pyrenaica*) and chamois (*Rupicapra rupicapra*) in an assemblage suggests hunting in alpine or mountainous regions (Acevedo and Cassinello, 2009; Nesti et al., 2010). Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*), particularly when found together, point to movements through forested landscapes. While red deer are ecologically flexible (Straus, 1981; Sommer et al., 2008), their coexistence with roe deer and wild boar in an assemblage strengthens this interpretation (Mauget, 1981; Danilkin, 1995). Aurochs (*Bos primigenius*) are thought to have inhabited semi-open riverine areas (Hall, 2008) and the presence of horses (*Equus* sp.) may indicate exploitation of open, colder habitats (Berger, 1986).

Analyzing the ecological requirements of other hunted taxa in a similar way can then build a wider picture of minimum potential movements made on the landscape by Neanderthals. It is important to consider, however, that Portuguese Estremadura during the Pleistocene did not have the same ecological conditions as today's, however, some habitat types such as altitude, river valleys, are consistent between the Pleistocene and modern times.

For Portuguese Estremadura, where complex landscapes provide access to several ecotonal zones, investigations into subsistence, foraging mobility and landscape use are particularly intriguing. The region is home to numerous well-known Middle Paleolithic sites that have provided information on Neanderthal subsistence, mobility and land use (e.g., Zilhão et al., 2010; Nabais and Zilhão, 2019; Carvalho et al., 2018; Fernández-Laso et al., 2015; Zilhão et al., 2020; Nabais et al., 2023; Haws et al., 2020a). Understanding the prey selection behaviors of Neanderthals provides a multidimensional perspective on Neanderthal lifeways helping to better understand their ecological niche, social organization and survival strategies in dynamic and often challenging environments. For example, evidence of selective hunting or opportunistic foraging can provide clues about their flexibility in survival strategies across different landscapes. It can also provide information past ecological conditions and whether Neanderthals practiced sustainable hunting or over-exploited specific resources, which may have influenced local fauna and ecosystems.

In Portuguese Estremadura, where current understanding of Neanderthal subsistence is both chronologically fragmented and based on only three sites, Neanderthal diets focused mostly red deer and ibex, with inputs from a wide -array of other ungulates and small prey (e.g., Fernández-Laso et al., 2015; Nabais, 2018; Carvalho et al., 2024; Nabais and Zilhão, 2019; Boneta Jiménez et al., 2025; Cardoso and Cascalheira, 2024). The consistent abundance of red deer in these non-contemporaneous anthropic assemblages could reflect stability in the red deer populations. Such stability may relate to the refugial nature of southern Europe and Iberia in particular (e.g., Figueiral and Terral, 2002; Gomez and Lunt, 2007); conversely, it could relate to the ecological flexibility of red deer (e.g., Straus, 1981). Regardless, it suggests Neanderthal hunting was not sufficiently intensive to negatively impact red deer populations.

During MIS 5, however, intensive exploitation of tortoises by Neanderthals evidenced at Gruta da Oliveira may have led to a localized extinction of this food resource at the beginning of MIS 4. This finding supports the notion of large enough Neanderthal population for overexploitation to occur (Nabais and Zilhão, 2019).

Lapa do Picareiro (Figure 1), a Paleolithic cave site situated in mountainous terrain of Estremadura, offers a unique opportunity to investigate these facets of behavior among the last Neanderthals in the region. The site contains a chronologically constrained multi-layer sequence of late Middle Paleolithic occupations with rich faunal assemblages, making it ideal for examining how Neanderthals navigated local landscapes and resources over time. With archaeological evidence spanning multiple occupation phases and accompanied by paleoenvironmental records, Lapa do Picareiro builds upon previous investigations into the relationship between subsistence choices and foraging mobility in Portuguese Estremadura.

This paper contributes to the growing regional record of Neanderthal subsistence and mobility strategies in Portuguese Estremadura by presenting new zooarchaeological and taphonomic data from multiple Middle Paleolithic occupations at Lapa do Picareiro. Using macro-mammalian faunal assemblages from three subunits of Level JJ, the latest Middle Paleolithic deposits at the site, we investigate subsistence and foraging mobility through time. These data are complemented by Picareiro's paleoenvironmental records, which allow for an evaluation of Neanderthal responses to climate change during MIS 3 (Benedetti et al., 2019; Carvalho et al., 2022).

We address the following research questions:

1. How did Neanderthals structure their subsistence at Picareiro, particularly in terms of prey selection?
2. What does the reconstructed Neanderthal subsistence, particularly their contribution to the faunal assemblages and prey choices, reveal about their movements across the landscape?
3. Do we see continuity or change and Neanderthal subsistence and foraging mobility in level JJ at Picareiro if change is observed, can this adaptation be linked to specific climate episodes?

2 Materials and methods

2.1 Study area and site

Portuguese Estremadura, a predominantly karstic region in central Portugal, is a key area for Middle Paleolithic research (Cardoso and Cascalheira, 2024), encompassing sites spanning MIS 5–3, such as Lapa do Picareiro (e.g., Bicho et al., 2003, 2009; Benedetti et al., 2019; Haws, 2006; Haws et al., 2020a, 2021), Gruta do Caldeirão (e.g., Zilhão et al., 2021a), Gruta da Figueira Brava (e.g., Antunes and Cunha, 1992; Raposo and Cardoso, 2000), Gruta da Oliveira (e.g., Zilhão et al., 2010, 2021b), Mira Nascente (e.g., Haws et al., 2020b), and Praia Rei Cortiço (e.g., Haws et al., 2010, 2020b). This region serves as a large-scale ecotone, where diverse marine ecosystems and terrestrial Mediterranean bioclimatic zones overlap (Haws et al., 2010). Its mosaic of montane islands, plains, and valleys supports Thermo- and Meso-Mediterranean vegetation and fauna, fed by the Tagus River Basin, associated drainages, and natural springs (Quézel, 1985).

During the Late Pleistocene, Estremadura was characterized by steppe and open mountain-type habitats, dominated by pine woodlands (González-Sampériz et al., 2010). These environments fluctuated between open and closed forested conditions in response to climatic variability (Carvalho et al., 2022). The region's proximity to the Atlantic Ocean, where ice-rafted debris floated during Heinrich events (Heinrich, 1988), suggests that cold and arid conditions during such events and other stadials could have been extreme, though direct evidence for their severity remains limited.

Neanderthal subsistence in Portuguese Estremadura is poorly understood due to the limited number of archaeofaunal assemblages directly linked to human activity (Nabais, 2018). However, evidence points to a broad diet dominated by cervids, supplemented by ibex and other ungulates such as horse and aurochs. Additionally, Neanderthals exploited small prey like rabbits (Mein and Antunes, 2000; Carvalho et al., 2018), tortoises (Nabais and Zilhão, 2019; Boneta Jiménez et al., 2025), crustaceans (Nabais et al., 2023), mollusks, and other marine resources (Zilhão et al., 2020). It has been suggested that this dietary breadth reflects a decreased need for high mobility strategies (Nabais, 2018).

Prey selection and raw material procurement strategies have led to the hypothesis that Neanderthals in this region practiced residential mobility within relatively restricted territories (Raposo, 1995; Zilhão, 2001). However, the scale of these territories remains poorly defined. A ^{87}Sr isotope study from Gruta da Oliveira and Gruta do Caldeirão suggests Neanderthal territories may have covered ~600 km², while later Upper Paleolithic humans operated within smaller territories of around 300 km² (Linscott et al., 2023). These estimates are based on limited data, and it is unlikely that territory sizes or mobility patterns remained static over tens of thousands of years, particularly given the cycles of climatic change during this period. To better understand the subsistence and foraging mobility of Estremaduran Neanderthals, we need multi-occupation, site-based subsistence records with good chronological control, and stratigraphic integrity to assess the behavioral and temporal variability of Neanderthals.

Lapa do Picareiro (Figure 1) is one such site, located on the west-facing slope of the Serra d'Aire about 100 km northeast of Lisbon. It is the highest-altitude Paleolithic cave site in Portugal (570 m a.s.l.) and lies ~40 km from the modern coastline. Since 1994, excavations have revealed large faunal assemblages, lithic artifacts, and charcoal spanning more than 40 stratigraphic units, covering occupations from the Middle Paleolithic to the Bronze Age (Benedetti et al., 2019; Bicho et al., 2000, 2003, 2006, 2009; Bicho, 2004; Haws, 2006; Haws et al., 2019, 2020a, 2021). Substantial radiocarbon dating with no significant inversions provide robust chronological control for these sequences. The Middle Paleolithic deposits are well-stratified, minimally disturbed, and contain evidence of multiple Neanderthal occupations associated with small lithic assemblages, primarily characterized by discoidal technology (Haws et al., 2020a).

The lithic evidence suggests that most Paleolithic occupations at Picareiro were short-term, potentially due to the site's challenging accessibility, though more intensive occupations occurred during the Magdalenian (Bicho et al., 2003, 2006, 2009; Bicho and Haws, 2012). However, it remains unclear whether the faunal record supports similarly short-term Neanderthal occupations. With one

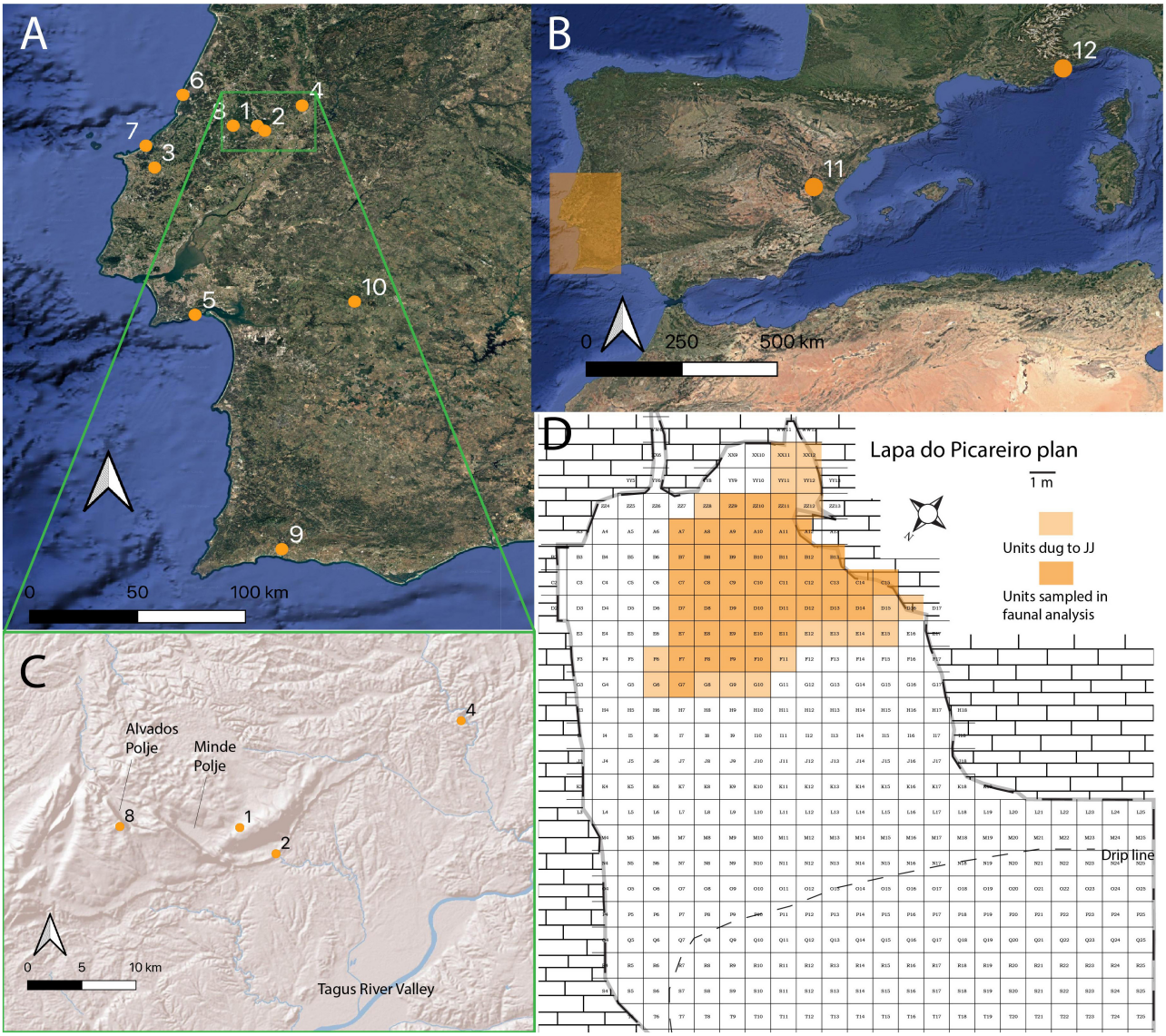

FIGURE 1
(A, B) Map showing the location of sites mentioned in the text: (1) Lapa do Picareiro located on the Serra d'Aire mountain, (2) Gruta da Oliveira, (3) Gruta Nova da Columbeira, (4) Gruta do Caldeirão, (5) Gruta da Figueira Brava, (6) Mira Nascente, (7) Praia Rei Cortiço, (8) Buraca Gloriosa, (9) Gruta da Companheira, (10) Gruta do Escoural, (11) Abrigo de la Quebrada, (12) Grotte du Lazaret. **(C)** Terrain inset map showing local geographic features near Picareiro mentioned in the text. **(D)** Site plan of Picareiro showing were Level JJ has been excavated and what units were sampled for this study.

of the largest Paleolithic faunal assemblages in Portugal, Picareiro has yielded tens of thousands of macro-, meso- and micro-mammal remains from Middle Paleolithic deposits alone. Additionally, abundant remains of birds, amphibians, and micromammals push the total number of skeletal remains even higher. Preliminary taphonomic studies indicate these assemblages were deposited by humans, carnivores, and raptorial birds (Haws et al., 2020a; Carvalho et al., 2023, 2024).

The stratigraphic sequence at Picareiro provides a strong paleoclimate signal. Variations in magnetic susceptibility and clast sizes align closely with the NGRIP curve (50–45 ka) and correspond to deep-sea pollen and sea surface temperature records (Benedetti et al., 2019). Isotopic zooarchaeology has identified Greenland Stadial and Interstadial signals in the sequence (Carvalho et al., 2022), corroborated by speleothem data from Buraca Gloriosa, a cave located <10 km away (Figure 1) (Denniston et al., 2018; Thatcher et al., 2020). Most archaeological horizons at Picareiro can be linked to specific climate events within MIS 3 (Benedetti et al., 2019), making the site ideal for examining how subsistence, foraging mobility, and landscape use responded to climatic downturns.

2.2 Level JJ

The assemblages analyzed in this study come from Level JJ, which represents the last Middle Paleolithic occupations at the

site. This deposit, over 1 meter thick, dates to ∼51.5–42.5 ka cal BP based on radiocarbon assays (Haws et al., 2020a). The lithic assemblage of Level JJ is comprised of primarily flakes and shatter, with few cores and one retouched piece (Haws et al., 2020a). Level JJ contains evidence of multiple Neanderthal occupation phases, with distinct lower and upper lithic horizons separated by a 25 cm-thick layer known as the JJ Dark Layer. This layer, composed of dark reddish-brown, organic-rich sediment, shows a notable decrease in lithic artifacts and faunal remains compared to the deposits above and below.

Picareiro's level JJ offers the opportunity to examine temporal and behavioral variability, as multiple phases of occupation have been observed. Level JJ and its associated faunal assemblages were divided into three subunits: **Lower JJ (LJJ), JJ Dark Layer (JJD)**, and **Upper JJ (UJJ)**, based on concentrations of archaeological materials (see Figure 2). These divisions, supported by stratigraphic integrity and age control, allow for assessments of subsistence and foraging mobility over time.

1. **Lower JJ (LJJ):** The base of Level JJ, ∼62 cm thick, and can be characterized by medium clasts in a matrix of very muddy reddish brown fine sediment (Benedetti et al., 2019). Radiocarbon dates range from 51.5 to 44.1 ka cal BP. This subunit contains a lithic artifact concentration dominated by quartzite, quartz, and chert. Magnetic susceptibility data identifies a signal corresponding to Greenland Interstadial 13 near the top of LJJ. Stable isotope zooarchaeology suggests a temperate forest environment with stable vegetation, transitioning to slightly more forested conditions during this period (Carvalho et al., 2022).
2. **JJ Dark Layer (JJD):** Situated directly above LJJ, this 25 cm-thick subunit contains medium to large clasts in an organic- and clay-rich matrix that is dark reddish brown. It has been radiocarbon dated to 45.4–44.2 ka cal BP. It contains few lithic artifacts ($n = 4$) and limited charcoal remains but thousands of skeletal remains of mammals (ranging from micro- to large-sized), amphibians, and birds. Magnetic susceptibility and isotopic data indicate that JJD formed during Heinrich Event 5, a period of environmental disturbance (Benedetti et al., 2019; Carvalho et al., 2022).
3. **Upper JJ (UJJ):** The top 45 cm of Level JJ contains medium to large clasts in a reddish brown clay-rich matrix. It represents the latest Middle Paleolithic occupation at Picareiro, dating to 44.9–42 ka cal BP. The lithic assemblage is characterized by quartz and quartzite, reflecting a shift in raw material procurement strategies that may indicate adaptation to the climatic instability of Heinrich Event 5 (Carvalho et al., 2022). Magnetic susceptibility data suggests signals for Greenland Stadial/Interstadial phases 12, 11, and 10, while isotopic data indicates fluctuating vegetation regimes, transitioning between open and closed temperate forests (Benedetti et al., 2019; Carvalho et al., 2022).

2.3 Methodology

2.3.1 Excavation methodology

The cave was mapped using a 1 × 1 m grid system. Each unit was excavated according to natural stratigraphy and 5 cm artificial levels within the geologic strata. All artifacts, bones (larger than 2 cm), and features were mapped in three dimensions using a total station. All sediment was sieved through nested 2 and 4 mm mesh screens to separate the finer sediment from the larger fraction which is mostly limestone éboulis. The larger fraction was sorted in the field. The remaining sediment in the 2 mm screen was water-sieved in the laboratory in order to recover small bones, lithics, and macrobotanical remains. This allowed for the recovery of small rabbit and micromammal elements, fish bones, shell fragments, stone chippage, personal ornaments and charcoal.

2.3.2 Zooarchaeological and taphonomic analysis

To reconstruct late Neanderthal subsistence and foraging mobility, we conducted zooarchaeological and taphonomic analyses on a sample of macro-mammalian remains from the three subunits of Level JJ. The skeletal remains analyzed included both *in situ* piece-plotted specimens and those recovered through sieving, with different taphonomic data recorded for each recovery method.

To investigate Neanderthal subsistence at Picareiro, we generated a comprehensive zooarchaeological and taphonomic dataset for the faunal assemblages of each subunit. Prey selection is assessed through species composition of each subunit. Identification of faunal remains was performed at the Interdisciplinary Center for Archaeology and Evolution of Human Behaviour (ICArEHB) at the Universidade do Algarve. Taxonomic and anatomical identifications were made using skeletal reference collections at the ICArEHB OsteoArchaeology Lab, supplemented by digital and printed atlases (e.g., Alimen and Lavocat, 1966; Hillson, 1996; Pales and Lambert, 1971; Schmid, 1972). Data entry was facilitated using the E5 configurable data entry program for archaeology (McPherron, 2022).

For each specimen, we recorded taxonomy, skeletal anatomy, portion, landmarks, and side, identifying remains to the lowest taxonomic level possible. Indeterminate fragments were categorized by morphology and size into large (300+ kg), medium (60–300 kg), or small (30–60 kg) ungulate size groups, based on cortical bone thickness and specimen dimensions.

We used the Number of Identified Specimens (NISP) as the primary analytical unit, following Grayson (1984) and Lyman (2008). Because the Picareiro dataset combines faunal remains from both piece-plotted and sieved material, which were excavated in arbitrary spits, and excavations are ongoing (i.e., the analysis presented here is based on a sample), derived measures like Minimum Number of Individuals or Minimum Number of Elements likely to be misleading. While NISP can also be misleading (in particular, issues of differential fragmentation and diagenesis can artificially inflate its numbers), in datasets with limitations such as the Picareiro dataset has, it is the preferred unit so long as these potential impacts are taken into account in drawing any conclusions (see Discussion in Lyman, 2008).

To distinguish between the contributions of different taphonomic agents, we recorded bone surface modifications and overall bone condition to distinguish what remains were deposited by humans vs. non humans. Observations included both anthropogenic modifications (e.g., cut marks, percussion marks, breakage patterns, fragmentation, and burning)

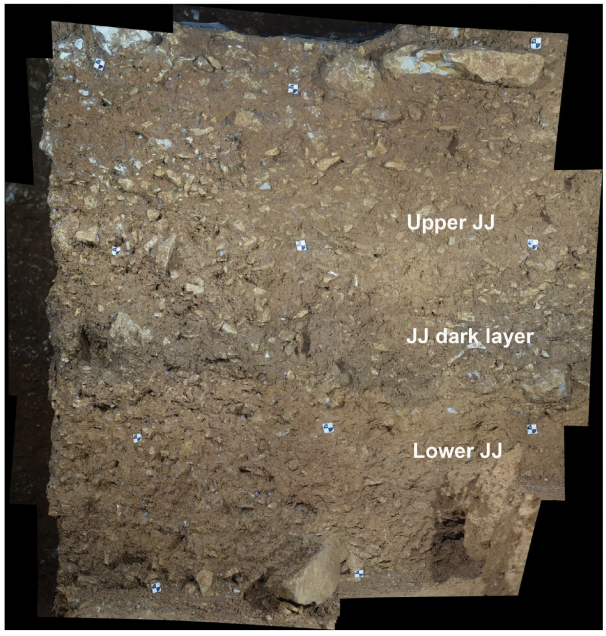

FIGURE 2
Composite image of a stratigraphic profile showing the dark layer in Level JJ.

TABLE 1 Numbers of identified specimens (NISP) and percentages of taxa identified in LJJ, JJD and UJJ units.

Faunal ID	LJJ NISP		JJD NISP		UJJ NISP	
B. primigenius	7	0.60%	2	0.25%	4	0.12%
C. pyrenaica	15	1.29%	1	0.12%	29	0.85%
R. rupicapra	5	0.43%	1	0.12%	8	0.24%
Capridae	16	1.38%	1	0.12%	33	0.97%
C. elaphus	106	9.15%	22	2.71%	197	5.80%
C. capreolus	1	0.09%	2	0.25%	7	0.21%
Cervidae	4	0.35%	1	0.12%	7	0.21%
S. scrofa	5	0.43%			5	0.15%
Equus sp.	5	0.43%	1	0.12%	8	0.24%
L. pardinus	4	0.35%			10	0.29%
F. silvestris	2	0.17%				
Canidae					2	0.06%
V. vulpes	4	0.35%			1	0.03%
Ursus sp.	2	0.17%				
Ind. carnivore					10	0.29%
S ungulate	18	1.55%	1	0.12%	47	1.38%
M ungulate	493	42.54%	658	80.93%	1,900	55.90%
L ungulate	1	0.09%			4	0.12%
S mammal	178	15.36%	16	1.97%	372	10.94%
M mammal	64	5.52%	4	0.49%	243	7.15%
L mammal	1	0.09%			6	0.18%
Indeterminate	228	19.67%	103	12.67%	506	14.89%
Total	1,159		813		3,399	

(Blumenschine, 1988; Pérez Ripoll, 1992; Fisher, 1995) and non-human modifications (e.g., digestive traces from both carnivores and raptorial birds, gnaw marks, and punctures) based on guidelines from Andrews (1990), Cruz-Uribe (1991), Fisher (1995), and Hockett (1996).

Human-related bone surface modifications provide insight into the prey selection behaviors of Neanderthals as well as the carcass processing strategies taking place at the site. Impact and percussion marks were recorded following the guidelines outlined by Vettese et al. (2020), with totals summarized for each subunit. All potential cut marks and burn marks were examined under a Dino-Lite Edge portable microscope (model: MSAM7915MZT) and Nikon microscope (model:SMZ800N). Burn color was recorded only for piece-plotted remains according to Cáceres (2002). Breakage patterns were classified as green, dry, modern and indeterminate fracture types for the most dominant fracture edge type for each specimen but were only recorded for piece plotted remains. Green fractures are indicative of fresh bone breakage during human or carnivore processing while dry fractures signal post-depositional breakage, a common observation in natural accumulations (Villa and Mahieu, 1991).

To assess the degree of fragmentation, which can indicate intensive human manipulation of bones (e.g., Binford, 1978), we measured and categorized piece-plotted remains into five size classes: 0–2.5, 2.5–5, 5–10, 10–20, and >20 cm. This analysis provides insight into the intensity of Neanderthal carcass processing and subsistence behaviors.

Species richness (the number of different taxa in an assemblage) provides insights into diet breadth, while species evenness (the relative abundance of each taxon) can reveal patterns of environmental use and hunting frequency (Jones, 2004). For example, a low evenness value could indicate reliance on a single or dominant prey species, suggesting systematic targeted hunting in specific environments. Conversely, higher evenness might suggest more generalized foraging or seasonal variation in prey choice. Variations in species richness and evenness can also reflect differences in environmental conditions, or broader hunting strategies (Jones, 2004; Grayson and Delpech, 2002; Lyman, 2008; Starkovich, 2017; Stiner, 2001). Assemblages with high evenness might indicate consistence use of diverse habitats, while changes in evenness could suggest shifts in Neanderthal mobility, resource availability or climatic influences. By integrating these measures, we aim to better understand the relationship between Neanderthal subsistence and their movements on the landscape. We assess species evenness through the reciprocal of Simpson's Dominance Index (Simpson, 1949; Faith and Du, 2018).

> *Do we see continuity or change and Neanderthal subsistence and foraging mobility in level JJ at Picareiro if change is observed, can this adaptation be linked to specific climate episodes?*

Besides prey selection, we also assess the continuity (or lack thereof) of carcass processing strategies observed among the subunits. Smaller fragments can be an indicator of greater processing effort or post-depositional fragmentation. We thus assess fragmentation size using a Mann-Whitney U Test for meaningful comparisons between two subunits (VanPool and Leonard, 2011). This test evaluates whether the distributions of fragment sizes differ significantly between groups based on ranks, which is particularly relevant for assessing relative fragmentation intensities. In this analysis we use Mann-Whitney to identify whether more intensive bone processing occurred in specific subunits. We set alpha at 0.05 and used the PAST4 software (Hammer et al., 2001) for all statistical tests.

3 Results

Of the 5,371 specimens analyzed in this study (Table 1), 1,159 came from LJJ, 813 in JJD, and 3,399 in UJJ. The highly fragmented assemblages made identifiability low, with the most abundant taxonomic categories being the M-sized ungulate: 42.5% of the NISP in LJJ, 80.9% in JJD and 55.8% in UJJ fall within this category. Of the remains identified to species or genus level, red deer was the most dominant in all three subunits, representing 9.1% of the LJJ assemblage, 2.7% in JJD and 5.8% in UJJ (Figure 3). Ibex was the second most dominant taxon identified in LJJ (1.4%) and UJJ (5.8%). Lower representations of other ungulates like aurochs, chamois, roe deer, wild boar, and horse were observed in all assemblages. Similar values of the Simpson's reciprocal index in LJJ (1/D = 1.80), JJD (1/D = 1.74) and UJJ (1/D = 1.67) indicate consistent interassemblage evenness.

Carnivore remains are rare. Low incidences of lynx (*L. pardinus*), wild cat (*F. silvestris*), canids, including red fox (*V. vulpes*) and bear (*Ursus* sp.) were identified in the LJJ and UJJ assemblages. No carnivores were identified in the JJD assemblage.

The representation of skeletal elements of ungulate taxa is presented in Table 2 (see Supplementary Table 1 for carnivore skeletal element representation). In the case of ungulates, elements of the appendicular skeleton are the most abundant (Table 2). For the most dominant taxon, red deer, metapodials and podials are the most abundant skeletal elements in all three assemblages (Figure 4), though cranial, axial and appendicular elements are all represented. In addition to the metapodials and podials, in all assemblages, the mandible, humerus, tibia and vertebrae were common in all three assemblages. Red deer scapulae were only encountered in the UJJ assemblage.

The bone surface modifications and breakage patterns typically associated with human (i.e., cutmarks, percussion marks, and burn marks) are present in all three assemblages to varying degrees (Table 3; Figure 5). The highest incidence of cutmarked specimens was observed in LJJ (2.4% of NISP), followed by UJJ (1.7%) then JJD (0.5%). In the JJD assemblage, cutmarks are only observed on red deer and in the medium-sized mammal and ungulate categories. In addition to red deer, cutmarks were encountered on aurochs and horse specimens in the LJJ and UJJ assemblages and ibex and chamois in UJJ (Figure 6). In the assemblages, cutmarks are most frequent on the appendicular and cranial portions of the skeleton, with cutmarks observed on a few ribs and thoracic vertebrae in the *C. elaphus* and medium taxon size category (Supplementary Table 2). Supplementary data on the frequency of cutmarks by skeletal element is available in Supplementary Table 2.

Percussion marks (notches, conchoidal fractures, etc.) were the most common anthropic marker encountered in the assemblages, with the highest incidences occurring in LJJ (4.8%), followed by UJJ (3.5%) and <1% of the JJD assemblage showing percussion marks. In all three assemblages red deer, small and medium sized mammal specimens showed the most evidence of percussion (Figure 7). Burning was the least common anthropic bone surface modification, with <1% of total NISP of each assemblage showing any evidence of burning (Figure 8). Of the plotted specimens with recorded burn color and stage, two exhibited stage 2 (brown), five showed stage 3 (black, charred), and one displayed stage 4 (gray). Anthropic bone surface modifications on red deer are most observed on the appendicular elements and mandibles, with occasional anthropic marks observed on the axial portion of the skeleton (Figure 9).

The assemblages are all highly fragmented (Figure 10). The Mann-Whitney U test showed no significant results (LLJ to JJD: $U = 2.5$, $p = 0.1316$, $r = 0.17$; JJD to UJJ: $U = 2$, $p = 0.1034$, $r = 0.08$; LJJ to UJJ: $U = 6.5$, $p = 0.2492$, $r = 0.045$; a Bonferroni correction was applied for all tests). Breakage patterns are dominated by green fractures in all assemblages, with more than 60% of the piece plotted remains showing green fractures and roughly 20% showing dry fractures (Figure 11) in all subunits.

Non-human bone surface modifications were encountered in small quantities, with similar proportions in the JJD and UJJ assemblages (Table 4; Figure 5), with the highest frequencies of non-human marks in LJJ (2.5% punctures, 1.2% gnawing, 3.6% digested).

4 Discussion

4.1 How did Neanderthals structure their subsistence at Picareiro, particularly in terms of prey selection?

The results presented here suggest that Neanderthals contributed significantly to the formation of the faunal assemblages at Picareiro, although non-human processes also played a lesser role in JJD and UJJ. Non-human modifications, such as punctures and digested remains, were most prevalent in the LJJ assemblage, though in small quantities. Generally, the higher frequency of anthropic marks compared to non-human indicators in the assemblages suggests that humans were the primary agents in shaping their accumulation.

The level JJ assemblages at Picareiro also displayed similar species richness and evenness, suggesting similar taxonomic composition. Prey selection during the late Middle Paleolithic at Picareiro is preferential toward red deer across all three occupation phases. Red deer remains showed consistent evidence of anthropic modification, reflecting a potential preference for the prey item typically observed among Neanderthals at Iberian sites (e.g., Straus,

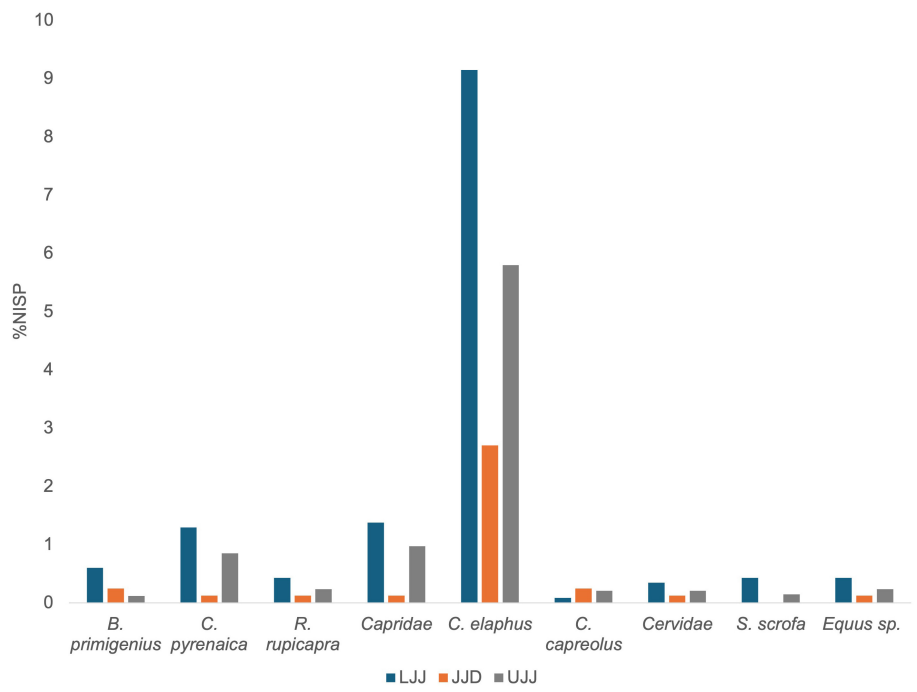

FIGURE 3
%NISP of ungulate taxa identified in the LJJ, JJD, and UJJ assemblages. Ungulate taxa identified were *B. primigenius* (aurochs), *C. pyrenaica* (Pyrenean ibex), *R. rupicapra* (chamois), *C. elaphus* (red deer), *C. capreolus* (roe deer), *S. scrofa* (wild boar), and *Equus sp.* (horse sp.).

2013; Marín et al., 2017; Marín-Arroyo and Sanz-Royo, 2021; see also references in Carvalho et al., 2022). Though a slight preference for red deer by Neanderthals seems evident at Picareiro, given that the small- and medium-sized categories also displayed high incidence of anthropic marks in all three subunits and the high degree of fragmentation observed in the assemblages, it is possible future proteomic and zooarchaeological analyses will increase the proportions of non-red deer ungulates into their diet. It is also possible future proteomic and zooarchaeological analysis of the heavily fragmented portion of the assemblage reflects a higher incidence of red deer, demonstrating a hunting strategy that is heavily focused on one prey item like that identified at sites in more northern latitudes where reindeer dominate assemblages (80–90% of NISP) (e.g., Costamagno et al., 2006; Discamps and Faivre, 2017; Rendu et al., 2023). Though rare, other ungulates also displayed anthropic bone surface modifications in all subunits, suggesting supplementation of a red deer-focused diet by aurochs, ibex, chamois, and horse. Currently, small and medium-sized categories do not provide much insight into prey selection.

At Picareiro, if the preference for red deer as a dietary resource is confirmed with future data, this would be indicative of a hunting behavior characterized by selection and not opportunism. The concept of selection refers to a human population's ability to recognize its needs and devise targeted strategies to meet them effectively (Rendu, 2022). This process involves anticipating future requirements, planning activities and utilizing appropriate technological tools to achieve these objectives (Rendu, 2022). Thus, at Picareiro, it seems that late Neanderthals occupying Picareiro had knowledge of the presence of red deer populations in this area, and perhaps visited the site in part to exploit this resource. The riverine valleys to the south of Picareiro, intermontane valleys, temperate forested environments (Carvalho et al., 2022), and polje that may have been a paleolake during the Late Pleistocene (Rodrigues, 1991) may have supported relatively stable red deer populations that Neanderthals could exploit within a 20 km radius of the site. On the other side of the coin, if future data suggest no preference for red deer but an exploitation of various ungulates in equal or similar proportions, an opportunistic hunting strategy would be assumed. Given Picareiro's location in an ecotone with proximity to various habitats, it could be that Neanderthals visited the site as a camp to exploit diverse hunting patches.

The skeletal representation across all taxonomic categories is dominated by appendicular elements, with cranial fragments being less frequent and axial elements rarely present. For red deer, the most abundant taxon and the one showing the highest incidences of anthropic bone surface modifications, this pattern holds true (Figure 9). This suggests that the appendicular skeleton, which includes meat-rich and marrow-bearing parts, was frequently transported to the cave for processing and consumption. Cranial fragments, which are nutrient and calorie rich, were also brought to the cave.

Axial elements are nearly absent across all ungulate taxa, with only one or two specimens identified for horse and wild boar, and slightly more for red deer (Table 1). This pattern may reflect selective transport of high-utility body parts to the cave, as carrying whole carcasses up the steep terrain would have been challenging. However, zooarchaeological studies emphasize that skeletal element abundances must be evaluated in light of density-mediated attrition, as post-depositional processes can heavily bias skeletal representation. Low-survival elements such as vertebrae

TABLE 2 Number of identified specimens of skeletal element representation of the ungulate taxa identified in the LJJ, JJD, and UJJ assemblages.

	B. primigenius			*C. pyrenaica*			*R. rupicapra*			*C. elaphus*			*C. capreolus*			*S. scrofa*			*Equus* sp.		
Element	LJJ	JJD	UJJ	LJJ	JJD	UJJ	LJJ	JJD	UJJ	LJJ	JJD	UJJ	LJJ	JJD	UJJ	LJJ	JJD	UJJ	LJJ	JJD	UJJ
Crania				3						5		2									
Mandible	1					5			1	8	1	13			1	1			1	1	
Teeth	1		2	7		15	3		3	36	7	46	1	2	3	2		3	2		2
Hyoid	1											1									
Atlas										1		1									
Axis										2	1										
Cervical										3		3									1
Thoracic										3		3									
Lumbar										2		2									
Sacrum																					
Indet. vertebra												1									2
Rib										3		12				1		2	1		
Sternabra																					
Scapula												7									
Humerus	2			1						3	1	14			2						
Radius									1		1	7									
Ulna										1		2									
Radioulna																					
Metacarpals				1		1	1		1	5	1	16									
Carpals						1				1		1									
Innominate				1						5	1					1					
Femur	1			1		3				7		16									
Patella							1														
Tibia	1		2					1	1	4	1	18			1			1	1		1
Metatarsals						1				7	4	14									
Tarsals						1				1		2									
Long bone fragments										3	1	5									
Indet. metapodia										2		8									
Phalanges		2		1	1	2			1	4	2	3									2
Sesamoids											1										
Total	7	2	4	15	1	29	5	1	8	106	22	197	1	2	7	5	0	6	5	1	8

Skeletal representation of all taxa identified to lower taxonomic level can be found in Supplementary material.

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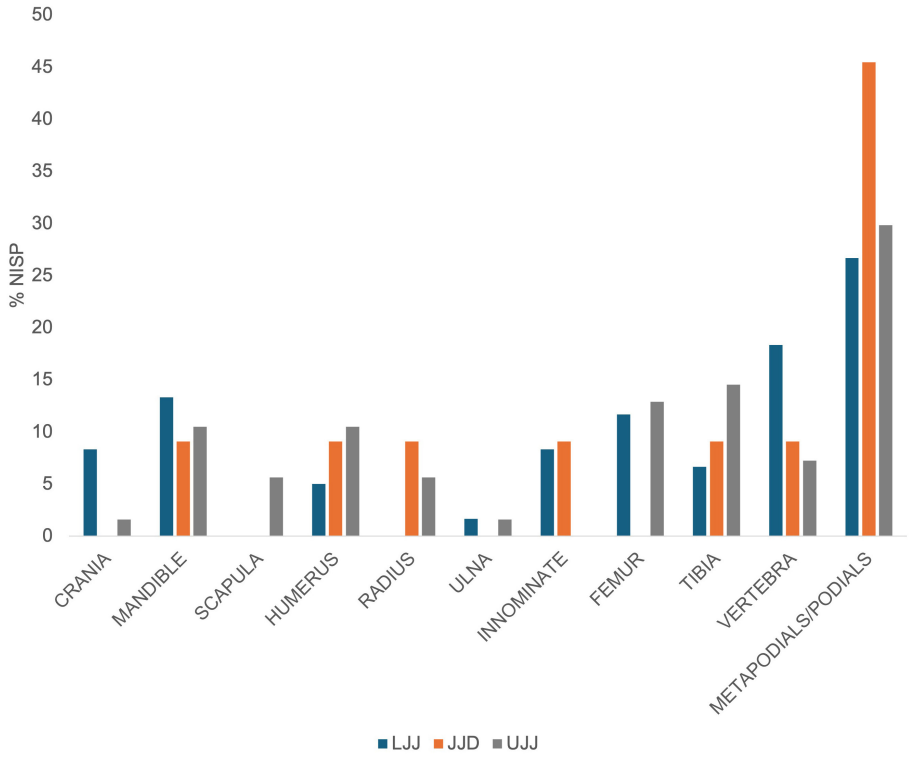

FIGURE 4
%NISP of aggregated skeletal element representation of *Cervus elaphus*.

and ribs are highly susceptible to weathering, microbial decay, and mechanical destruction from trampling, significantly reducing their likelihood of preservation (Lyman, 1994, 2021; Stiner, 2002; Faith and Thompson, 2018). This attritional overprint can obscure original transport decisions, meaning that the skeletal pattern observed at Picareiro may not solely reflect human selection. While carnivore modifications are not frequent in the assemblage, gnawing and digestion traces suggest that occasional scavenging may have further contributed to the depletion of fragile axial elements. Despite this, the presence of elements representing the entire red deer skeleton at Picareiro indicates that whole carcasses may have occasionally been brought to the cave. Even so, given the potential effects of post-depositional attrition, we focus our behavioral interpretations primarily on high-survival skeletal elements to minimize taphonomic bias. The palimpsestic nature of the site may also contribute to the observed pattern, as repeated occupations could have resulted in differential preservation and secondary displacement of skeletal elements.

Analysis of anthropic bone surface modifications at Lapa do Picareiro reveals various carcass processing activities. Cutmarks are most frequently observed on meat-rich limb elements (Supplementary Table 2), suggesting meat fileting and stripping (e.g., Binford, 1978, 1981; Bunn et al., 1986; Dominguez-Rodrigo, 1997). Cranial fragments with cutmarks indicate attempts to access nutrient- and fat-rich resources, such as the brain (e.g., Lyman, 2005). Mandibular cutmarks on red deer, aurochs, and ibex suggest butchering focused on tongue and cheek meat extraction (e.g., Dominguez-Rodrigo, 1997) or as part of the marrow extraction process (Blumenschine and Marean, 1993). Less commonly, cutmarks on an ibex phalanx and a red deer incisor root suggest specialized butchery practices. Cutmarks on phalanges, which are low-yield elements with little muscle tissue, may indicate hide removal (Binford, 1981) or intensive carcass processing (Lyman, 2005). Similarly, cutmarks on tooth roots are rare but may reflect removal of mandibular or maxillary flesh, particularly tongue and cheek meat, leaving traces on the mandible, maxilla, and occasionally the tooth roots (e.g., Dominguez-Rodrigo, 1997).Cutmarks on red deer and medium-sized taxa ribs suggest activities related to fileting and meat removal (e.g., Binford, 1981), trimming fat or sinew (Lupo and O'Connell, 2002), or accessing internal organs.

TABLE 3 Number of identified specimens displaying presence of cutmarks, percussion marks, or burn marks in the LJJ, JJD, and UJJ assemblages.

	Cutmarks		Percussion		Burnmarks		Total	
Sublevel	NISP	%	NISP	%	NISP	%	NISP	%
UJJ	57	1.7	119	3.5	22	0.6	198	5.8%
JJD	4	0.5	7	0.9	7	0.9	18	2.2%
LJJ	28	2.4	56	4.8	3	0.3	87	7.5%

At Picareiro, the presence of cutmarks on meat- and nutrient-rich portions of the skeleton suggests that Neanderthals had primary access to carcasses, rather than scavenging remains left by

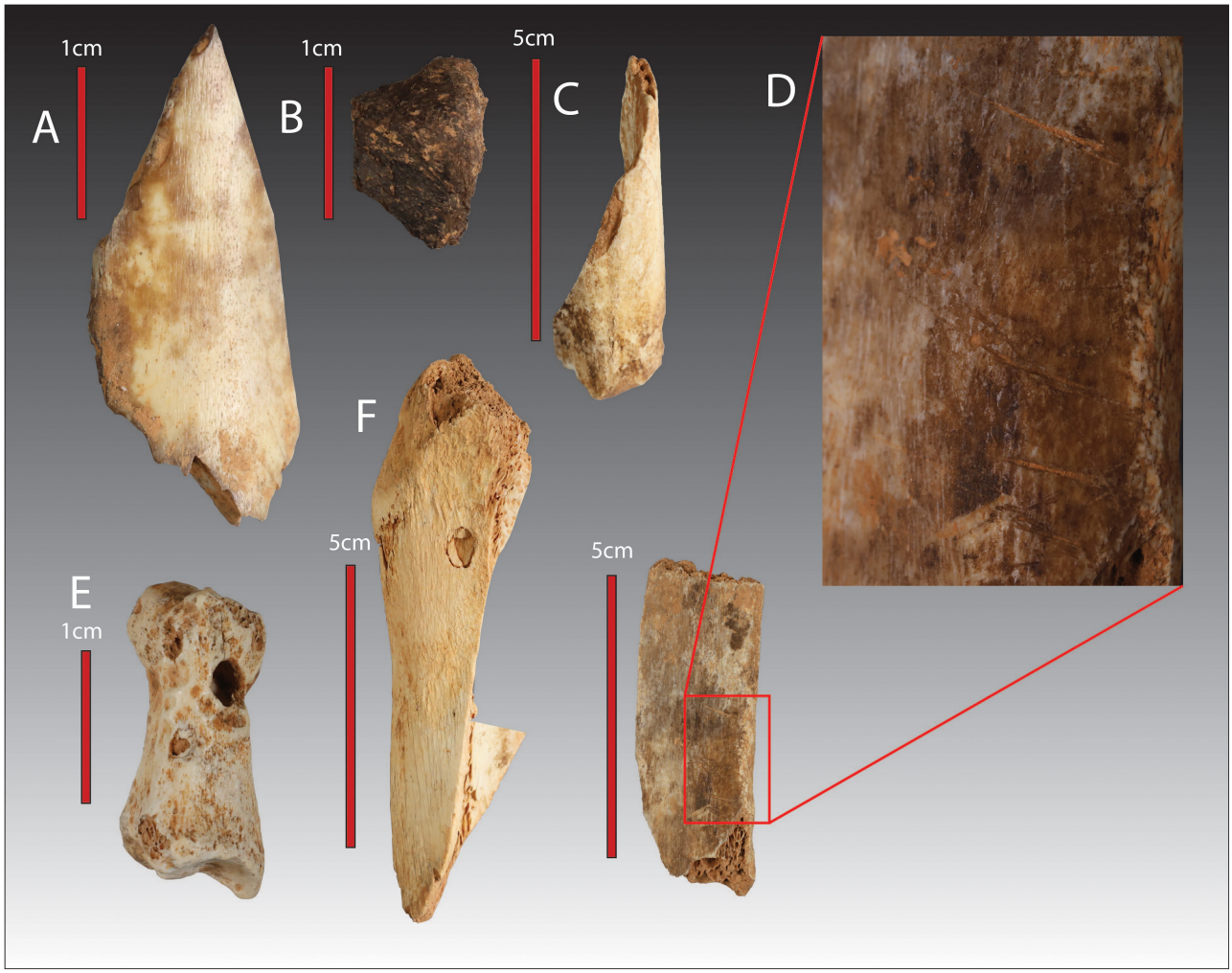

FIGURE 5
Types of bone surface modifications typically encountered in the Level JJ assemblages. **(A, B)** Burned bones (different stages of burning); **(C)** Percussion mark and green spiral fracture; **(D)** Cutmarks on rib fragment; **(E)** Punctured and digested phalanx; **(F)** Crush mark resulting in a puncture.

other predators. However, both ethnographic and archaeological evidence indicate that butchery strategies varied significantly, depending on environmental conditions, dietary needs, and cultural preferences (e.g., Dominguez-Rodrigo, 1997; Lyman, 2005; Lupo and O'Connell, 2002). On-going analyses on cutmark location and morphology will help unravel carcass exploitation and transport strategies.

Archaeological and ethnographic evidence points to humans as primary depositional agents in assemblages with processed long bones and skulls to extract marrow and contents of the brain cavity (e.g. Blumenschine, 1995; Blumenschine and Marean, 1993; Dominguez-Rodrigo, 1997). Percussion marks, typically associated with marrow extraction activities (see Discussion in Vettese et al., 2020) were identified in all three subunits indicating that Neanderthals at Picareiro maximized their calorie intake from these carcasses.

Evidence of burning which can be an indicator roasting or using bone fuel (e.g., Binford, 1978; Costamagno et al., 2006; David, 1990) is severely limited. Of the piece plotted remains where burning color or stage are recorded, two brown specimens (Stage 2) indicated exposure to low-temperature fires (200–300°C) which may be indicative of low-intensity or indirect heat exposure, five charred black (stage 3) specimens suggesting exposure to fires with moderate heat (300–500°C), and one gray calcined (stage 4) bone that was burned at higher temperatures (~600°C and above) (Cáceres, 2002). With such scarce data, little can be said about whether burn marks observed in the Picareiro assemblage relate to intentional cooking activities or simply their proximity to fires. Spatial analysis and categorization of the burned specimens encountered during sieving will be critical for resolving this issue, but at this time, we cannot confidently interpret these remains as being a result of anthropogenic burning.

The slightly higher frequencies of red deer exploitation at Picareiro mirrors other Neanderthal-affiliated zooarchaeological assemblages in Portuguese Estremadura where red deer is the taxon that is most exploited (e.g., Cardoso et al., 2002; Zilhão et al., 2010; Brugal and Raposo, 1999). However, given the very limited and temporally fragmented subsistence record in the region, whether this is a regional pattern needs further investigation through the analysis of Neanderthal-affiliated zooarchaeological assemblages

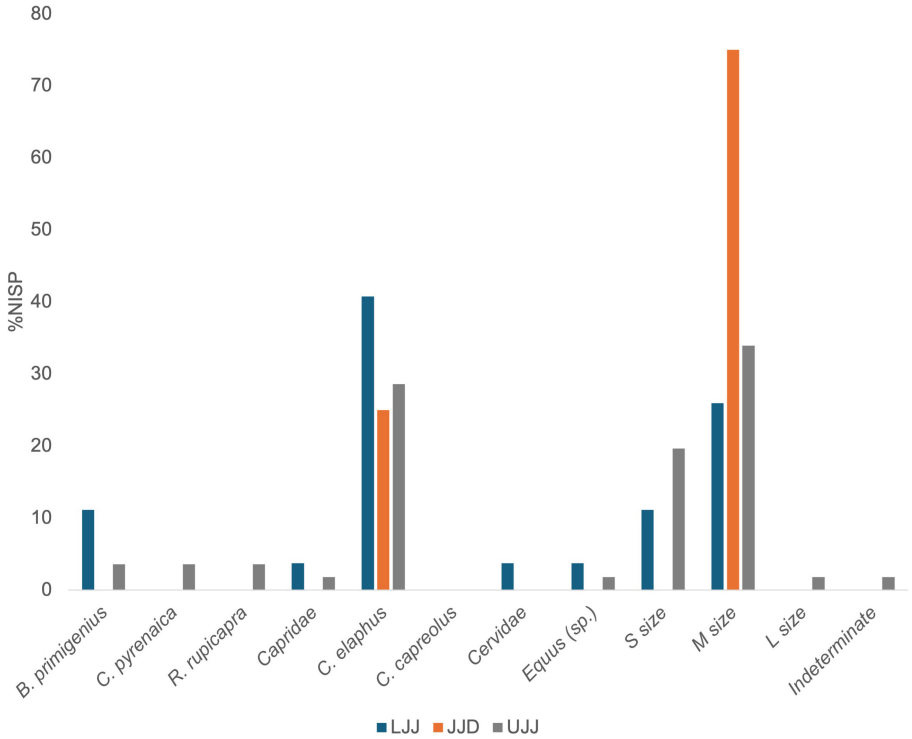

FIGURE 6
%NISP carrying cutmarks by taxon. Cutmarks were encountered on *B. primigenius* (aurochs), *C. pyrenaica* (Pyrenean ibex), *R. rupicapra* (chamois), *C. elaphus* (red deer), *C. capreolus* (roe deer), *S. scrofa* (wild boar), *Equus sp.* (horse sp.), cervids, caprids, small, medium and large ungulates, and indeterminate fragments.

from other sites. Picareiro is unique, however, in that its faunal assemblages relating to the Middle Paleolithic studied thus far show no evidence of extinct Pleistocene fauna which are present at Gruta da Oliveira, a site located on the other side of the Serra d'Aire, during MIS5 (Zilhão et al., 2010). In addition, preliminary results of an ongoing analysis of meso-fauna from Level JJ at Picareiro (Carvalho et al., 2023, 2024) indicate that with the exception of rabbits, exploitation of other small prey items such as tortoises or aquatic taxa by Neanderthals have not been identified thus far. This is in stark contrast to sites like Figueira Brava and Gruta da Oliveira, where regular exploitation of tortoises and marine prey by Neanderthals has been identified (e.g., Nabais et al., 2023; Nabais and Zilhão, 2019; Zilhão et al., 2020). Future analyses at Picareiro and recently excavated sites like Gruta da Companheira (e.g., Barbieri et al., 2023) and Gruta do Escoural will provide a better picture on Neanderthal subsistence behaviors in westernmost Iberia.

Neanderthals at Picareiro appear to have targeted prey similar to that found at other Iberian sites, primarily focusing on equids, cervids, and caprids. This pattern seems largely driven by the availability of these animals in the surrounding landscape (e.g., Eixea et al., 2020; Marín-Arroyo and Sanz-Royo, 2021; Yravedra et al., 2016; Nabais, 2018; Sánchez-Hernández et al., 2020a,b). For example, red deer are often the most common taxon in zooarchaeological assemblages across many Iberian regions (e.g., Blasco, 2008; Blasco and Peris, 2012; Salazar-García et al., 2013; Marín-Arroyo and Sanz-Royo, 2021; Ruiz et al., 2021; Yravedra et al., 2016). In contrast, sites in high-altitude alpine settings frequently exhibit a dominance—or even a specialization (exceeding 70% of the assemblage)—of either ibex or chamois (e.g., Yravedra et al., 2014; Real et al., 2019; Yravedra and Cobo-Sánchez, 2015; Yravedra, 2013). Additionally, in more open Pleistocene environments, such as at Abrigo de la Quebrada in Valencia, there is a clear preference for equid remains (Real et al., 2019). These observations support the hypothesis that, like other Neanderthal groups across Iberia, those at Picareiro exploited locally available fauna, with their prey selection primarily influenced by the immediate environmental context (see Discussion in Jones and Carvalho, 2023).

4.2 What does the reconstructed Neanderthal subsistence reveal about their movements across the landscape?

Assessing the duration of site occupations often involves analyzing site formation processes and the density of archaeological materials, the presence of living floors or structures, and the types of modifications observed on those materials (e.g., Stiner, 2013; Marín et al., 2019). However, most archaeological sites are palimpsests—composites of materials accumulated through repeated occupations rather than discrete single events (Bailey, 2008; Bailey and Galanidou, 2009), meaning that distinguishing

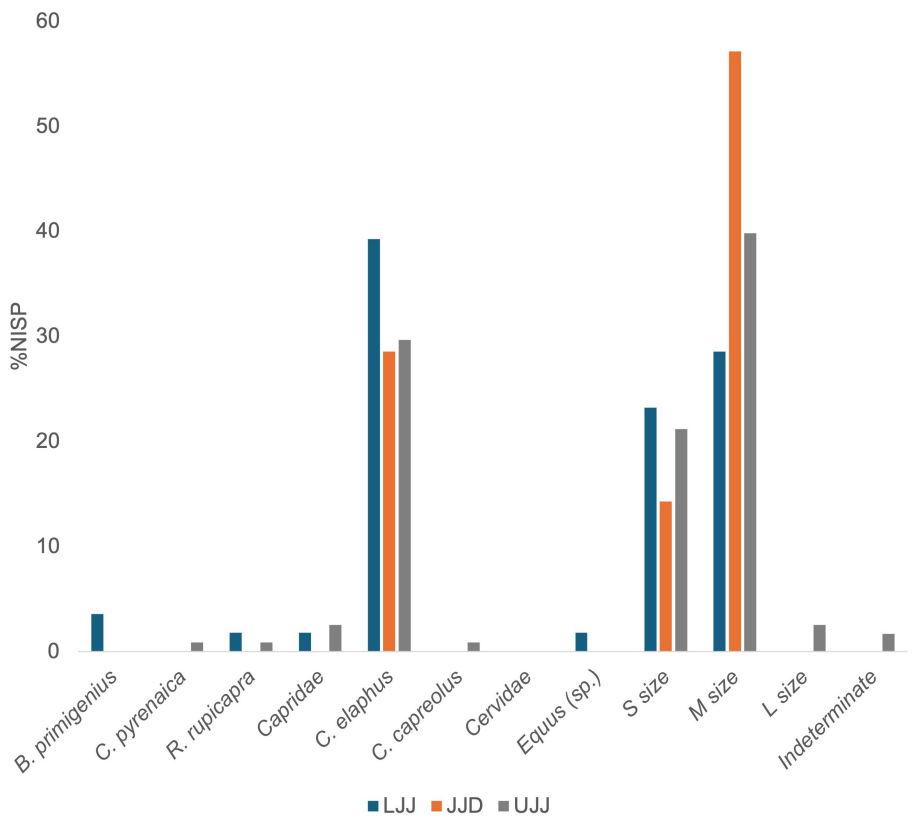

FIGURE 7
%NISP carrying percussion mark by taxon. Percussion marks were encountered on were encountered on *B. primigenius* (aurochs), *C. pyrenaica* (Pyrenean ibex), *R. rupicapra* (chamois), *C. elaphus* (red deer), *C. capreolus* (roe deer), *S. scrofa* (wild boar), *Equus sp*. (horse sp.), cervids, caprids, small, medium and large ungulates, and indeterminate fragments.

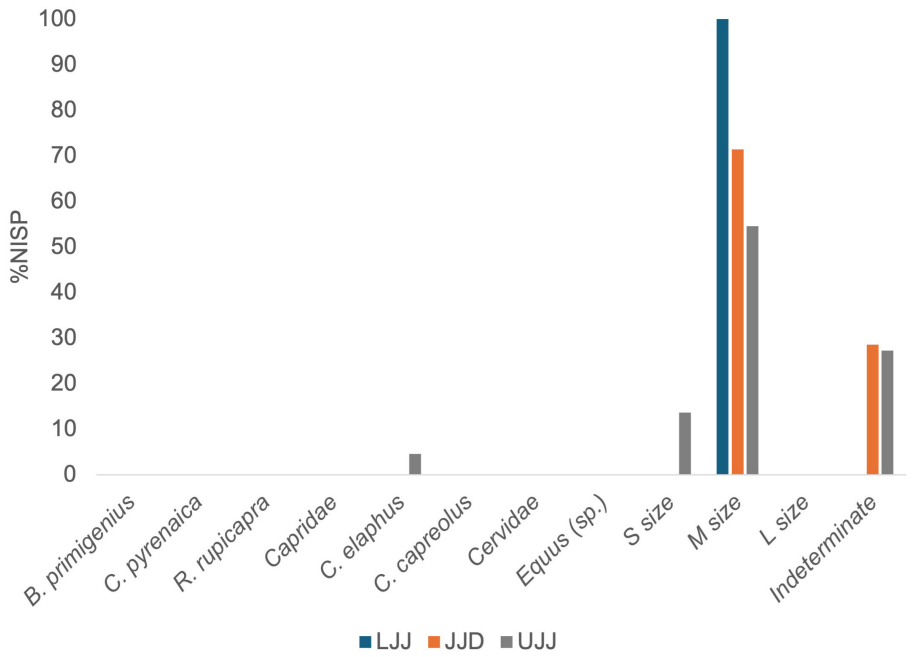

FIGURE 8
%NISP carrying burn marks by taxon. Burn marks were only encountered on *C. elaphus* (red deer), small medium and large ungulate categories, and indeterminate fragments.

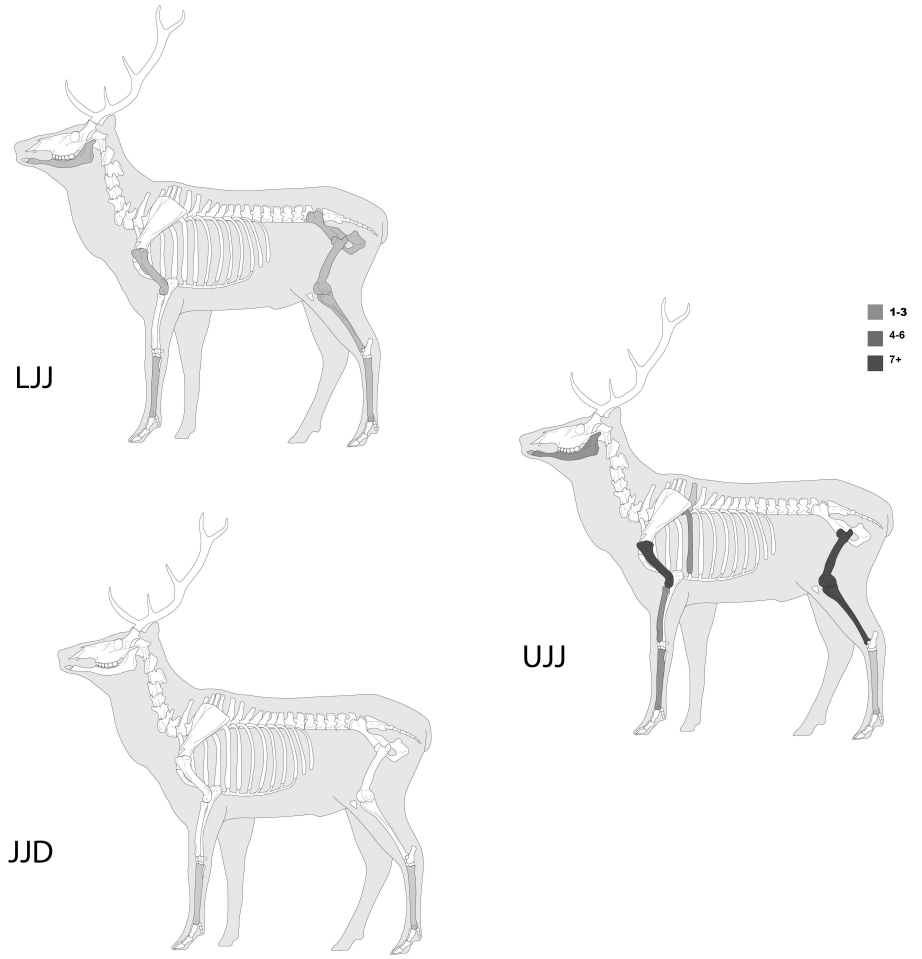

FIGURE 9
Schematic showing the frequency of red deer elements with anthropic modifications (cut marks, burning, or percussion marks) in LJJ, JJD, and UJJ. Only specimens with anthropic modifications are represented.

between short- and long-term occupations isn't straightforward, and requires multiple lines of evidence (Moncel and Rivals, 2011). Lithic indices proposed for assessing site occupation durations based on tool the presence of retouched tools (Riel-Salvatore and Barton, 2004) have shown contradicting results (Bicho and Cascalheira, 2020), demonstrating the need for multiple lines of evidence.

At Lapa do Picareiro, the evidence for occupation appears somewhat contradictory. The small lithic assemblage from Level JJ—dominated by flakes, some shatter, and very few formal or retouched tools (Haws et al., 2020a)—suggests a low-density human presence. Moreover, the predominance of flakes over other tool types may indicate a segmented chaîne opératoire, a pattern often associated with short-term occupations (Naudinot and Marchand, 2020), where a more segmented sequence typically reflects briefer site use. However, further detailed lithic analyses are needed at Picareiro to confirm this interpretation.

In addition, the limited input from both humans and non-human agents (such as carnivores and predatory birds), along with the presence of carnivore taxa within the assemblages, supports the idea of intermittent human activity interspersed with animal use of the cave. This, combined with the general absence of features like stacked hearths, structures, or living floors—elements that would signal more intensive, long-term occupation—reinforces the hypothesis that the cave was used for relatively short durations.

It is important to note, however, that the site's low sedimentation rate (0.1–0.3 mm a^{-1}; Benedetti et al., 2019) indicates a palimpsest deposit. Thus, additional spatial, lithic, and geoarchaeological data are required to conclusively determine the duration of occupations at Picareiro. Based on the current evidence, we hypothesize that the occupations were brief rather than intensive.

Neanderthal prey selection at Picareiro reflects a primarily local mobility strategy center on exploiting the site's location in an ecotonal environment. Red deer, the dominant prey species across all subunits, though sometimes used as indicator of forested environments, have been shown to display dietary and ecological flexibility, foraging in riverine valleys, forests and alpine environments during the winter (Schmid, 1972; Hofmann, 1989; Fonseca, 1998; Azorit et al., 2012; Berlioz et al., 2017; Gebert and Verheyden-Tixier, 2001; Sánchez-Hernández et al., 2020a,b; Straus, 1981). The location of Picareiro (Figure 1) fits this description

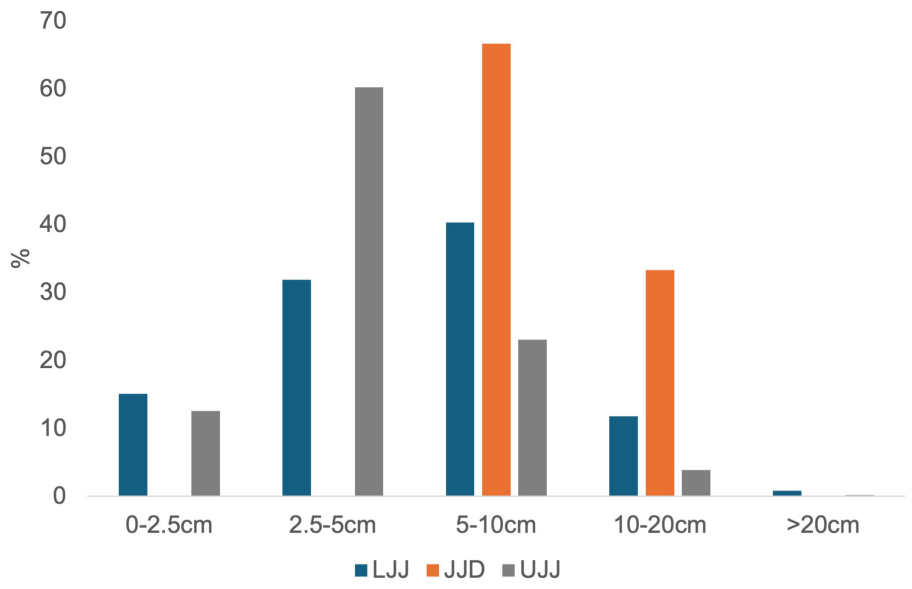

FIGURE 10
Percentage of piece plotted remains identified per specimen size category of LJJ, JJD, and UJJ assemblages.

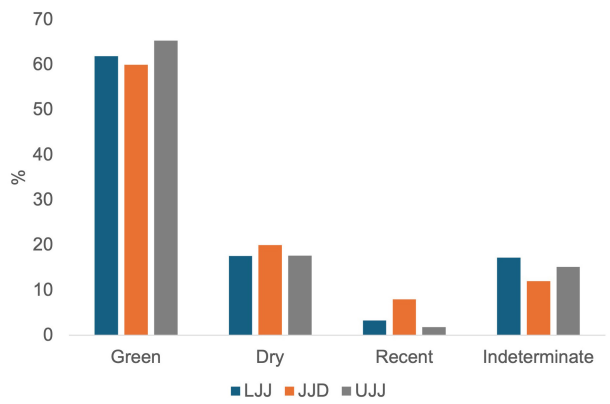

FIGURE 11
Percentage of piece plotted remains in breakage pattern profiles categories in LJJ, JJD, and UJJ assemblages.

TABLE 4 Number of identified specimens displaying the presence of punctures, gnawing, digestion and carnivore scoring.

	Puncture		Gnawing		Digested		Scoring	
Sublevel	NISP	%	NISP	%	NISP	%	NISP	%
UJJ	54	1.6	21	0.6	42	1.2	1	0.02
JJD	5	0.6	1	0.1	4	0.5		
LJJ	29	2.5	14	1.2	42	3.6	3	0.3

as it is characterized by a large-scale ecotone with mountainous, valleys and plains. Several water sources, the Poljes of Mira-Minde (>5 km away) and Alvados (20 km away), and the Tagus river valley and its tributaries could have supported red deer and other ungulate populations.

Red deer populations are generally sedentary, with some modern populations migrating seasonally to access food, reduce competition, or avoid snow in higher latitudes (e.g., Mysterud et al., 2011). However, archaeological evidence suggests that such movements were relatively limited in the past (Steele, 2002). ^{87}Sr analysis of red deer from MIS 6 at Lazaret Cave (France) indicates that while some individuals moved seasonally, their travel distances did not exceed 20 km (Barakat et al., 2023). In Portuguese Estremadura, similar ^{87}Sr studies further support the presence of red deer year-round during MIS 5, with no evidence of long-distance migration (Linscott et al., 2023). Given the c. 680 m elevation of the Serra d'Aire, any localized movements by red deer in this region were likely minor and driven by food availability rather than adverse climatic conditions (Linscott et al., 2023). If red deer populations were present year-round during both MIS 5 and MIS 3, this continuity suggests a longstanding healthy demography among Pleistocene red deer populations in the region, with localized groups persisting in the region across climatic fluctuations. These findings indicate that Neanderthals at Picareiro had a stable and predictable red deer resource throughout the year, reinforcing the interpretation that this species played an important role in their subsistence strategy.

The presence of ibex and occasional chamois in the assemblages suggests that Neanderthals may have frequented mountainous environments to hunt these species (Acevedo and Cassinello, 2009; Nesti et al., 2010). While ibex has been found at Paleolithic sites in Iberia across a range of settings, from montane to coastal environments, chamois are typically associated with steeper, high-altitude habitats (Yravedra and Cobo-Sánchez, 2015). Although Neanderthals specialized in hunting alpine taxa in classic rocky, high-altitude settings, sites where ibex and chamois appear in smaller frequencies do not necessarily

need to be mountainous (Yravedra and Cobo-Sánchez, 2015), as seen at Picareiro. Nevertheless, the inclusion of these taxa in the assemblage raises the possibility of movements to local mountainous areas such as the Serra d'Aire, where Picareiro is located, or to other nearby ranges like Montejunto or Serra da Estrela, situated 30–40 km southwest and northeast of the site, respectively.

The presence of aurochs and horse among the anthropic remains suggests that Neanderthals ventured into more open environments to hunt these species. Aurochs, which typically forage in low-lying, semi-open riverine areas (Hall, 2008), may have drawn Neanderthals to the riverine plains of the Tagus, located approximately 10–15 km southeast of the site. Horses, on the other hand, could have been encountered in nearby patches of open landscapes, as Portuguese Estremadura during the Late Pleistocene was characterized by steppe-like vegetation and open mountain habitats dominated by pine woodlands (González-Sampériz et al., 2010). Isotopic zooarchaeology indicates that this region fluctuated between mosaics of semi-closed forests, open vegetation, and much drier steppe environments over time (Carvalho et al., 2022).

All of the prey items that Neanderthals procured at Picareiro were presumably available within a 15–20 km radius from the site, with patches of high-altitude environments from which ibex and chamois could be procured 30–40 km away. If Neanderthals did not travel to Montejunto or Serra da Estrela to procure prey given the existence of habitats suitable for the ungulates consumed by Neanderthals no more than 15–20 km away, it is possible that Neanderthals had a minimum subsistence territory of 225–400 km^2. However, if longer distance trips were required for encountering ungulate populations, subsistence territories could be as large as 1,600 km^2, assuming Neanderthals occasionally traveled to Montejunto or Serra da Estrela, to hunt ibex and chamois. However, considering ibex's ecological versatility, along with local mobility signal inferred by the presence of red deer and presence of aurochs and horse that may have been available within a 15 km radius, it is likely that Neanderthals primarily exploited a much more localized environment. The smaller estimated territory of 225–400 km^2 is smaller than the 600 km^2 territory proposed for Neanderthals at Gruta da Oliveira, based on ^{87}Sr studies of human and ungulate remains (Linscott et al., 2023). Because ^{87}Sr values provide direct evidence of the territory of an animal during one point of its life, it is not unreasonable to assume that our estimation, based on the proximity of patches in which targeted prey were encountered, is an underestimation.

4.3 Do we see continuity or change and Neanderthal subsistence and foraging mobility in Level JJ at Picareiro if change is observed, can this adaptation be linked to specific climate episodes?

Currently available paleoenvironmental indicators from Picareiro point to some sort of environmental disturbance linked with Heinrich Event 5 during the deposition of the JJD subunit (Benedetti et al., 2019; Carvalho et al., 2022). Though based on limited data, paleoenvironmental reconstructions based on isotope zooarchaeology point to rapidly oscillating environments from more open to more closed temperate forests in JJD. Thus, if we observe changes in Neanderthal subsistence before, during and after the deposition of JJD, it could be that ecological instability in Heinrich Event 5 forced Neanderthals to change their subsistence to adapt. However, if continuity is observed, this would indicate resilience in Neanderthal subsistence behaviors and/or population stability among targeted taxa. In other words, though regional environmental conditions may have oscillated, continuity in Neanderthal subsistence would suggest this part of Portuguese Estremadura consistently supported animal populations.

The absence of statistically significant differences in prey selection across the three JJ assemblages indicates that Neanderthal subsistence and mobility strategies remained largely consistent during the late Middle Paleolithic at Lapa do Picareiro. Across all subunits, the persistent exploitation of red deer underscores the resilience of these strategies—red deer served as a dependable resource despite climatic instability, likely due to the species' inherent ecological stability. This continuity is particularly striking given the isotopic evidence of environmental disturbance in red deer remains from JJD (Carvalho et al., 2022).

Although Heinrich events may have fragmented Neanderthal territories in other parts of southern Europe during periods of climatic downturn (Melchionna et al., 2018), the subsistence behavior at Picareiro appears unaffected. In contrast, the lithic record from the site reveals a shift in raw material procurement strategies: before Heinrich Event 5, there was a broader use of quartz, quartzite, and chert, whereas after the event, the assemblage relies primarily on quartz and quartzite, with chert largely omitted (Carvalho et al., 2022). Despite this change in lithic practices, the faunal evidence confirms a stable pattern of red deer exploitation—a trend that is consistent with other Iberian sites where red deer remain the preferred prey even amid cycles of environmental change (e.g., Jones et al., 2019; Marín-Arroyo and Sanz-Royo, 2021).

5 Conclusion

Our results suggest Neanderthals were the primary agents shaping the Level JJ faunal assemblages at Picareiro, with a consistent preference on red deer, supplemented occasionally by other ungulates such as aurochs, ibex, chamois, and horse. Skeletal remains were primarily appendicular and cranial elements, reflecting the transport of meat-rich and marrow-bearing parts to the cave for processing, were largely absent because they either were not transported to the site, or suffered attrition due to site formation processes. Cutmarks and percussion marks reveal butchering practices such as defleshing, fileting and marrow extraction, suggesting efficient resource use. The stable ecological conditions of surrounding riverine valleys and temperate forests likely supported red deer populations, enabling Neanderthals to exploit this key resource through variable hunting strategies while adapting their behaviors to the challenges of the landscape and environment.

The evidence from Lapa do Picareiro suggests that Neanderthal occupations were likely brief and characterized by intermittent use rather than long-term, intensive habitation. Although the small

lithic assemblage and the absence of clear structural or living floor features point to low-density, short-term site use, the palimpsest nature of the deposits and the need for multiple lines of evidence caution against definitive conclusions. At the same time, the subsistence data—marked by the consistent exploitation of red deer alongside occasional hunting of ibex, chamois, aurochs, and horse—indicates that Neanderthals were effectively exploiting a diverse, ecotonal environment within a relatively localized territory, potentially ranging from 225 to 400 km^2.

Despite environmental disturbances during Heinrich Event 5, the evidence from Picareiro demonstrates that Neanderthal subsistence strategies remained remarkably resilient. While shifts in lithic raw material procurement signal adaptive responses to changing conditions, the consistent exploitation of red deer across assemblages underscores a stable, reliable resource base. This continuity suggests that, even amid oscillating environments, the landscape of Portuguese Estremadura consistently supported key prey populations, enabling Neanderthals to maintain effective subsistence and mobility strategies throughout the late Middle Paleolithic. These findings highlight the dynamic interplay between ecological stability, environmental pressures, and Neanderthal subsistence and mobility strategies in the late Middle Paleolithic.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this study analyzes archaeological animal remains that are tens of thousands of years old. Since no research is conducted on modern or live specimens, no ethical approval is required for research.

Author contributions

MC: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition, Methodology, Project administration, Visualization. JH: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. EJ: Conceptualization, Investigation, Methodology, Supervision, 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.

Generative AI statement

The author(s) declare that no Gen AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2025.1545249/full#supplementary-material

References

Acevedo, P., and Cassinello, J. (2009). Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus. *Mamm. Rev.* 39, 17–32. doi: 10.1111/j.1365-2907.2008.00138.x

Alimen, M.-H., and Lavocat, R. (1966). *Atlas de préhistoire. v.3. Faunes et flores préhistoriques de l'Europe occidentale*. Paris: N. Boubée.

Altuna, J. (1992). *Asociaciones de macromamíferos del Pleistoceno superior en el Pirineo occidental y el Cantábrico. The Late Quaternary of the Pyrenean Region*. Bilbao: Universidad del Pais Vasco.

Andrews, P. (1990). *Owls, Caves, and Fossils*. Chicago, IL: Natural History Museum Publications.

Antunes, M. T., and Cunha, A. S. (1992). Neanderthalian remains fromFigueira Brava cave, Portugal. *Geobios* 25, 681–692. doi: 10.1016/0016-6995(92)80108-P

Azorit, C., Tellado, S., Oya, A., and Moro, J. (2012). Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. *Anim. Prod. Sci.* 52:720. doi: 10.1071/AN12016

Bailey, G. (2008). "Time perspectivism: origins and consequences," in *Time in Archaeology: Time Perspectivism Revisited*, eds. S. Holdaway and L. Wandsnider (Salt Lake City, UT: University of Utah Press), 13–30.

Bailey, G., and Galanidou, N. (2009). Caves, palimpsests and dwelling spaces: examples from the Upper Palaeolithic of south-east Europe. *World Archaeol.* 41:215e241. doi: 10.1080/00438240902843733

Barakat, S., Le Corre, M., Willmes, M., Cohen, J., Vuillien, M., Desclaux, E., et al. (2023). Laser ablation strontium isotopes and spatial assignment show seasonal mobility in red deer (*Cervus elaphus*) at Lazaret Cave, France (MIS 6). *Front. Ecol. Evol.* 11:988837. doi: 10.3389/fevo.2023.988837

Barbieri, A., Regala, F. T., Cascalheira, J., and Bicho, N. (2023). The sediment at the end of the tunnel: geophysical research to locate the Pleistocene entrance of Gruta da Companheira (Algarve, Southern Portugal). *Archaeol. Prospect.* 30, 117–134. doi: 10.1002/arp.1881

Benedetti, M. M., Haws, J. A., Bicho, N. F., Friedl, L. and Ellwood, B. B. (2019). Late Pleistocene site formation and paleoclimate at Lapa do Picareiro, Portugal. *Geoarchaeology* 34, 698–726. doi: 10.1002/gea.21735

Berger, J. (1986). *Wild Horses of the Great Basin: Social Competition and Population Size*. Chicago, IL: University of Chicago Press.

Berlioz, E., Azorit, C., Blondel, C., Ruiz, M. S. T., and Merceron, G. (2017). Deer in an arid habitat: dental microwear textures track feeding adaptability. *Hystrix* 28, 222–230. doi: 10.4404/HYSTRIX-28.2-12048

Bicho, N. (2004). "The middle paleolithic occupation of Southern Portugal," in *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age, vol. II*, ed N. Conard (T?bingen: Kerns Verlag), 513–531.

Bicho, N., and Cascalheira, J. (2020). "Use of lithic assemblages for the definition of short-term occupations in hunter-gatherer prehistory," in *Short-Term Occupations in Paleolithic Archaeology: Definition and Interpretation*, eds. J. Cascalheira, and A. Picin (Cham: Springer International Publishing), 19–38.

Bicho, N., and Haws, J. (2012). The Magdalenian in central and southern Portugal: human ecology at the end of the Pleistocene. *Quat. Int.* 272–273, 6–16. doi: 10.1016/j.quaint.2012.02.055

Bicho, N., Haws, J., and Hockett, B. (2006). Two sides of the same coin—rocks, bones and site function of Picareiro Cave, central Portugal. *J. Anthropol. Archaeol.* 25, 485–499. doi: 10.1016/j.jaa.2006.03.009

Bicho, N. F., Haws, J., Gibaja, J. F., and Hockett, B. (2009). Lapa do Picareiro, un asentamiento de caza magdaleniense en la Estremadura portuguesa. *Complutum* 20, 71–82.

Bicho, N. F., Haws, J., Hockett, B., and Markova, A. K. (2003). Paleoecologia e ocupa..o humana da Lapa do Picareiro: resultados preliminares. *Revista portuguesa de Arqueologia* 6, 49–81.

Bicho, N. F., Hockett, B., Haws, J., et al. (2000). Hunter–gatherer subsistence at the end of the Pleistocene: preliminary results from Picareiro Cave, Central Portugal. *Antiquity* 74, 500–506. doi: 10.1017/S0003598X00059834

Binford, L. R. (1978). *Nunamiut Ethnoarchaeology*. New York, NY: Academic Press.

Binford, L. R. (1981). Behavioral archaeology and the "Pompeii premise". *J. Anthropol. Res.* 37, 195–208. doi: 10.1086/jar.37.3.3629723

Blasco, R. (2008). Human consumption of tortoises at level IV of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839–2848. doi: 10.1016/j.jas.2008.05.013

Blasco, R., Cochard, D., Colonese, A. C., Laroulandie, V., Meier, J., Morin, E., et al. (2022). "Small animal use by Neanderthals," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (London: Academic Press), 123–143.

Blasco, R., and Peris, J. F. (2012). A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quat. Int.* 252, 16–31 doi: 10.1016/j.quaint.2011.03.019

Blasco, R., Rosell, J., Rufà, A., Marco, A. S., and Finlayson, C. (2016a). Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quat. Int.* 421, 62–77. doi: 10.1016/j.quaint.2015.10.040

Blasco, R., Rosell, J., Sánchez-Marco, A., Gopher, A., and Barkai, R. (2019). Feathers and food: human-bird interactions at Middle Pleistocene Qesem Cave, Israel. *J. Hum. Evol.* 136:102653. doi: 10.1016/j.jhevol.2019.102653

Blasco, R., Rosell, J., Smith, K. T., Maul, L. C., Sañudo, P., Barkai, R., et al. (2016b). Tortoises as a dietary supplement: a view from the Middle Pleistocene site of Qesem Cave, Israel. *Quat. Sci. Rev.* 133, 165–182. doi: 10.1016/j.quascirev.2015.12.006

Blumenschine, R. J. (1988). An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483–502. doi: 10.1016/0305-4403(88)90078-7

Blumenschine, R. J. (1995). Percussion marks, tooth marks and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29, 21–52.

Blumenschine, R. J., and Marean, C. W. (1993). "A carnivore's view of archaeological bone assemblages," in *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains. Occasional Paper 21*, ed. J. Hudson (Carbondale: Center for Archaeological Investigations, Southern Illinois University), 273–300.

Boneta Jiménez, I., Cardoso, J. L., and Pérez-García, A. (2025). The turtles from the middle Paleolithic site of Gruta Nova da Columbeira (Bombarral, Portugal): update through an archaeozoological perspective. *Anat. Rec.* 308, 1677–1691. doi: 10.1002/ar.25229

Brugal, J. P., and Raposo, L. (1999). Foz do Enxarrique (Ródão, Portugal): preliminary results of the analysis of a bone assemblage from a Middle Palaeolithic open site. *Monogr. Römisch Germanischen Zentralmuseums* 42, 367–379.

Bunn, H. T., Kroll, E. M., Ambrose, S. H., Behrensmeyer, A. K., Binford, L. R., Blumenschine, R. J., et al. (1986). Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania [and comments and reply]. *Curr. Anthropol.* 27, 431–452. doi: 10.1086/203467

Cáceres, I. (2002). *Tafonomía de yacimientos antrópicos en karst. Complejo Galería (Sierra de Atapuerca, Burgos), Vanguard Cave (Gibraltar) y Abric Romaní* (Capellades, Barcelona) (Ph.D. thesis). Dpt. Història i Geografia. Rovira i Virgili, Tarragona, 1–304.

Cardoso, J. L., and Cascalheira, J. (2024). 40,000 years later: what we know about the presence of Neanderthals in Portuguese territory and their extinction. *Estudos Arqueológicos de Oeiras* 34, 9–52. doi: 10.5281/zenodo.12731989

Cardoso, J. L., Raposo, L., and Ferreira, V. (2002). *A Gruta Nova da Columbeira Bombarral*. Bombarral: Câmara Municipal do Bombarral.

Carvalho, M., Benedetti, M., Cascalheira, J., Friedl, L., and Haws, J. (2023). "Neanderthals and early modern humans in western Iberia: Taphonomy and diet at Lapa do Picareiro (central Portugal)," in *Poster Presented at the European Society for the Study of Human Evolution Annual Meeting, Aarhus, Denmark, 21–22 September* (Aarhus).

Carvalho, M., Ellis, G., Benedetti, M., Friedl, L., Cascalheira, J., Bicho, N., et al. (2024). "Human diet and ecology during the Middle to Upper Paleolithic Transition in Portuguese Estremadura: The case from Lapa do Picareiro," in *Paper presented at the European Association of Archaeologists Annual Meeting, Rome, Italy, 28–31 August* (Rome).

Carvalho, M., Jones, E. L., Ellis, M. G., Cascalheira, J., Bicho, N., Meiggs, D., et al. (2022). Neanderthal palaeoecology in the late Middle Palaeolithic of western Iberia: a stable isotope analysis of ungulate teeth from Lapa do Picareiro (Portugal). *J. Quat. Sci.* 37, 300–319. doi: 10.1002/jqs.3363

Carvalho, M., Pereira, T., and Manso, C. (2018). Rabbit exploitation in the Middle Paleolithic at Gruta Nova da Columbeira, Portugal. *J. Archaeol. Sci.* 21, 821–832. doi: 10.1016/j.jasrep.2018.09.003

Cochard, D., Brugal, J. P., Morin, E., and Meignen, L. (2012). Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. *Quat. Int.* 264, 32–51. doi: 10.1016/j.quaint.2012.02.014

Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M. D., Lozano-Francisco, M. C., Vera-Peláez, J. L., Finlayson, C., et al. (2011). Earliest known use of marine resources by Neanderthals. *PLoS ONE* 6:e24026. doi: 10.1371/journal.pone.0024026

Costamagno, S., Liliane, M., Cédric, B., Bernard, V., and Bruno, M. (2006). Les Pradelles (Marillac-le-Franc, France): a mousterian reindeer hunting camp? *J. Anthropol. Archaeol.* 25, 466–484. doi: 10.1016/j.jaa.2006.03.008

Cruz-Uribe, K. (1991). Distinguishing hyena from hominid bone accumulations. *J. Field Archaeo.* 18, 467–486. doi: 10.2307/530408

Danilkin, A. (1995). *Behavioural Ecology of Siberian and European Roe Deer*. Netherlands: Springer. Available online at: https://books.google.it/books?id=ugPa5Siepr4C

Darlas, A., and Psathi, E. (2016). "The middle and upper Paleolithic on the western coast of the Mani peninsula (southern Greece)," in *Paleoanthropology of the Balkans and Anatolia* (Dordrecht: Springer), 95–117.

Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., et al. (2017). Neanderthal selective hunting of reindeer? The case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011. doi: 10.1007/s12520-017-0580-8

David, B. (1990). *How Was This Bone Burnt? in Problem Solving in Taphonomy: Archaeological and Palaeontological Studies From Europe, Africa and Oceania, Vol. 2*, eds. S. Solomon, I. Davidson and D. Watson (Brisbane, QLD: Tempus), 65–79.

Denniston, R. F., Houts, A. N., Asmerom, Y., Wanamaker Jr. A. D., Haws, J. A., Polyak, V. J., et al. (2018). A stalagmite test of North Atlantic SST and Iberian hydroclimate linkages over the last two glacial cycles. *Clim. Past* 14, 1893–1913. doi: 10.5194/cp-14-1893-2018

Discamps, E., and Faivre, J. P. (2017). Substantial biases affecting Combe-Grenal faunal record cast doubts on previous models of Neanderthal subsistence and environmental context. *J. Archaeol. Sci.* 81, 128–132. doi: 10.1016/j.jas.2017.03.009

Dominguez-Rodrigo, M. (1997). Meat-eating by early hominids at the FLK 22Zinjanthropussite, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *J. Hum. Evol.* 33, 669–690. doi: 10.1006/jhev.1997.0161

Eixea, A., Chacón, M. G., Bargalló, A., Sanchis, A., Romagnoli, F., Vaquero, M., et al. (2020). Neanderthal spatial patterns and occupation dynamics: a focus on the central region in Mediterranean Iberia. *J. World Prehist.* 33, 267–324. doi: 10.1007/s10963-020-09143-3

Evins, M. A. (1982). The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. *Paléorient* 8, 37–58. doi: 10.3406/paleo.1982.4308

Fa, J. E., Stewart, J. R., Lloveras, L., and Vargas, J. M. (2013). Rabbits and hominin survival in Iberia. *J. Hum. Evol.* 64, 233–241. doi: 10.1016/j.jhevol.2013.01.002

Faith, J. T., and Du, A. (2018). The measurement of taxonomic evenness in zooarchaeology. *Archaeol. Anthropol. Sci.* 10, 1419–1428. doi: 10.1007/s12520-017-0467-8

Faith, J. T., and Thompson, J. C. (2018). "Low-survival skeletal elements track attrition, not carcass transport behavior in Quaternary large mammal assemblages," in *Zooarchaeology in Practice: Case Studies in Methodology and Interpretation in Archaeofaunal Analysis*, eds. C. M. Giovas, and M. J. LeFebvre (Cham: Springer), 109–126.

Fernández-Laso, M. C., Brugal, J. P., and Raposo, L. (2015). Gruta Nova da Columbeira (Bombarral, Portugal): un modelo de ocupación en cueva durante el Paleolítico Medio. Resultados del estudio del registro de macromamíferos. *Trabajos de Prehistoria* 72, 304–326. doi: 10.3989/tp.2015.12156

Figueiral, I., and Terral, J. F. (2002). Late quaternary refugia of Mediterranean taxa in the Portuguese Estremadura: charcoal based palaeovegetation and climatic reconstruction. *Quat. Sci. Rev.* 21, 549–558. doi: 10.1016/S0277-3791(01)00022-1

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., et al. (2012). Birds of a feather: neanderthal exploitation of raptors and corvids. *PLoSONE* 7:e45927. doi: 10.1371/journal.pone.0045927

Fisher, J. W. (1995). Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory* 2, 7–68. doi: 10.1007/BF02228434

Fonseca, M. M. (1998). *Plasticity of mating behaviour in red deer (Cervus elaphus) in a Mediterranean environment* (Doctoral dissertation). University College London, London, United Kingdom.

Gaudzinski-Windheuser, S., and Niven, L. (2009). "Hominin subsistence patterns during the Middle and Late Paleolithic in Northwestern Europe," in *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*, eds. J.-J. Hublin, and M. P. Richards (Dordrecht: Springer), 99–111.

Gebert, C., and Verheyden-Tixier, H. (2001). Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. *Mamm. Rev.* 31, 189–201. doi: 10.1111/j.1365-2907.2001.00090.x

Goffette, Q., Rots, V., Abrams, G., Pirson, S., Di Modica, K., Bray, F., et al. (2024). Neanderthal exploitation of birds in north-western Europe: Avian remains from Scladina Cave (Belgium). *Front. Environ. Archaeol.* 3:1441926. doi: 10.3389/fearc.2024.1441926

Gomez, A., and Lunt, D. H. (2007). "Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula," in *Phylogeography of Southern European Refugia*, eds. S. Weiss, and N. Ferrand (Dordrecht: Springer), 155–188.

González-Sampériz, P., Leroy, S. A., Carrión, J. S., Fernández, S., García-Antón, M., Gil-García, M. J., et al. (2010). Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. *Rev. Palaeobot. Palynol.* 162, 427–457. doi: 10.1016/j.revpalbo.2010.03.009

Grayson, D. K. (1984). *Quantitative Zooarchaeology*. New York, NY: Academic Press.

Grayson, D. K., and Delpech, F. (2002). Specialized early Upper Palaeolithic hunters in southwestern France? *J. Archaeol. Sci.* 29, 1439–1449. doi: 10.1006/jasc.2002.0806

Hall, S. J. (2008). A comparative analysis of the habitat of the extinct aurochs and other prehistoric mammals in Britain. *Ecography* 31, 187–190. doi: 10.1111/j.0906-7590.2008.5193.x

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electro.* 4:9.

Hardy, B. L., and Moncel, M. H. (2011). Neanderthal use of fish, mammals, birds, starchy plants and wood 125-250,000 years ago. *PLoS ONE* 6:e23768. doi: 10.1371/journal.pone.0023768

Hardy, B. L., Moncel, M. H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., et al. (2013). Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). *Quat. Sci. Rev.* 82, 23–40 doi: 10.1016/j.quascirev.2013.09.028

Haws, J., Benedetti, M., Carvalho, M., and Ellis, G. (2021). Human adaptive responses to climate andenvironmental change during the Gravettian of Lapa do Picareiro (Portugal). *Quat. Int.* 587, 4–18. doi: 10.1016/j.quaint.2020.08.009

Haws, J. A. (2006). "Late Upper Paleolithic large mammal exploitation at Lapa do Picareiro," in *Animais na Pré-história e Arqueologia da Península Ibérica. Actas IV Congreso de Arqueología Peninsula Vol. 3*, ed. N. F. Bicho (Faro: Universidade do Algarve), 179–195.

Haws, J. A., Benedetti, M. M., Cascalheira, J. M., Bicho, N. F., et al. (2019). "Human occupation during the Late Pleniglacial at Lapa do Picareiro (Portugal)," in *Human Adaptations to the Last Glacial Maximun: The Solutrean and Its Neighbors*, eds I. Schmidt, J. Cascalheira, N. Bicho, and G. C., Weniger (Cambridge: Cambridge Scholar Publishing), 188.

Haws, J. A., Benedetti, M. M., Funk, C. L., Bicho, N. F., Daniels, J. M., Hesp, P. A., et al. (2010). Coastal wetlands and the Neanderthal settlement of Portuguese Estremadura. *Geoarchaeology* 25, 709–744. doi: 10.1002/gea.20330

Haws, J. A., Benedetti, M. M., Funk, C. L., Bicho, N. F., Pereira, T., Marreiros, J., et al. (2020b). Late Pleistocene landscape and settlement dynamics of Portuguese Estremadura. *J. Field Archaeol.* 45, 222–248. doi: 10.1080/00934690.2020.1733780

Haws, J. A., Benedetti, M. M., Talamo, S., Bicho, N., Cascalheira, J., Ellis, M. G., et al. (2020a). The early Aurignacian dispersal of modern humans into westernmost Eurasia. *Proc. Natl. Acad. Sci. U. S. A.* 117, 25414–25422. doi: 10.1073/pnas.2016062117

Heinrich, H. (1988). Origin and consequences of cyclic ice rafting in the northeast Atlantic Ocean during the past 130,000 years. *Quat. Res.* 29, 142–152. doi: 10.1016/0033-5894(88)90057-9

Higham, T., Douka, K., Wood, R., et al. (2014). The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* 512, 306–309. doi: 10.1038/nature13621

Hillson, S. (1996). *Mammal Bones and Teeth: An Introductory Guide to Methods of Identification*. London: Institute of Archaeology, University College London.

Hockett, B. S. (1996). Corroded, thinned and polished bones created by golden eagles (Aquila chrysaetos): taphonomic implications for archaeological interpretations. *J. Archaeol. Sci.* 23, 587–591. doi: 10.1006/jasc.1996.0055

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78, 443–457. doi: 10.1007/BF00378733

Jones, E., and Carvalho, M. (2023). Ecospaces of the middle to upper paleolithic transition: the archaeofaunal record of the iberian Peninsula. *J. Hum. Evol.* 177:103331. doi: 10.1016/j.jhevol.2023.103331

Jones, E. L. (2004). Dietary evenness, prey choice, and human–environment interactions. *J. Archaeol. Sci.* 31, 307–317. doi: 10.1016/j.jas.2003.08.011

Jones, J. R., Richards, M. P., Reade, H., Bernaldo de Quirós, F., and Marín-Arroyo, A. B. (2019). Multi-Isotope investigations of ungulate bones and teeth from El Castillo and Covalejos caves (Cantabria, Spain): implications for paleoenvironment reconstructions across the Middle-Upper Palaeolithic transition. *J. Archaeol. Sci. Rep.* 23, 1029–1042. doi: 10.1016/j.jasrep.2018.04.014

Linscott, B., Pike, A. W., Angelucci, D. E., Cooper, M. J., Milton, J. S., Matias, H., et al. (2023). Reconstructing Middle and Upper Paleolithic human mobility in Portuguese Estremadura through laser ablation strontium isotope analysis. *Proc. Nat. Acad. Sci. U. S. A.* 120:e2204501120. doi: 10.1073/pnas.2204501120

Livraghi, A., Fanfarillo, G., Dal Colle, M., Romandini, M., and Peresani, M. (2021). Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: a study on De Nadale cave, Italy. *Quat. Int.* 586:24–41. doi: 10.1016/j.quaint.2019.11.024

Lupo, K. D., and O'Connell, J. F. (2002). Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. *J. Archaeol. Sci.* 29, 85–109. doi: 10.1006/jasc.2001.0690

Lyman, R. L. (1994). *Vertebrate Taphonomy*. New York, NY: Cambridge University Press.

Lyman, R. L. (2005). Analyzing cut marks: lessons from artiodactyl remains in the northwestern United States. *J. Archaeol. Sci.* 32, 1722–1732. doi: 10.1016/j.jas.2005.06.003

Lyman, R. L. (2008). *Quantitative Paleozoology*. New York, NY: Cambridge University Press.

Lyman, R. L. (2021). "Bone density and bone attrition," in *Manual of Forensic Taphonomy*, eds. J. T. Pokines and S. A. Symes (Boca Raton, FL: CRC Press), 79–102.

Marin, J., Daujeard, C., Saladi,é, P., Rodríguez-Hidalgo, A., Vettese, D., Rivals, F., et al. (2020). Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). *Quat. Sci. Rev.* 243:106472. doi: 10.1016/j.quascirev.2020.106472

Marín, J., Rodríguez-Hidalgo, A., Vallverdú, J., de Soler, B. G., Rivals, F., Rabuñal, J. R., et al. (2019). Neanderthal logistic mobility during MIS3: zooarchaeological perspective of abric romaní level P (Spain). *Quat. Sci. Rev.* 225:106033. doi: 10.1016/j.quascirev.2019.106033

Marín, J., Saladié, P., and Rodríguez-Hidalgo, A., and Carbonell, E. (2017). Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence. *PLoS ONE* 12:e0186970. doi: 10.1371/journal.pone.0186970

Marín-Arroyo, A. B., and Sanz-Royo, A. (2021). What Neanderthals and AMH ate: reassessment of the subsistence across the Middle–Upper Palaeolithic transition in the Vasco-Cantabrian region of SW Europe. *J. Quat. Sci.* 37, 320–334. doi: 10.1002/jqs.3291

Martínez-Moreno, J., Mora, R., and De la Torre, I. (2004). "Methodological approach for understanding Middle Palaeolithic settlement dynamics at La Roca dels Bous (Noguera, Catalunya, Northeast Spain)," in *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age, Vol. 2*, ed. N. J. Conard (Tübingen: Kerns Verlag), 393–413.

Mauget, R. (1981). "Behavioural and reproductive strategies in wild forms of Sus scrofa (European wild boar and feral pigs)," in *The Welfare of Pigs*, ed. W. Sybesma (The Hague: Martinus Nijhoff Publishers), 3–13.

McPherron, S. P. (2022). *E5 [Computer software]*. Available online at: https://github.com/surf3s/E5

Mein, P., and Antunes, M. T. (2000). "Gruta da Figueira Brava: petits mammifères – Insectívora, Chiroptera, Lagomorpha," in *Últimos Neandertais em Portugal – evidência, odontológica e outra*, ed M. T. Antunes (Lisboa: Academia das Ciências de Lisboa), 163–177.

Melchionna, M., Di Febbraro, M., Carotenuto, F., Rook, L., Mondanaro, A., Castiglione, S., et al. (2018). Fragmentation of Neanderthals' pre-extinction distribution by climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 496, 146–154. doi: 10.1016/j.palaeo.2018.01.031

Moncel, M.-H., and Rivals, F. (2011). On the question of short-term neanderthal site occupations: payre, France (MIS 8-7), and Taubach/Weimar, Germany (MIS 5). *J. Anthropol. Res.* 67, 47–75. doi: 10.3998/jar.0521004.0067.104

Morin, E., and Laroulandie, V. (2012). Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE* 7:e32856. doi: 10.1371/journal.pone.0032856

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes–a role for density dependence? *Oikos* 120, 1817–1825. doi: 10.1111/j.1600-0706.2011.19439.x

Nabais, M. (2018). Neanderthal subsistence in Portugal: what evidence?. *Archaeol. Int.* 21, 95–100. doi: 10.5334/ai-376

Nabais, M., Dupont, C., and Zilhão, J. (2023). The exploitation of crabs by last interglacial Iberian Neanderthals: The evidence from Gruta da Figueira Brava (Portugal). *Front. Environ. Archaeol.* 2:1097815. doi: 10.3389/fearc.2023.1097815

Nabais, M., and Zilhão, J. (2019). The consumption of tortoise among last interglacial Iberian Neanderthals. *Quat. Sci. Rev.* 217, 225–246. doi: 10.1016/j.quascirev.2019.03.024

Naudinot, N., and Marchand, G. (2020). *Take Shelter! Short-Term Occupations of the Late Paleolithic and the Mesolithic in the French Far West. Short-Term Occupations in Paleolithic Archaeology: Definition and Interpretation*. Springer Nature, 121–146.

Nesti, I., Posillico, M., and Lovari, S. (2010). Ranging behaviour and habitat selection of Alpine chamois. *Ethol. Ecol. Evol.* 22, 215–231. doi: 10.1080/03949370.2010.502316

Orbach, M., and Yeshurun, R. (2021). The hunters or the hunters: human and hyena prey choice divergence in the Late Pleistocene Levant. *J. Hum. Evol.* 160:102572. doi: 10.1016/j.jhevol.2019.01.005

Pales, L., and Lambert, C. (1971). *Atlas ostéologique pour servir à l'identification des mammifères du quaternaire*. Paris: Éditions du Centre national de la recherche scientifique.

Patou-Mathis, M. (2000). Neanderthal subsistence behaviours in Europe. *Int. J. Osteoarchaeol.* 10, 379–395. doi: 10.1002/1099-1212(200009/10)10:5<379::AID-OA558>3.0.CO;2-4

Pelletier, M., Desclaux, E., Brugal, J. P., and Texier, P. J. (2019). The exploitation of rabbits for food and pelts by last interglacial Neandertals. *Quat. Sci. Rev.* 224:105972. doi: 10.1016/j.quascirev.2019.105972

Peresani, M., Fiore, I., Gala, M., Romandini, M., and Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky BP, Italy. *Proc. Nat. Acad. Sci. U. S. A.* 108, 3888–3893. doi: 10.1073/pnas.1016212108

Pérez Ripoll, M. (1992). *Marcas de carniceria, fracturas intenciona-das y mordeduras de carnivoros en huesos prehistoricos del mediterráneo español*. Alicante: Instituto de Cultura Juan Gil Albert (Coleccion Patrimonio 15).

Quézel, P. (1985). "Definition of the Mediterranean region and the origin of its flora," in *Plant Conservation in the Mediterranean Area*, ed. C. Gómez-Campo (Dordrecht: Dr. W. Junk Publishers), 9–24.

Raposo, L. (1995). Ambientes, territorios y subsistencia en el Paleolítico Medio de Portugal. *Complutum*, 6, 57–78.

Raposo, L., and Cardoso, J. L. (2000). "Mousterian industries of the Gruta da Figueira Brava," in Memórias da Academia das Ciências de Lisboa (Lisbon: Academia das Ciências de Lisboa), 319–337.

Real, C., Eixea, A., Sanchis, A., Morales, J. V., Klasen, N., Zilhão, J., et al. (2018). Abrigo de la Quebrada level IV (Valencia, Spain): interpreting a middle palaeolithic palimpsest from a zooarchaeological and lithic perspective. *J. Paleolit. Archaeol.* 3, 187–224. doi: 10.1007/s41982-018-0012-z

Real, C., Sanchis, A., Eixea, A., and Villaverde, V. (2019). Neanderthal subsistence and short-term human occupation patterns during MIS 5. New data from Abrigo de la Quebrada (Valencia, Spain). *J. Archaeol. Sci.* 28:102056. doi: 10.1016/j.jasrep.2019.102056

Rendu, W. (2022). "Selection versus opportunism: a view from Neanderthal subsistence strategies," in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic*, eds. F. Romagnoli, F. Rivals, and S. Benazzi (Amsterdam: Academic Press; Elsevier), 109–122.

Rendu, W., Renou, S., Koliasnikova, A., Baumann, M., Plisson, H., Discamps, E., et al. (2023). Neanderthal subsistence at Chez-Pinaud Jonzac (Charente-Maritime, France): a kill site dominated by reindeer remains, but with a horse-laden diet? *Front. Ecol. Evol.* 10:1085699h. doi: 10.3389/fevo.2022.1085699

Richards, M. P., Pettitt, P. B., Trinkaus, E., Smith, F. H., Paunović, M., and Karavanić, I. (2000). Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *Proc. Nat. Acad. Sci. U. S. A.* 97, 7663–7666. doi: 10.1073/pnas.120178997

Riel-Salvatore, J., and Barton, C. M. (2004). Late Pleistocene technology, economic behavior, and land-use dynamics in southern Italy. *Am. Antiq.* 69, 257–274. doi: 10.2307/4128419

Rodrigues, M. L. (1991). Depósitos e evolução quaternária das vertentes nas depressões de Minde e de Alvados (Maciço Calcário Estremenho, Portugal). *Finisterra* XXVI, 5–26. doi: 10.18055/Finis1907

Rosell, J., Blasco, R., Rivals, F., Chacon, M. G., Arilla, M., Camaros, E., et al. (2017). A resilient landscape at teixoneres cave (MIS 3; Moi a, Barcelona, Spain): the Neanderthals as disrupting agent. *Quat. Int.* 435:195e210. doi: 10.1016/j.quaint.2015.11.077

Ruiz, M. N., Benito-Calvo, A., Alonso-Alcalde, R., Alonso, P., de la Fuente, H., Santamaría, M., et al. (2021). Late Neanderthal subsistence strategies and cultural traditions in the northern Iberia Peninsula: Insights from Prado Vargas, Burgos, Spain. *Quat. Sci. Rev.* 254:106795. doi: 10.1016/j.quascirev.2021.106795

Salazar-García, D. C., Power, R. C., Serra, A. S., Villaverde, V., Walker, M. J., and Henry, A. G. (2013). Neanderthal diets in central and southeastern Mediterranean Iberia. *Quat. Int.* 318, 3–18. doi: 10.1016/j.quaint.2013.06.007

Sánchez-Hernández, C., Gourichon, L., Blasco, R., Carbonell, E., Chacón, G., Galván, B., et al. (2020b). High-resolution Neanderthal settlements in mediterranean Iberian Peninsula: A matter of altitude? *Quat. Sci. Rev.* 247:106523. doi: 10.1016/j.quascirev.2020.106523

Sánchez-Hernández, C., Gourichon, L., Soler, J., Soler, N., Blasco, R., Rosell, J., et al. (2020a). Dietary traits of ungulates in northeastern Iberian Peninsula: did these Neanderthal preys show adaptive behaviour to local habitats during the Middle Palaeolithic? *Quat. Int.* 557, 47–62. doi: 10.1016/j.quaint.2020.01.008

Schmid, E. (1972). *Atlas of animal bones. For prehistorians, archaeologists and Quaternary geologists. Knochenatlas. Für Prähistoriker, Archäologen und Quartärgeologen*. Amsterdam: Elsevier.

Simpson, E. H. (1949). Measurement of diversity. *Nature* 163, 688–688. doi: 10.1038/163688a0

Sommer, R. S., Zachos, F. E., Street, M., Jöris, O., Skog, A., and Benecke, N. (2008). Late quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quat. Sci. Rev.* 27, 714–733. doi: 10.1016/j.quascirev.2007.11.016

Starkovich, B. M. (2017). Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). *J. Hum. Evol.* 111, 63–84. doi: 10.1016/j.jhevol.2017.04.005

Steele, T. E. (2002). *Red deer: Their ecology and how they were hunted by Late Pleistocene hominids in Western Europe* (Doctoral dissertation). Stanford University, Stanford, CA, United States.

Stepanchuk, V. N., Vasilyev, S. V., Khaldeeva, N. I., Kharlamova, N. V., and Borutskaya, S. B. (2017). The last Neanderthals of Eastern Europe: Micoquian layers IIIa and III of the site of Zaskalnaya VI (Kolosovskaya), anthropological records and context. *Quat. Int.* 428, 132–150. doi: 10.1016/j.quaint.2015.11.042

Stiner, M. C. (1994). *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton, NJ: Princeton Univ. Press.

Stiner, M. C. (2001). Thirty years on the "Broad Spectrum Revolution" and Paleolithic demography. *Proc. Natl. Acad. Sci. U. S. A.* 98, 6993–6996. doi: 10.1073/pnas.121176198

Stiner, M. C. (2002). On in situ attrition and vertebrate body part profiles. *J. Archaeol. Sci.* 29, 979–991. doi: 10.1006/jasc.2001.0798

Stiner, M. C. (2013). An unshakable middle paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. *Curr. Anthropol.* 54, S288–S304. doi: 10.1086/673285

Straus, L. G. (1981). On the habitat and diet of *Cervus elaphus*. *Munibe* 33, 175–182.

Straus, L. G. (1992). *Iberia Before the Iberians: The Stone Age Prehistory of Cantabrian Spain*. Albuquerque: University of New Mexico Press.

Straus, L. G. (2013). "Iberian archaeofaunas and hominin subsistence during marine isotope stages 4 and 3," in *Zooarchaeology and Modern Human Origins*, eds. J. L. Clark, J. D. Speth (Dordrecht: Springer), 97–128.

Terlato, G., Livraghi, A., Romandini, M., and Peresani, M. (2019). Large bovids on the Neanderthal menu: exploitation of Bison priscus and Bos primigenius in northeastern Italy. *J Archaeol. Sci. Rep*. 25, 129–143. doi: 10.1016/j.jasrep.2019.04.006

Thatcher, D. L., Wanamaker, A. D., Denniston, R. F., Ummenhofer, C. C., Regala, F. T., Jorge, N., et al. (2020). Linking the karst record to atmospheric, precipitation, and vegetation dynamics in Portugal. *Chem. Geol.* 558:119949. doi: 10.1016/j.chemgeo.2020.119949

Vallverdú, J., Allue, E., Bischoff, J. L., C aceres, I., Carbonell, E., Cebri a, A., et al. (2005). Short human occupations in the middle palaeolithic level iof the abric Romaní rock-shelter (Capellades, Barcelona, Spain). *J. Hum. Evol.* 48:157e174. doi: 10.1016/j.jhevol.2004.10.004

Van Neer, W., and Wouters, W. (2009). "Les restes de Poissons des niveaux du Paléolithique moyen et supérieur de la grotte Walou," in *La grotte Walou à Trooz (Belgique)*, eds. S. Pirson, C. Draily, and M. Toussaint (Namur: Etudes et Documents Archéologie 21; Département du Patrimoine & Institut du Patrimoine Wallon), 68–81.

VanPool, T. L., and Leonard, R. D. (2011). *Quantitative Analysis in Archaeology*. Hoboken, NJ: John Wiley & Sons.

Vettese, D., Blasco, R., Cáceres, I., Gaudzinski-Windheuser, S., Moncel, M.-H., Hohenstein, U. T., et al. (2020). Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeol. Anthropol. Sci.* 12:48. doi: 10.1007/s12520-019-00972-8

Vidal-Cordasco, M., Ocio, D., Hickler, T., and Marín-Arroyo, A. B. (2022). Ecosystem productivity affected the spatiotemporal disappearance of Neanderthals in Iberia. *Nat. Ecol. Evol.* 6, 1644–1657. doi: 10.1038/s41559-022-01861-5

Villa, P., and Mahieu, E. (1991). Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48. doi: 10.1016/0047-2484(91)90034-S

Villa, P., Soriano, S., Pollarolo, L., Smriglio, C., Gaeta, M., D'orazio, M., et al. (2020). Neandertals on the beach: Use of marine resources at Grotta dei Moscerini (Latium, Italy). *PLoS ONE* 15:e0226690. doi: 10.1371/journal.pone.0226690

Villaverde, V., Martínez, R., Guillem, P. M., and Fumanal, M. P. (1996). "Mobility and the role of small game in the paleolithic of the central region of the Spanish Mediterranean: a comparison of Cova Negra with other paleolithic deposits," in *The Last Neanderthals, the First Anatomically Modern Humans*, eds. E. Carbonell and M. Vaquero (Tarragona: Universitat Rovira i Virgili), 267–288.

Wood, R. E., Barroso-Ruíz, C., Caparrós, M., Jordá Pardo, J. F., Galván Santos, B., and Higham, T. F. (2013). Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. *Proc. Nat. Acad. Sci. U. S. A.* 110, 2781–2786. doi: 10.1073/pnas.1207656110

Yaroshevich, A., Oron, M., and Sharon, G. (2023). Big-game hunting during the late Middle Paleolithic in the Levant: insights into technology and behavior from Nahal Mahanayeem Outlet, Upper Jordan River, Israel. *J. Archaeol. Sci.* 47:103777. doi: 10.1016/j.jasrep.2022.103777

Yravedra, J. (2013). "New contributions in the subsistence of Middle-Upper Palaeolithic in northern Spain," in *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene*, eds. J. Clark and J. D. Speth (New York, NY: Springer), 77–95.

Yravedra, J., and Cobo-Sánchez, L. (2015). Neanderthal exploitation of ibex and chamois in southwestern Europe. *J. Hum. Evol.* 78, 12–32. doi: 10.1016/j.jhevol.2014.10.002

Yravedra, J., Gómez-Castanedo, A., Aramendi-Picado, J., Montes-Barquín, R., Sanguino-González, J. (2016). Neanderthal and Homo sapiens subsistence strategies in the Cantabrian region of northern Spain. *Archaeol. Anthropol. Sci.* 8: 779–803. doi: 10.1007/s12520-015-0253-4

Yravedra, J., Gómez-Castanedo, A., Picado, J. A., and Preysler, J. B. (2014). Specialised hunting of Iberian ibex during Neanderthal occupation at El Esquilleu Cave, northern Spain. *Antiquity* 88, 1035–1049. doi: 10.1017/S0003598X00115303

Zilhão, J. (2001). "Middle Paleolithic settlement patterns in Portugal," in *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age*, ed N. Conard (T?bingen: Kerns Verlag), 597–608.

Zilhão, J., Angelucci, D., Argant, J., Brugal, J. P., Carrión, J. S., Carvalho, R., et al. (2010). "Humans and hyenas in the middle Paleolithic of Gruta da Oliveira (Almonda karstic system, Torres Novas, Portugal)," in *Actas de la 1ª Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica* (Murcia: Museo Arqueológico de Murcia), 298–308.

Zilhão, J., Angelucci, D. E., Arnold, L. J., Demuro, M., Hoffmann, D. L., and Pike, A. W. (2021b). *A Revised, Last Interglacial Chronology for the Middle Palaeolithic Sequence of Gruta da Oliveira (Almonda karst system*). Lisbon: UNIARQ - Centro de Arqueologia da Universidade de Lisboa.

Zilhão, J., Angelucci, D. E., Arnold, L. J., d'Errico, F., Dayet, L., Demuro, M., et al. (2021a). Revisiting the Middle and Upper Palaeolithic archaeology of Gruta do Caldeirão (Tomar, Portugal). *PLoS ONE* 16:e0259089. doi: 10.1371/journal.pone.0259089

Zilhão, J., Angelucci, D. E., Igreja, M. A., Arnold, L. J., Badal, E., Callapez, P., et al. (2020). Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* 367:eaaz7943. doi: 10.1126/science.aaz7943

Zilhão, J., and Villaverde, V. (2008). "The Middle Paleolithic of Murcia," in *Treballs d'Arqueologia* (Barcelona: Departament de Prehistòria; Universitat Autònoma de Barcelona), 229–248.

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Cut from the same cloth? Comparing Neanderthal processing of faunal resources at Amud and Kebara caves (Israel) through cut-marks analyses

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Amud and Kebara caves (northern Israel) are two broadly contemporaneous Middle Paleolithic sites dated to ca. 70–50 Ka BP, both located in the Mediterranean realm of the southern Levant. Neanderthal occupations at these sites are represented by considerable amounts of lithic artifacts, combustion features and abundant faunal material as well as human remains. As similar mammalian taxonomic distributions were observed in these two Neanderthal cave sites, we explore the complexity and diversity of their animal resources processing techniques by comparing cut-marks characteristics and patterns. A total of 344 animal bone fragments bearing cut-marks were selected from specific stratigraphic contexts from both sites, and studied using macroscopic and microscopic techniques (i.e., Focus Variation microscopy) to quantify, characterize, and measure the cut-marks left on the bones. The observations were compared across the stratigraphic units and between the sites. Despite comparable taxonomic distributions, there are notable differences in the density and layout of cut-marks between the two caves. The micro-morphometric characteristics of these marks also highlight intra- and inter-site differences and similarities. This evidence might suggest distinctive butchering strategies between the Neanderthal populations in Amud and Kebara caves despite comparable occupation intensities, similar lithic technologies, and access to similar food resources. Such discrepancies could possibly reflect inter-group cultural differences related to carcass processing preferences, organization of tasks within the group, or socially transmitted traditions.

KEYWORDS

cut-marks, Middle Paleolithic, Southern Levant, animal resources processing, subsistence practices, bone surface modifications

1 Introduction

Neanderthal diet was diverse and flexible, with the composition of faunal assemblages in sites occupied by Neanderthals across Eurasia shown to vary depending on the eco-geographical location of the sites. This suggests that Neanderthals were capable of adapting to different landscapes, environments, and local resources (e.g., Lorenzen et al., 2011; Blasco et al., 2013, 2016; Morin et al., 2015; Rivals et al., 2022; Romagnoli et al., 2022).

Faunal studies and isotopic analyses demonstrated that the diet of Neanderthal was rich in animal proteins from large and small game, including the consumption of red and yellow bone marrow (Rendu, 2022; Rivals et al., 2022; Vettese et al., 2022 and references therein). Studies of the observed ratios of fallow deer to gazelle in Mediterranean Middle Paleolithic sites have reinforced the already suggested notion of a human bias in favor of gazelles in this region, potentially reflecting a specific human choice of prey (Orbach and Yeshurun, 2021 and references therein). Evidence suggests that the strategies for transport and butchering of animal carcasses adopted by Middle Paleolithic populations were dependent on many factors, including: the distance from residential camps to the hunting locations, the composition and size of the hunting party, the presence of scavenging carnivores near the kill-sites, the number of carcasses to be processed, as well as the size of the prey, and the differential utility of the various body parts (e.g., Binford, 1981; Bunn, 1986; O'Connell et al., 1988, 1990; Metcalfe and Barlow, 1992; Gifford-Gonzalez, 1998, 2018; Monahan, 1998; Faith et al., 2009; Speth, 2012; Schoville and Otárola-Castillo, 2014 and references therein). These factors lead to the hypothesis that large animals were more likely to be butchered at the kill-site, with a selection of body parts with a high yield of meat or fat, while smaller animals were brought whole to the occupation site, a phenomenon commonly referred to as the "schlepp effect" (Gifford-Gonzalez, 1998).

Levantine Late Middle Paleolithic (MP) sites, dated roughly between 75 and 45 Ka BP (corresponding to MIS 4 to MIS 3) are characterized mainly by shared similarities in settlement organization, the overall reduction of exploited territories in comparison to previous periods, as well as similar yet highly variable lithic technological practices (Hovers, 2009; Hovers and Belfer-Cohen, 2013; Abadi et al., 2020). Cave sites usually exhibit evidence for fire use and spatial differentiation of activities. Some of these spatial patterns, for instance the spatial coincidence of knapping activities with hearths, or the presence of specific areas designated for the discard of material and/or deposition of human remains, are common to several sites (Meignen et al., 2006). Reoccurring occupations maintaining consistent locations of these activities over time are also observed, mainly in cave sites (Hovers, 2001; Meignen et al., 2006). These various observations raise the question of knowledge-transmission and specific cultural practices within and between groups. These aspects of MP human behavior, most often discussed with regards to lithic assemblage characteristics, are here investigated from the perspective of animal resources processing. We compare butchery cut-mark patterns from two geographically close and broadly contemporaneous MP sites: Amud Cave and Kebara Cave.

Among the Levantine Middle Paleolithic sites, Amud Cave and Kebara Cave, situated some 70 km apart in Northern Israel (Figure 1), stand out for their richness in lithic artifacts, Neanderthal remains, and faunal remains, which attest to the occupation intensity at the sites. These two sites, located in the Mediterranean ecological zone of the southern Levant, are well-dated and have yielded broadly contemporaneous archeological layers within the time range of ca. 60-50 Ka BP (Valladas et al., 1987, 1999; Rink et al., 2001; Rebollo et al., 2011). Analyses of dental remains suggested for both sites at the corresponding stratigraphic units that occupations took place mainly between late fall to early spring (Speth and Clark, 2006; Speth and Tchernov, 2007; Rendu and Speth, 2019; Jallon et al., 2025), and that their occupants probably had access to a similar range of food resources. Similarities in the lithic assemblages, the nature of the deposits, and the modalities of occupation of Amud and Kebara caves have been extensively demonstrated by previous studies (Hovers, 1998, 2004, 2007; Albert et al., 2007; Shahack-Gross et al., 2008; Hovers et al., 2011; Meignen and Bar-Yosef, 2019 and references therein; see detailed site descriptions provided in the Section 2 below), making these two cave sites suitable for in-depth comparative analyses. Publications describing the bone assemblages from these two sites reveal that, notwithstanding slight differences, both reflect the Late Middle Paleolithic range of variability, focusing mainly on mountain gazelles, fallow deer, and other middle- to large-sized ungulates. Based on these similarities, we could therefore assume that similar butchering strategies were used at both sites. However, considerable differences were observed in the taphonomic characteristics of both faunal assemblages (Rabinovich and Hovers, 2004; Speth, 2019 and references therein). For instance, at Amud Cave, burnt remains appear to be particularly numerous and the bone material is highly fragmented, which could either

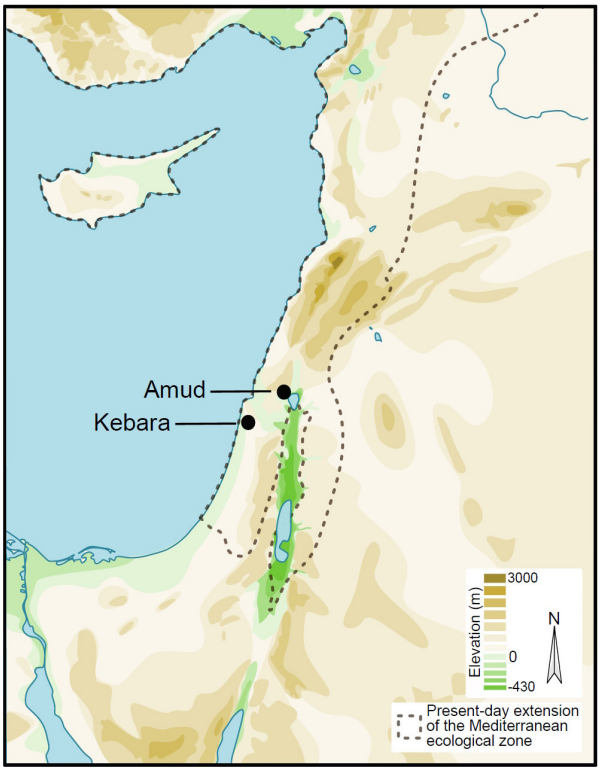

FIGURE 1
Map of the Levant situating Amud and Kebara caves. Map made with the software Inkscape (version 1.0.2). Present-day extension of the Mediterranean ecological zone based on Asouti et al. (2015).

Abbreviations: MP, Middle Paleolithic; BSG, Body-size group; OA, Opening angle; RD, Floor radius; WIS, Width at the surface.

reflect intentional human action (cooking, marrow extraction, or waste management), or be due to post-depositional processes such as trampling and repetitive sets of fireplaces throughout the occupations of the site (Rabinovich and Hovers, 2004; see also Mallol et al., 2013; Pérez et al., 2017; and Gallo et al., 2025 on bone post-depositional fragmentation and burning). Based on previous published work, the two sites also appear to differ in the frequency of butchery marks identified across the assemblages, with only 1%−3% of the remains studied from Amud bearing cut-marks (Rabinovich and Hovers, 2004), against 15% of the identified remains from Kebara (Speth, 2019). These differences in fragmentation and cut-mark frequency could reflect differing human behaviors at the two sites, but they could also be due to differing post-depositional processes, or to differences in zooarcheological analytical strategies and sample sizes. Because of the intense fragmentation, a standard approach to the study of cut-marks is particularly challenging for Amud, since cut-marks are most often observed on undetermined bone fragments. Therefore, in an effort to highlight the potential evidence of site-specific human behaviors and untangle them from taphonomic biases, the present study proposes to complement previous work on the faunal material from Amud and Kebara by focusing our analyses exclusively on the fragments bearing cut-marks and on their macro- and microscopic characteristics. We hypothesize that the absence of differences in cut-mark patterns among the two faunal assemblages may indicate that Neanderthal groups inhabiting the two sites used similar butchering strategies. On the contrary, if different cut-mark patterns can be observed within and between the two faunal assemblages, these differences might reflect differing behaviors. This approach aims to use cut-marks analyses to further explore the complexity and diversity of the animal resources processing techniques adopted at the two sites, despite the challenges inherent to the study of highly fragmented material.

Pioneered by Lartet (1860) and Martin (1909), the study of cut-marks has been widely applied over the last 70 years to explore the traces resulting from various carcass processing strategies, as they can be an important source of evidence to reconstruct ancient butchery practices (e.g., White, 1952; Binford, 1981; Lyman, 1994, 1995; Blumenschine et al., 1994; Domínguez-Rodrigo and Pickering, 2003). Experimental and analytical work led to a better understanding of cut-marks macro- and micro-morphological characteristics, allowing for a better understanding of variations in frequency and morphology of butchery marks resulting from the tools used and the force applied during the butchering process (e.g., Walker, 1978; Potts and Shipman, 1981; Bello and Soligo, 2008; Bello et al., 2009; Bello, 2011; Greenfield et al., 2013; Galán and Domínguez-Rodrigo, 2014; Moretti et al., 2015). The frequency, location, and morphology of cut-marks have been suggested to differ depending on the specific butchery process (i.e., skinning, defleshing, disarticulation, fileting of meat; e.g., Binford, 1981; Vigne, 2006; Soulier and Morin, 2016; Soulier and Costamagno, 2017; Otárola-Castillo et al., 2018; Wallduck and Bello, 2018; Bello and Galway-Witham, 2019; Soulier, 2021). The emergence of new methodologies significantly improved our understanding of ancient butchery activities, providing high-precision microscopic tools for cut-mark identification and analysis (e.g., Bello and Soligo, 2008; Bello et al., 2009, 2013; Bello, 2011; Maté-González et al., 2017; Yravedra et al., 2017; Bello and Galway-Witham, 2019; Courtenay et al., 2019; Domínguez-Rodrigo, 2019). High-resolution cut-mark analyses therefore have the potential to provide additional insights into ancient human behaviors and how ancient groups exploited the faunal resources available to them. With this approach, we aim to evaluate the potential effects of resource selection (e.g., faunal composition, anatomical parts butchered), differential use of the cave space, and cultural behavior on site-specific butchery practices.

Our study focuses on the following objectives: firstly, we aim to assess whether cut-mark patterns differ diachronically or spatially within Amud cave, to evaluate whether animal carcasses might have been processed differently over the successive occupations represented in the sequence or within different areas of the cave. Secondly, we explore potential differences in cut-mark patterns in relation to prey-size within Kebara Cave, to evaluate whether specific types of prey could have been processed differently. Finally, we aim to investigate whether strategies of faunal resource exploitation appear similar across the two sites or differed in any way, and, if differences are identified, whether the patterns observed in relation to chronology, site area, or prey size could help explain these discrepancies. Furthermore, an effort is maintained throughout the study to assess the impact of potentially different post-depositional processes between the two sites on cut-mark preservation, in order to formulate our interpretations with caution. However, other factors, and in particular the palimpsest nature of the deposits considered here, limit our ability to confidently explore the full complexity of human behaviors associated with these butchery activities. As such, our objectives are approached as a means of generating informed hypotheses rather than definitive behavioral reconstructions.

2 Archeological sites—background

2.1 Amud cave

Amud Cave is located in the Nahal Amud valley, 5 km northwest of the Sea of Galilee on the edge of the Jordan Valley (Figure 1). It is situated at the top of a steep cliff, ca. 30 m above the present valley floor. The site was first excavated between 1961 and 1964 by a Japanese expedition (Suzuki and Takai, 1970) and re-opened later between 1991 and 1994 by a joint Israeli-American team. The sequence of Amud Cave displays two main stratigraphic units: the uppermost unit A, which mostly consists of mixed Holocene sediments, and, underlying it, unit B formed by anthropogenic Middle Paleolithic sediments (Shahack-Gross et al., 2008; Zeigen et al., 2019; see Supplementary Figure 1). Within this latter stratigraphic unit, four sub-units were identified, well dated by Thermoluminescence and ESR-U series (Valladas et al., 1999; Rink et al., 2001) and numbered B1–B4 from surface to bottom (See Supplementary Data 1.1 for further detail). The uppermost sub-units, B1 and B2, are thought to represent a continuous deposition phase and were dated to ca. 55 Ka BP. The deepest and oldest sub-unit, B4, dated to 68.5–70 Ka BP, is separated from B2 by sub-unit B3, a sterile layer resulting from the collapse of

the cave's roof. The sub-units are not all uniformly distributed among the two main excavated areas of the cave. In particular, sub-unit B1 can be found exclusively in Area (A) along the northern wall of the cave, while sub-unit B4 was encountered mainly in the central part of the cave in the two contingent Areas B and C. All the deposits yielded a large amount of lithic and faunal material, in association with ash, hearths, and other combustion features, especially in the central part of the cave. Taken together, these suggest an intense occupation (Shahack-Gross et al., 2008). In Areas B–C, organized lithic production is associated with hearths, whereas Area A is characterized by higher frequencies of cortical flakes, exhausted, and broken tools, as well as bones in different burning states found within the cemented ash. This led Area A to be interpreted as a discard area (Alperson-Afil and Hovers, 2005; Zeigen et al., 2019). Neanderthal remains were retrieved exclusively from Area A (Hovers et al., 1995, 2000).

In a sample of 5,340 specimens published by Rabinovich and Hovers (2004), one of the main observations was the high degree of fragmentation of the remains resulting in the dominance of small shaft fragments and splinters. This fragmentation pattern considerably constrained taxonomic analyses and the number of identifiable bones available for study. Nonetheless, results from this Rabinovich and Hovers' (2004) study identified the mountain gazelle (*Gazella gazella*) as the most-represented species (12%−14% of the assemblage), which is also part of the most abundant ungulate body size group (BSG) represented in the assemblage (BSG-D: body mass of 15–40 kg, as defined in Rabinovich and Hovers, 2004). Depending on the sub-unit, this size group is between 58% and 60% of the assemblage. Gazelle remains were mostly of juveniles and adults (up to 4–5 years-old). While amounting to <5% of the NISP, the next most represented species are the fallow deer (*Dama mesopotamica*), wild goat (*Capra* sp.), and red deer (*Cervus elaphus*). These taxa were all classified as falling in BSG B and C (80–250 kg and 40–80 kg, respectively, ranging between 5% and 10% of the NISP depending on the sub-units). Other, less abundant taxa included wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). Represented by only a few isolated remains are the common fox (*Vulpes vulpes*) and aurochs (*Bos primigenius*). Rabinovich and Hovers (2004) also suggested the possible presence of larger taxa such as rhinoceros (*Stephanorhinus* sp.), whose remains (mostly long bone splinters) might be misidentified as those of the aurochs, with both taxa falling into the same BSG A (>1,000 kg). Gazelle and fallow deer were shown to be represented by both cranial and post-cranial elements, suggesting that carcasses were likely transported complete to the site, in contrast to larger animals (body mass > 1,000 kg) which were only represented by long bone shafts, fragmented limbs and a few teeth (Rabinovich and Hovers, 2004).

The presence and impact of carnivores was observed to be negligible at Amud cave (Rabinovich and Hovers, 2004), with a notable absence of bone surface alterations caused by carnivores (tooth marks, scratching marks and gnawing marks) on the fauna, a rare phenomenon in Middle Paleolithic cave sites. Burnt bones were reported to represent up to 40% of the identified remains, and the burning colors exhibited were interpreted as likely indicating indirect exposure to fire (Rabinovich and Hovers, 2004). Cut-marks were observed on long bone shafts on 1%−3% of the total assemblage (Rabinovich and Hovers, 2004).

2.2 Kebara cave

Kebara cave is located on the western flank of Mt Carmel (Figure 1), ca. 60 m above current sea level and 2.5 km from the modern seashore. The excavation campaigns at Kebara were initiated by F. Turville-Petre in 1931 and continued by M. Stekelis between 1951 and 1965. Later campaigns were undertaken between 1982 and 1990 (Bar-Yosef and Meignen, 2007; Meignen and Bar-Yosef, 2019, and references therein). Kebara cave displays a long Mousterian sequence, subdivided into 12 units dated from around 60–48 Ka BP (Valladas et al., 1987; See Supplementary Data 1.2 for further details). Large amounts of lithic material, animal remains as well as laminated hearths were uncovered in most of these units. Given the nature of the sediments, the concentration of combustion features and the density of finds, it has been suggested that the cave served mainly as a base-camp during the Mousterian occupation phases (Meignen et al., 2006, 2017).

Two major Middle Paleolithic occupation episodes were identified on the basis of the faunal remains found at Kebara. The first one, referred to as the "midden period," corresponds to units XII to VIII and is characterized by an abundance of fauna and lithic material, as well as by high concentrations of burning evidence, such as cemented hearths and charred/burnt bones (Speth, 2019; Supplementary Figure 2). The bones are heterogeneously distributed, with a higher concentration along the northern wall of the cave and a very low density over the cave floor in the other zones, which has been shown to be independent from diagenetic processes (Weiner et al., 1993, 2007). The bone fragments concentrated in the northern zone show a higher incidence of burning, lower fragmentation rate and lower economic utility [according to Binford's (1978) criteria], suggesting that they were intentionally deposited there as a discard midden over successive human occupations of the cave (Speth, 2019). The over-representation of exhausted cores and cortical elements in this zone in comparison to the rest of the lithic assemblage reinforces this interpretation (Bar-Yosef et al., 1992). In contrast, the "post-midden period" (Units VII–V) shows a lower density of bone remains, with a significantly decreased contrast between the central and northernmost areas of the cave (Speth and Tchernov, 2007; Speth, 2019).

The faunal assemblage collected during the latest excavation campaigns (1982–1990) has been studied extensively by Speth (2019, and references therein), who assessed over 20,670 specimens across the seven Middle Paleolithic units. He identified the mountain gazelle (*Gazella gazella*) as being invariably the most abundant taxa, representing 45.6% of the total NISP, the fallow deer (*Dama mesopotamica*) representing 24.7% of the NISP, aurochs (*Bos primigenius*) 14.3% of the NISP, and red deer (*Cervus elaphus*) 8% of the NISP. Other represented taxa are bears (*Ursus* sp., 3.9% of the NISP) and Equids (2.1% of the NISP). Finally, wild goat (*Capra* sp.), roe deer (*Capreolus capreolus*), hartebeest (*Alcelaphus bucephalus*), and steppe rhinoceros (*Stephanorhinus hemitoechus*) represent <1% of the total number of remains.

TABLE 1 Total number of specimens assessed (*N*) per stratigraphic unit for Amud and Kebara caves, with number of specimens bearing cut-marks ($n_{cut-marked}$), and the number of cut-marked specimens selected for further macro- and micro-morphometric analyses ($n_{detailed-sample}$).

Site	Stratigraphic unit	*N**	$n_{cut-marked}$	$n_{detailed-sample}$
Amud	B1	2,618	10	10
	B2	7,514	107	19
	B4	784	130	14
	Unclear stratigraphic context	569	2	0
	Total Amud	*11,485*	*249*	*43*
Kebara	Unit IX (Total)	1,226	95	34

*Number of specimens assessed, based on the data collected for this study, as well as on published and unpublished data from previous work by R. Rabinovich and J. Speth (Rabinovich and Hovers, 2004; Speth, 2019). Note that for specimens from Amud, *N* refers to the total number of remains (NR), while for those from Kebara, it refers to the number of identified specimens (NISP).

The taphonomic analyses conducted on this assemblage showed no marked difference in the representation of cranial vs. postcranial elements. Evidence of carnivore damage was observed on 9.09% of the NISP in unit IX (Speth, 2019: Table 3.9), and burnt bones were found to represent 9% of the NISP, with burning traces observed more frequently on smaller taxa. The incidence of these burning traces was higher on limbs than on other skeletal elements, and more frequent on diaphysis fragments than on epiphyses, which was interpreted as indication that the burning events were likely related to cooking processes. Cut-marked bones were reported to represent up to 15% of the NISP (excluding dental elements; Speth, 2019).

3 Materials and methods

3.1 Identification and taphonomic assessment of cut-marked specimens

Both Amud and Kebara faunal collections are stored and curated at the National Natural History Collections of the Hebrew University of Jerusalem. A comprehensive faunal study of the main stratigraphic units of Amud is currently in progress by one of the authors (A.J.). Data from previous zooarcheological studies (Rabinovich and Hovers, 2004; Speth, 2019) as well as unpublished databases, were combined to these newly collected data to form our faunal assemblage (*N*, Table 1). Within the assemblage, the specimens recorded as bearing cut-marks ($n_{cut-marked}$ in Table 1) were identified and re-examined to confirm the presence of cut-marks, following published work on the differentiation of butchery marks from taphonomic damage (e.g., Shipman and Rose, 1983; Behrensmeyer et al., 1986; Andrews, 1995; Blasco et al., 2008; Domínguez-Rodrigo et al., 2009; Fernández-Jalvo and Andrews, 2016). For Amud, the studied specimens derive from stratigraphic sub-units B4, B2, and B1, dated respectively to ca. 70 Ka BP and to ca. 56 Ka BP (Valladas et al., 1999; Rink et al., 2001). Across the faunal remains assessed to date within these stratigraphic sub-units ($N = 11{,}485$), 249 bones were identified as bearing cut-marks, accounting for 2.2% of this assemblage (Table 1). For Kebara, we selected specimens from unit IX ($N = 1{,}226$), which is dated to 58.4 ± 0.4 Ka BP (Valladas et al., 1987) and is therefore broadly contemporaneous with the younger sub-units from Amud Cave. Cut-marks were identified on 95 bone fragments from this unit, representing 8.4% of the identified specimens (Table 1).

The specimens bearing cut-marks ($n_{cut-marked}$, Table 1) were first examined and described to record the following parameters for each cut-marked specimen:

Identifications and prey size classification. Osteological and taxonomic identification was conducted for each specimen using previous identifications provided in the collections databases as well as the comparative osteological and archaeozoological collections housed at the National Natural History Collections at the Hebrew University of Jerusalem. To facilitate comparisons between sites and stratigraphic units and evaluate the influence of prey size on the butchery patterns observed, the specimens were grouped using the following body size classification:

- Prey size 1: Small ungulates, 15–45 kg (e.g., gazelle, roe deer; BSG D in Rabinovich and Hovers, 2004).
- Prey size 2: Medium-sized ungulates, 45–200 kg (e.g., red deer, fallow deer, wild goat, boar; BSG B–C in Rabinovich and Hovers, 2004).
- Prey size 3: Large ungulates, 500–1,200 kg (e.g., aurochs, equids; BSG A in Rabinovich and Hovers, 2004)

General taphonomic assessment. The degree of preservation and alteration of the cut-marked specimens was evaluated using the following parameters:

- Exposure (direct or indirect) to fire, assessed on the basis of surface coloring. Specimens partially or fully carbonized and calcined (corresponding to categories 1–6 of Stiner et al., 1995) were categorized as "burnt," while cream-colored fresh-looking specimens (category 0 from Stiner et al., 1995) were categorized as "unburnt." Bone fragments presenting a solid color in shades of brown or orange, which do not show clear signs of charring but whose color is likely the result of indirect exposure to high temperatures, were classified as "likely burnt."
- Element's completeness: classification of each specimen into four categories based on the percentage of preserved bone (Rabinovich et al., 2012): less than half the element preserved (<50%); around half of the element preserved (∼50%), more than half of the element preserved (>50%), complete or nearly complete element (∼100%).
- Evidence of anthropogenic bone fracture: percussion damage (e.g., adhesive flakes, notches, percussion grooves, scraping marks and striations as referred to by Vettese et al., 2020; see also references therein), were identified and recorded when present.
- Presence/absence of other taphonomic alterations that may interfere with the reading of cut-marks (water dissolution,

weathering, root-marks, gnawing etc.) were also recorded using taphonomy manuals and atlases (Fernández-Jalvo et al., 2010; Pokines et al., 2021; Fernández-Jalvo and Andrews, 2016) as well as reference material from the National Natural History Collections of the Hebrew University of Jerusalem.

3.2 Macroscopic and micro-morphometric cut-marks analyses

A sub-sample of specimens bearing cut-marks was further selected for detailed macroscopic assessment and micro-morphometric analyses (hereafter "detailed sample," Table 1). For the Amud material, 43 specimens were selected in such a way that all of the studied sub-units and spatial areas of the cave would be equally represented, while excluding specimens from disturbed contexts or uncertain stratigraphic attribution (Supplementary Figures 1B, C). For Kebara, 34 specimens were selected for detailed analyses and originate from three squares situated in proximity to the northern cave wall (F19, G19, H19, and I13; Supplementary Figure 2B). Specimens in this sub-sample were measured and analyzed using macro- and microscopic techniques to quantify, characterize, and measure the cut-marks. They represent, respectively, 17.3% and 35.8% of the specimens identified as bearing cut-marks from Amud and Kebara, and account, respectively, for 0.4% and 3% of the total assemblages.

Macroscopic analyses. The selected specimens were first cleaned by applying acetone with a soft brush to remove the sediment embedded in the incisions or overlaying glue residues masking the marks. With the aid of a binocular lens (magnification: 10x−30x), the bone surfaces were assessed, drawn to record the location and morphology of the cut-marks, and measured with a caliper. The following parameters were recorded or calculated:

- Surface area (cm²): Quantification of the cortical surface area of each specimen. The shape of each specimen was simplified as a combination of smaller regular geometric figures (rectangles, isosceles or right-angled triangles, semicircles, etc.) whose areas were calculated separately and added together (Supplementary Figure 3A).
- Number of cut-marks per fragment (n_{cut}, Table 1).
- Cut-marks density per fragment: number of cut-marks per specimen relative to its surface area.
- Linearity of each incision in plan-view: linear (i.e., "straight") or non-linear (curved, sinuous or drawing a broken-line; Supplementary Figure 3B). The number of linear incisions identified was then divided by the total number of incisions observed on the specimen to calculate the linearity frequency for each specimen (ranging from 0—no incisions are linear, to 1—all incisions are linear).
- Layout of the cut-marks: qualitative description of how the cut-marks were organized (parallel to or overlapping other marks, close or far from each other, etc.), quantitative evaluation of the number of incisions crossing at least one other incision and the number of intersection points formed.
- Quantitative assessment of complete cut-marks vs. cut-marks interrupted by the breakage of the bone edge (note: cut-marks partially covered by concretions or altered were considered uninformative and not included in this assessment).

Micro-morphometric analyses. The selected specimens were studied using two Focus Variation microscopes, the Alicona InfiniteFocus G5+ (AIF) and the Portable Alicona RL (ARL) optical surface measurement systems (Optimax Ltd, Market Harborough, UK). These instruments are housed at the Imaging and Analysis Centre, Science Innovation Platforms, at the Natural History Museum (London, UK). The portable ARL system was transported and used directly at the National Natural History Collections of the Hebrew University of Jerusalem for the first phase of data collection. These optical systems allow for the non-destructive and non-invasive three-dimensional (3D) analysis of microscopic surface features. They create a series of individual image planes and overlapping focus levels to produce a virtual reproduction of the object in 3D. The recorded *x*, *y*, and *z* coordinates of each reconstructed pixel can be then used to conduct linear measurements of the surface features using the AIF software IF-MeasureSuite (Bello and Soligo, 2008; Bello and Galway-Witham, 2019). For both microscopes, a 10x lens was used to capture the finer detail of the cut-marks (AIF: working distance = 17.5 mm; numerical aperture = 0.3; vertical resolution = 100 nm; ARL: working distance = 17.5 mm; numerical aperture = 0.3; vertical resolution = 150 nm). Both systems offer the same level of accuracy and precision [finest lateral topographic resolution, AIF = 1.76 μm; ARL = 2 μm; Minimum measurable profile roughness (Ra), AIF = 0.5 μm, ARL = 0.55 μm], and are therefore expected to yield comparable outputs.

Linear and profile variables of the cut-marks were recorded following the methodology proposed by Bello and Soligo (2008), Bello et al. (2009), and Bello et al. (2013), by extracting a 2D profile from the mid-point of each incision (Figure 2). The following variables were considered:

- Length: Maximum length of the incision.
- Width of the incision at the surface (WIS): maximal length between the two points where each slope forming the incision intersects with the unaffected bone surface.
- Depth of the incision (D): maximum depth of the incision, measured by drawing a line perpendicular to the WIS from the lowest point of the cut-mark profile.
- Opening angle (OA): angle at the convergence point between two lines fitted onto the left and right slopes of the incision.
- Floor radius (Rd): radius of a circle fitted to the floor of the incision, where the profiles of the left and right slopes start to converge.

3.3 Statistical analyses

The data were analyzed across the sites and stratigraphic units to evaluate whether specific cut-marks patterns could be observed. Results were compared between the Amud and Kebara samples, as

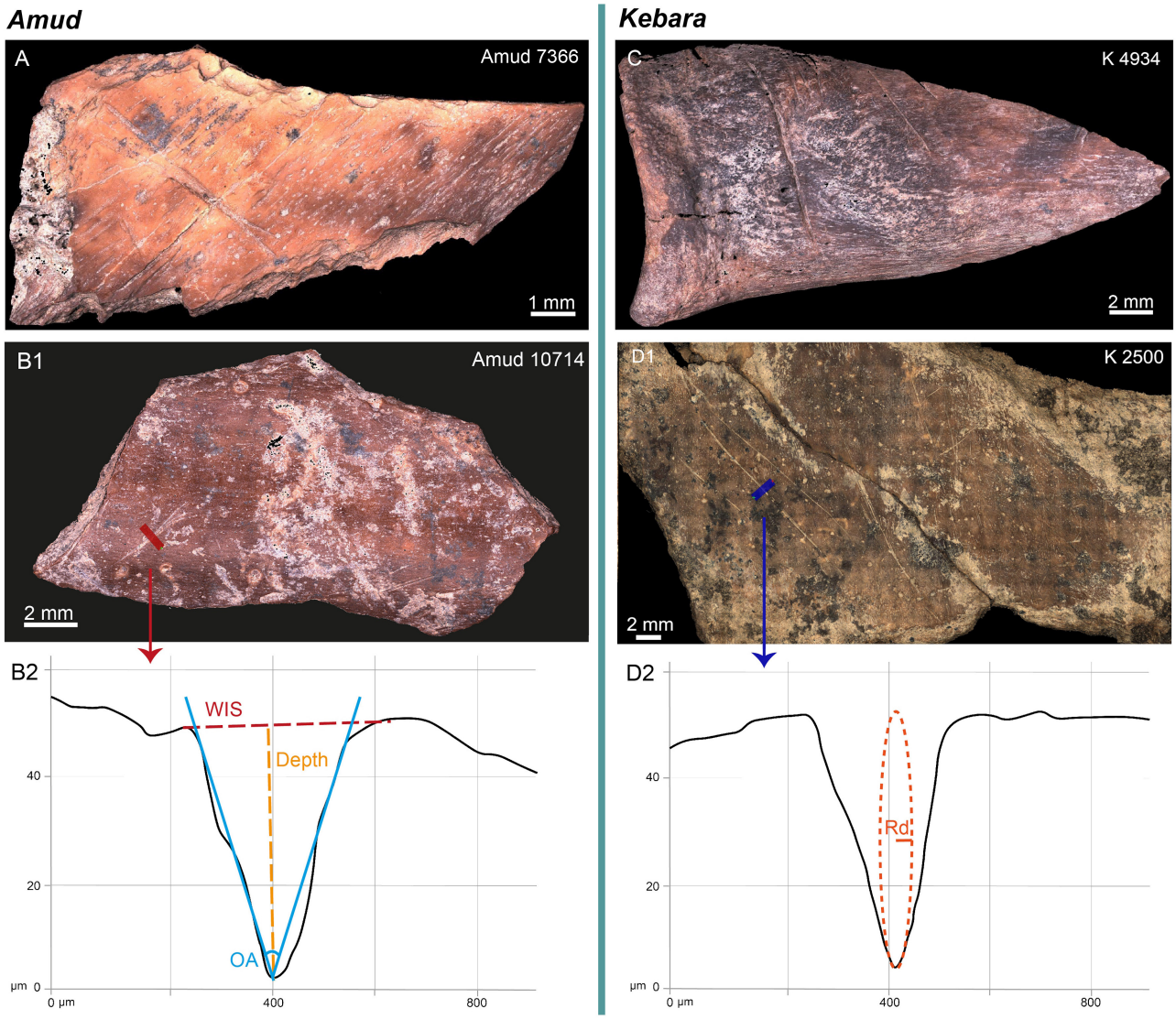

FIGURE 2
Alicona images (10× lens) of specimens from Amud **(A, B)** and Kebara **(C, D)**, with examples of the associated profile diagrams showing the variables measured at the mid-point of the cut-marks studied, with: in **(B2)**, the width of the incision on the surface (WIS), the depth of the incision **(D)**, the opening angle of the incision (OA); in **(D2)**, the floor radius (Rd) of the incision. Note: due to the difference in scale between the *X*- and *Y*-axes, the circle used to calculate the floor radius (Rd) appears elliptical.

well as between and within the Amud sub-units to assess intra-site spatial and chronological variability for this site. The spatial analysis of cut-marked specimens from Amud focused on sub-units B1–B2, to compare specimens from Area A to specimens from Areas B–C (Supplementary Figure 1).

Descriptive statistics and plots were computed using R Studio (version 2022.12.0+253, Posit Team, 2022; "*ggplot*" Wickham, 2006), and statistical tests were carried out using Past (version 4.05; Hammer et al., 2001) or R Studio. Statistical comparisons between groups were only carried out for sample sizes ≥ 5. For quantitative variables, the data was analyzed using non-parametric tests as the data was skewed and did not follow a normal distribution: Mann-Whitney-Wilcoxon or Mann-Whitney *U* tests (α 0.05) were used for pairwise comparisons, and Kruskal-Wallis tests followed by Dunn tests (where relevant) were used for comparisons between three groups or more. Qualitative data was analyzed using Chi square tests for independence (α 0.05) to determine whether any observed difference between samples were statistically significant. Chi square *post-hoc* tests include residuals analyses and, when significant differences were revealed for a contingency table of a matrix larger than 2 × 2, Fisher's exact test was applied to the collapsed contingency tables following DeViva (2014; see Sharpe, 2015). In addition, the micro-morphometric measurements were further tested across samples through a series of Principal Component Analyses (PCA) performed in R studio ("*factoextra*"; Kassambara and Mundt, 2017) on a covariance matrix, using all five variables (length, WIS, depth, OA, and Rd) as a way to assess the overall micro-morphometric variation of cut-marks across samples when analyzed as three-dimensional features. To prepare the data for PCA, the variable OA was converted from circular to linear

data (OA_{linear}) following Courtenay et al. (2021) and Valtierra et al. (2024), to ensure all the variables considered were linear.

4 Results

4.1 Identifications and taphonomic assessment of cut-marked specimens

Species and prey size representation. While the same taxa were exploited at both sites, taxon representation is highly heterogeneous between the two sites (Figure 3A). This is reflected in our cut-marked samples. The Amud sample comprises almost exclusively taxa falling into prey size 1 (73.9%), and fewer from prey size 2 (7.2%) and includes a few unidentified specimens (not included in prey size comparisons). The sample from Kebara is mostly represented by specimens from prey size 1 and 2 (40% and 42.1%, respectively), and comprises also large ungulates (i.e., prey size 3, 17.9%).

Body parts representation. Long bone shafts are the most represented anatomical elements across Amud sub-units, where they constitute 60%−91.6% of the cut-marked specimen. They represent only 35.8% of the Kebara sample, where the distribution of body parts in the Kebara sample is relatively balanced and all body parts are well-represented (Figure 3B).

These proportions are roughly equivalent in the detailed samples (Supplementary Figure 4D). Long bone shafts represent up to 78.6% of the selected specimens from Amud and 29.4% of the Kebara detailed sample. Prey size 1 is the most prominent category represented in the detailed samples of Amud, and represents 50% of the Kebara detailed sample. However, it is worth mentioning that only three specimens of aurochs and equid are present in the detailed sample from Kebara (Supplementary Figure 4).

Exposure to fire. The majority of Amud cut-marked specimens was identified as likely burnt (n = 172, 68.5%). Another 52 were recognized as "burnt" (20.7%), and 27 as unburnt (10.7%). The majority of Kebara specimens was classified as unburnt (n = 90, 89.1%). An additional seven specimens were identified as heavily burnt (6.9%), and four (<0.1%) as likely burnt (Table 2 and Figure 3C). The differences between the two sites are statistically significant, as well as intra-site differences within Amud, with sub-layer B1 showing less burnt specimens than the other sub-units (χ^2 = 202.42, df = 2, $p < 0.001$; Supplementary Table 1).

Element completeness. Out of the 249 Amud cut-marked specimens, the greater majority (97.8%) represent less than half of a complete skeletal element; one was complete (0.4%), three were preserved to more than 50% (1.2%), and four were preserving half of the element (1.6%). Out of the 95 cut-marked specimens from Kebara, 16 items were complete (15.8%), the rest of the specimens (84.2%) preserved less than half of the skeletal element (Table 2 and Figure 3D). Chi² tests confirmed these inter-sites differences were significant (χ^2 = 19.682, df = 2, $p < 0.001$), and reveal further differences within the Amud cut-marked assemblage, with B1 presenting more complete elements than the other sub-units (χ^2 = 9.615, df = 2, $p = 0.008$; Supplementary Table 1).

Taphonomic bone surface alterations. Carnivore impact on the faunal remains is practically non-existent at both sites. Other major fossildiagenetic alterations, such as striations due to trampling, root-marks, water dissolution and drying cracks are also minimal and, when present, did not affect the reading of the butchery marks (Table 3).

Anthropogenic bone surface modifications. Considering all sub-units together, specimens bearing cut-marks represent 2.2% of the assessed assemblage for Amud, while they account for 7.8% of the Kebara layer IX assemblage. These numbers are in line with those provided in previous publications of both assemblages, i.e., 1%−3% of the remains studied from Amud depending on the sub-units (Rabinovich and Hovers, 2004), and 15% of the identified remains from Kebara (Speth, 2019). For Amud, we recognized 10 cut-marked bones bearing impact notches. In Kebara, two cut-marked specimens displayed impact notches. Both specimens from Kebara and four from Amud were included in our detailed sample.

The difference observed in the frequencies of burnt and fragmented specimens in both samples, as well as the scarcity of other anthropogenic and non-anthropogenic bone surface modifications, are mirrored in the detailed samples of both sites (Supplementary Table 2 and Supplementary Figure 4).

4.2 Amud cave: spatial and chronological cut-mark variability

4.2.1 Macroscopic analyses

Surface area. At Amud, differences in the dimensions of surface areas were observed between sub-units, with specimens from sub-unit B1 being bigger (median = 5.8 cm², IQR = 3.88) compared to specimens in sub-units B2 (median = 1.65 cm², IQR = 1.45) and B4 (median = 2 cm², IQR = 2.17). The difference is statistically significant [$H_{(2)} = 13.86$, $p < 0.001$; Dunn's *post-hoc* test $p_{B1/B2} < 0.001$, $p_{B1/B4} < 0.001$, $p_{B2/B4} = 0.468$].

Number of cut-marks and cut-marks density. While the number of cut-marks per specimen is similar across the different sub-units and areas of the site (Tables 4A, C), there are differences in cut-mark density between the two main occupations areas, with a higher density of incisions per fragment on specimens from Areas B–C (median = 0.082; IQR = 0.094) compared to specimens from Area A (median = 0.015; IQR = 0.015; $U = 46$, $p = 0.026$; Figures 4A, B).

Linearity of the incisions. Within the Amud cave sequence, sub-unit B4 significantly differs from B1 and B2, featuring fewer linear incisions (χ^2 = 17.787, df = 2, F-exact$_{B1+B2/B4}$ $p < 0.001$, F-exact$_{B1/B2}$ $p = 0.128$; Table 4A and Supplementary Table 3E). No difference was found across the areas of the site (Table 4C and Supplementary Table 3D).

4.2.2 Micro-morphometric analyses

Length of the cut-marks. There is no significant difference in incision length between the Amud sub-units [$H_{(2)} = 1.1629$, $p = 0.559$; Table 5A and Supplementary Table 4E], nor between Amud's peripheral area (Area A) and the central part of the cave (Areas B and C; $W = 574$, $p = 0.313$; Table 5C and Supplementary Table 4D).

Width of the incisions at the surface (WIS). Significant differences are found between the Amud sub-units [$H_{(2)} = 15.558$, $p < 0.001$], with specimens from B1 presenting wider cut-marks than specimens from B2 and B4 (Table 5A and

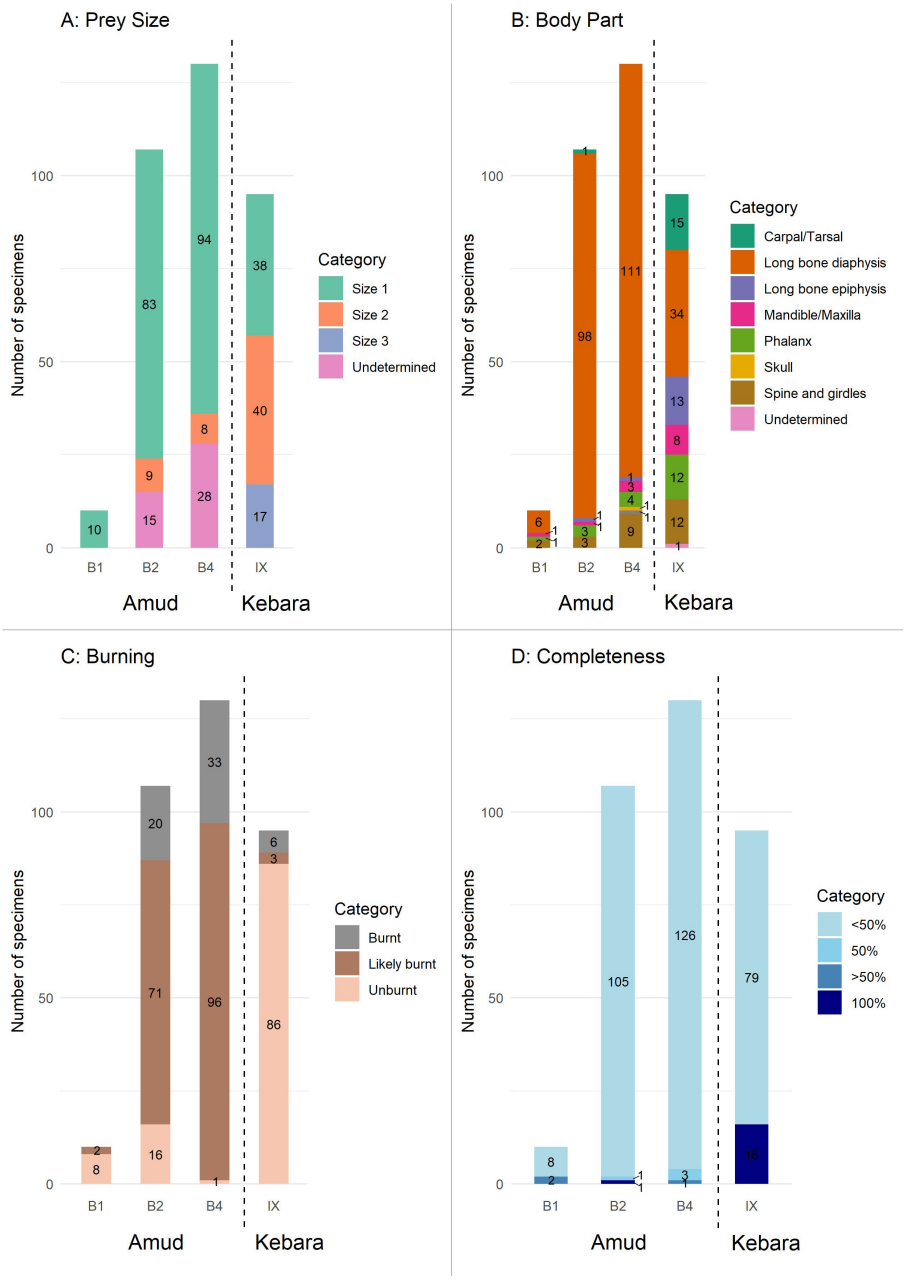

FIGURE 3
Cut-marked assemblage composition and main evidence of anthropic modifications for each site and relevant sub-units. **(A)** Prey size representation, **(B)** body part representation, **(C)** proportion of specimens with identified evidence of exposure to fire/heat source, and **(D)** completeness of the specimens.

Supplementary Table 4E). WIS values differ between the two areas, with significantly wider cut-marks found in Area A (median = 208.72 µm, IQR = 168.92) compared to Areas B–C (median = 151.24 µm, IQR = 147.48; W = 1,234, p = 0.022; Table 5C and Supplementary Table 4D).

Depth of the incisions. Depth values are relatively homogenous across sub-units within the Amud sample [$H_{(2)}$ = 4.8372, p = 0.089; Table 4B and Supplementary Table 4E]. No significant difference was found for the depth of the incisions when comparing cut-marks from Area A to Areas B–C (W = 1,009, p = 0.684; Table 5C and Supplementary Table 4D).

Opening angle (OA). There are significant differences in OA values across the Amud sub-units [$H_{(2)}$ = 7.9675, p = 0.019], with B2 presenting significantly lower OA values compared to B1 and B4 (Table 4A and Supplementary Table 4E). Incisions present significantly higher OA values in Area A (median = 134.94°, IQR = 35.66) than in Areas B–C (median = 119°, IQR = 32.98; W = 1,198, p = 0.047; Table 5C and Supplementary Table 4D).

Floor radius (Rd). Rd was found to differ significantly across the Amud sub-units [$H_{(2)}$ = 44.858, p < 0.001], with higher values in B1 (median = 53.77 µm; IQR = 53.06) compared to B2 (median = 26.1 µm; IQR = 26.23) and B4 (median = 32.81 µm; IQR = 33.78;

TABLE 2 General taphonomic assessment of the cut-marked samples, for each site/sub-unit.

Site	Unit/sub-unit	Sample size ($n_{cut-marked}$)	Exposure to fire/heat source			State of completeness			
			Burnt	Likely burnt	Unburnt	<50%	50%	>50%	100%
Amud	B1	10	0	2 (20%)	8 (80%)	8 (80%)	0	2 (20%)	0
	B2	107	20 (18.7%)	71 (66.3%)	16 (15%)	105 (98.1%)	1 (0.95%)	0	1 (0.95%)
	B4	130	33 (25.4%)	96 (73.8%)	1 (0.8%)	126 (96.9%)	3 (2.3%)	1 (0.8%)	0
	Unclear	2	0	1 (50%)	1 (50%)	2 (100%)	0	0	0
	All sub-units	**249**	*53 (21.3%)*	*170 (68.3%)*	*26 (10.4%)*	*241 (96.8%)*	*4 (1.6%)*	*3 (1.2%)*	*1 (0.4%)*
Kebara	Layer IX	**95**	6 (6.3%)	3 (3.2%)	86 (90.5%)	79 (83.2%)	0	0	16 (16.8%)

Evidence of exposure to fire/heat source is presented as the total number of specimens identified as "burnt" or "unburnt," or classified as "likely burnt." The state of completeness is presented using the following categories: <50% (less than half of the skeletal element is preserved); 50% (about half of the element is preserved), >50% (more than half of the element is preserved), 100% (the element is complete or nearly complete). The percentages provided in parentheses reflect the proportion of specimens displaying the relevant modification, relative to the sample ($n_{cut-marked}$).

TABLE 3 Number of cut-marked specimen bearing additional anthropogenic and non-anthropogenic bone surfaces alterations, per site and stratigraphic unit.

Site	Stratigraphic unit	Sample size ($n_{cut-marked}$)	P	R	E	D	W	G	Total
Amud	B1	10	1 (10%)	0	3 (30%)	0	3 (30%)	0	7 (70%)
	B2	107	1 (0.9%)	5 (4.7%)	11 (10.3%)	2 (1.9%)	5 (4.7%)	0	24 (22.4%)
	B4	130	8 (6.2)	5 (3.8%)	11 (8.5%)	1 (0.8)	7 (5.4%)	0	32 (24.6)
	Unclear	2	0	1 (50%)	0	0	0	0	1 (50%)
	Total Amud	**249**	*10 (4%)*	*11 (4.4%)*	*25 (10%)*	*3 (1.2%)*	*15 (6%)*	*0*	*64 (25.7%)*
Kebara	Unit IX (Total)	**95**	8 (8.4%)	0	6 (6.3%)	0	4 (4.2%)	1 (1%)	19 (20%)

P, percussion notches; R, root marks; E, exfoliated cortical surface; D, water dissolution patches; W, weathering (causing longitudinal cracks and scaling of the cortical surface); and G, Gnawing marks. The percentages provided in parentheses reflect the proportion of specimens displaying the relevant modification, relative to the sample ($n_{cut-marked}$).

Table 5A). Incisions differ significantly in their Rd values between the two main occupation areas ($W = 1{,}478$, $p < 0.001$), with significantly larger floor radii for specimens from Area A (median = 70.58 µm, IQR = 65.15) compared to Areas B–C (median = 26.19 µm, IQR = 27.88; Table 5C and Supplementary Table 4D).

Principal component analysis. The first two components (PC1 and PC2) explain 37.9% and 32.2% of the variance, respectively (Supplementary Table 5B). PC1 is mostly influenced by OA and Depth, which contribute positively to this component. PC2 is mostly influenced by WIS and Rd, which contribute negatively to this component. When comparing the variability of the incisions' overall form, cut-marks from B1 display clearly a wider range of values compared to all the other samples (Figures 5B, C).

4.3 Amud and Kebara: comparisons of the butchering marks between sites (detailed sample)

4.3.1 Macroscopic analyses

Surface area. The 43 specimens of Amud selected for further analysis are all fragmented, whereas seven out of the 34 specimens from Kebara are complete (20.6%). The median fragment surface area is significantly smaller in Amud (median = 2.49 cm², IQR = 2.92) compared to Kebara (median = 17.78 cm², IQR = 20.9; $U = 118$; $p < 0.001$; Figure 4C and Table 4). The surface areas are more variable in Kebara, with fragments ranging from 1.3 to 97.7 cm², while fragment surface areas at Amud are within a much narrower size range (between 0.3 and 9.4 cm²). As expected, at Kebara, the specimen surface area differs significantly according to prey size [$H_{(2)} = 6.142$, $p < 0.001$], with smaller ungulates producing smaller bone fragments.

To test whether the difference in surface area between the two sites might be due to differences in the prey sizes represented in each sample (i.e., Amud dominated by small ungulates), we compared the surface area of fragments from Amud and Kebara only for specimens attributed to prey size 1. Specimens from Kebara are significantly larger ($U = 95$, $p < 0.001$) and more variable in size compared to those from Amud (Amud: $n = 38$, median = 2.53 cm², IQR = 2.79; Kebara: $n = 17$, median = 7.40 cm², IQR = 18.44).

Number of cut-marks and cut-mark density. Altogether, 936 cut-marks were observed on the 43 specimens studied from Amud, and 736 on the 34 specimens studied from Kebara, which corresponds to an average of 21.3 and 21.4 incisions per specimen, respectively, with comparable variances (Table 4). When scaling the number

TABLE 4 Assessment of the anthropogenic modifications in the detailed-samples for (A) each site/sub-unit, (B) each prey size category, and (C) for each occupation Area at Amud Cave (sub-units B1–B2).

Site	Unit/sub-unit	Sample size (*n*)	Surface area (mm^2)		n_{cuts}		Cut-marks density		Linearity freq.	
			Median	IQR	Median	IQR	Median	IQR	Median	IQR
(A)										
Amud	B1	10	580.12	387.74	14.50	13	0.023	0.025	0.80	0.27
	B2	19	164.58	145.46	13	14.50	0.082	0.100	0.70	0.44
	B4	14	199.90	216.75	8	41.50	0.051	0.100	0.65	0.48
	All sub-units	43	*248.69*	*291.93*	*13*	*18*	*0.046*	*0.094*	*0.70*	*0.48*
Kebara	Layer IX	34	1778.41	2090.45	14	15.75	0.009	0.014	0.90	0.29
(B)										
Amud	Size 1	38	252.87	278.68	13	18.50	0.052	0.094	0.69	0.46
	Size 2	2	498.67	66.30	19	8	0.037	0.011	0.65	0.20
Kebara	Size 1	17	740.30	1844.50	15	15	0.010	0.017	1	0.08
	Size 2	14	2618.46	2242.76	10	14.50	0.008	0.006	0.79	0.17
	Size 3	3	2609.70	1898.88	15	47.50	0.014	0.009	0.67	0.03
(C)										
Amud (B1–B2)	A	4	633.14	394.97	11	16.5	0.015	0.015	0.81	0.08
	B–C	9	164.58	145.20	11	14	0.082	0.094	0.82	0.55

Median values and interquartile ranges (IQR) are reported for each sample when assessing surface area (in mm^2), number of cut-marks per fragment ("n_{cuts}"), number of cut-marks per fragment relative to the surface area ("cut-marks density"), and number of linear incisions per fragment relative to curved/sinuous incisions ("linearity freq.").

of incisions to fragment size (n incisions/cm^2), we find that the density of incisions is significantly higher at Amud (mean = 10.34, median = 4.55) compared to Kebara (mean = 1.58, median = 0.89; $U = 211$, $p < 0.001$). Fragments attributed to prey size 1 display a much higher variability in cut-mark density compared to any other prey size categories in either site (Supplementary Table 3 and Figure 4A). When considering prey size 1 only, cut-mark density is higher at Amud (values are, mean = 9.3; median =5.8) compared to Kebara (are, mean = 2.1, median = 0.9).

Linearity of incisions. In both detailed samples, the majority of the cut-marks are linear. However, specimens from Amud present significantly more curved or sinuous incisions compared to specimens from Kebara ($\chi^2 = 51.777$, df = 1, $p < 0.001$; Table 4). The Amud sample also shows a greater variability per specimen, with more specimens presenting both linear and curved incisions on a same fragment compared to Kebara. Differences between prey size categories also appear for both sites: in Kebara, small ungulates (prey size 1) display more linear cut-marks than other prey size categories, while large ungulates (prey size 3) feature more sinuous incisions compared to the other two prey size classes ($\chi^2 = 12.733$, df = 2, F-exact$_{1+2/3}$ $p = 0.012$, F-exact$_{1/2}$ $p = 0.011$). For Amud, the trend is reversed, with small ungulates displaying less linear cut-marks than medium-sized ungulates ($\chi^2 = 13.437$, df = 1, $p < 0.001$; note, however, the disparity of sample sizes between the two groups).

Layout and completeness of cut-marks. We counted 191 incisions crossing at least one other mark on the bones from the Amud sample (37.3% of the total number of cut-marks), and 112 on those from the Kebara sample (15.2%). The cut-marks on specimens in the Amud sample tend to cross other incisions more often than those in the Kebara sample: we counted a minimum of 308 intersection points between incisions on the specimens from Amud, compared to a minimum of 127 intersection points from Kebara (e.g., Figure 6). The completeness of the cut-marks was evaluated for 671 incisions in the Amud sample, and 536 incisions (in the Kebara sample). Similar proportions of complete cut-marks (i.e., uninterrupted by bone fracture) were found at both sites: 465 cut-marks (86.8%) were complete at Kebara, while 559 cut-marks (83.3%) were complete at Amud.

4.3.2 Micro-morphometric analyses

Length of the cut-marks. Cut-mark length differs significantly between the two sites (Amud median = 1.88 mm, $n = 288$; Kebara median = 3.38 mm, $n = 232$; Table 5A and Figure 6). Incisions from Kebara present a higher range of lengths (IQR = 3.7) compared to Amud (IQR = 1.36; $W = 12{,}219$, $p = 1.341\text{e-}15$). When considering prey size, no significant difference in incision length can be observed between the various prey size categories within the Amud sample ($W = 1765.5$, $p = 0.476$). More variation in lengths can be observed within the Kebara sample [$H_{(2)} = 14.74$, $p = 0.0006$], with longer incisions observed for prey size 2 (median = 3.77 mm, IQR = 4.04) and prey size 3 (median = 4.71 mm, IQR = 5.2; Table 5B). Cut-marks on specimens from prey size 1 are significantly longer at Kebara compared to Amud ($W = 5{,}958$, $p = 0.001$; Supplementary Table 4B).

Width of the incision at the surface (WIS). No significant difference was found between the two sites (Amud median =

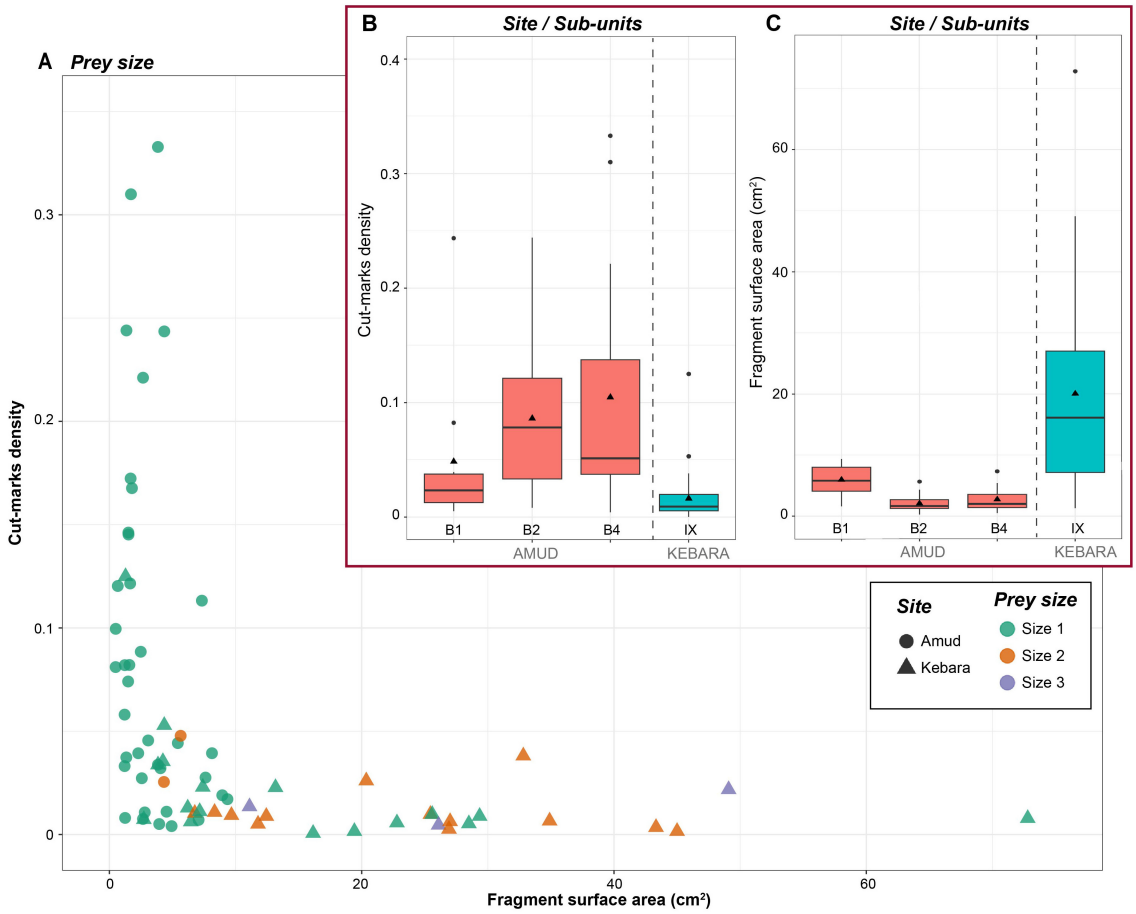

FIGURE 4
Cut-marks density for the Amud and Kebara samples, **(A)** per prey size (Size 1: small ungulates; Size 2: medium-sized ungulates; Size 3: large ungulates), and **(B)** per site and sub-units, and **(C)** Fragment surface area (cm²) per site and sub-units; (boxplots, median and interquartile range; triangles, mean; dots, outliers).

170.04 µm; IQR = 149.35; Kebara median = 182.33 µm, IQR = 147.3; W = 29,975, p = 0.170; Table 5A and Figure 6). WIS values are relatively homogeneous across prey size categories within the Amud sample (W = 1,994, p = 0.489). At Kebara these values are more variable [$H_{(2)}$ = 11.11, p = 0.004], with significantly wider incisions observed on prey size 3 (i.e., large-sized; median = 294.36 µm, IQR = 166.35) compared to size 2 (median = 166.72 µm, IQR = 114.04) and size 1 (median = 182.01 µm, IQR = 143.23; Table 5B). When focusing on prey size 1, no significant difference in width was found between the Amud and Kebara samples (W = 11,437, p = 0.887; Supplementary Table 4B).

Depth of the incisions. Cut-marks on specimens from Kebara display a wider range of depths (median = 31.17 µm; IQR = 54.96) than those from Amud (median = 26.16 µm; IQR = 34.68), although this difference is not statistically significant (W = 30,612, p = 0.101; Table 5A and Figure 6). The depth of the incisions differs significantly depending on prey size within the Kebara sample [Kebara: $H_{(2)}$ = 7.0547, p = 0.029; Amud: W = 1,773, p = 0.089; Table 4B]: in Kebara, prey size class 3 specimens bear deeper cut-marks (median = 45.33 µm, IQR = 34.67) than size class 2 specimens (median = 26.2 µm, IQR = 50.52). When focusing on prey size 1, no significant difference in depth was found between Amud and Kebara (W = 10,931, p = 0.164; Supplementary Table 4B).

Opening angle (OA). The opening angle of the incisions does not differ significantly between the two sites (Amud median = 130.37°, IQR = 32.88; Kebara median = 126.08°, IQR = 38.46; W = 36,082, p = 0.116; Table 5A and Figure 6). No significant difference in OA values was observed between prey size categories within the Kebara sample [$H_{(2)}$ = 2.2033, p = 0.332]. In contrast, in the Amud sample, there are significantly higher OA values on specimens from prey size 1 (W = 3,240, p = 0.002; Table 5B). Prey size 1 specimens in Kebara have significantly lower OA values (W = 13,874, p = 0.029; Supplementary Table 4B) compared to Amud.

Floor radius (Rd). No significant difference in incision floor radius was found between the two sites (Amud median = 38.22 µm; IQR = 44.32; Kebara median = 39.71 µm, IQR = 38.71; W = 29,743, p = 0.29; Table 5A and Figure 6). Rd values are relatively homogeneous across prey sizes within both samples [Amud: W = 2,155, p = 0.910; Kebara: $H_{(2)}$ = 2.6993, p = 0.259; Supplementary Table 4C]. When focusing on prey size 1, no significant difference in Rd was found between the Amud and Kebara samples (W = 11,968, p = 0.302; Supplementary Table 4B).

TABLE 5 Cut-marks micro-measurements per (A) each site/sub-unit, (B) each prey size category represented, and (C) each occupation area (i.e., Area A or Areas B–C) within the Amud sub-units B1–B2.

Site	Sub-unit/layer	*n*	Length (mm)		WIS (μm)		Depth (μm)		OA (°)		Floor radius (μm)	
			Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
(A)												
Amud	B1	97	1.91	1.19	206.27	178.82	28.91	39.53	133.26	34.16	53.77	53.06
	B2	82	1.94	1.42	153.83	153.96	27.20	31.32	121.96	31.00	26.10	26.23
	B4	109	1.69	1.52	150.35	99.43	23.40	31.53	134.56	31.32	32.81	33.78
	All sub-units	*288*	*1.88*	*1.36*	*170.04*	*149.35*	*26.16*	*34.68*	*130.37*	*32.88*	*38.22*	*44.32*
Kebara	Layer IX	232	3.38	3.70	182.33	147.30	31.17	54.96	126.08	38.46	39.71	38.71
(B)												
Amud	Size 1	230	1.94	1.31	171.65	152.08	27.41	34.31	133.59	33.47	39.43	44.73
	Size 2	20	1.85	2.06	194.87	202.71	35.82	50.44	105.62	43.13	44.91	44.44
Kebara	Size 1	105	2.60	2.43	182.01	143.23	32.87	62.49	122.85	40.84	37.58	42.30
	Size 2	98	3.77	4.04	166.72	114.04	26.20	50.52	127.11	39.92	44.93	42.28
	Size 3	29	4.71	5.20	294.36	166.35	45.33	34.67	128.44	45.61	38.92	24.74
(C)												
Amud (B1/B2)	A	48	1.87	0.94	208.72	168.92	44.47	63.29	134.94	35.66	70.58	65.15
	B–C	40	1.96	1.51	151.24	147.48	28.76	30.02	119.00	32.98	26.19	27.88

The median and interquartile range (IQR) is presented for each variable: Length, Width of the Incision at the Surface (WIS), Depth, Opening Angle (OA), and Floor radius. n represents the total number of individual cut-marks measured for each sample.

Principal component analysis (PCA). The first two components (PC1 and PC2) explain 39.6% and 26.7% of the variance, respectively (Supplementary Table 5A). PC1 is mostly influenced by WIS and Depth, which contribute negatively to this component. PC2 is mostly influenced by Rd (positively) and OA (negatively). Visualization of overall cut-marks form patterns through PCAs shows that cut-marks greatly overlap in their measurements across sites and sub-units, although samples from Amud B1 and Kebara IX are the most variable in terms of cut-marks form, while Amud B2 and B4 display consistently shorter, shallower, and narrower cut-marks (Figure 5 and Supplementary Table 5A).

5 Discussion

Within a broader unified technological tradition of the Late MP in the Levant, (e.g., the use of similar flaking methods to produce artifacts of similar shape), the stone tools from Kebara and Amud show some technological variations (e.g., Meignen, 1995) interpretable as local traditions accumulated through social learning (e.g., Hovers and Belfer-Cohen, 2013). Here we investigate whether the exploitation of faunal resources at the two sites, as evidenced in this study, might also reveal local traditions that varied depending on resource selection, differential use of the cave space, and site-specific butchery practices.

Previous studies of the faunal assemblages suggested an overall comparable species composition at both sites for medium- and large-sized ungulates, at the same time highlighting some variations between the two sites. Specifically, large ungulates such as aurochs (*Bos primigenius*) or equids (*Equus* sp.) are better represented at Kebara compared to Amud (Speth and Tchernov, 2001; Rabinovich and Hovers, 2004). Signs of burning were observed in Kebara on 9% of the identified bone remains ($n = 913$; Speth, 2019). In contrast, up to 40% of Amud identified remains were burnt [$n = 2{,}124$; in addition to another 14% ($n = 3{,}212$) observed on unidentifiable bone fragments; Rabinovich and Hovers, 2004]. Finally, specimens from Amud were heavily fragmented, with recorded fragment sizes averaging around 27.4 mm in length but <1 mm in width, while the length recorded for the specimens of Kebara averages around 35.8 mm (Rabinovich and Hovers, 2004; Speth, 2019 and references therein). In the present study, analyses of the cut-marked specimens replicate these observations (Sections 3.1, 3.2), confirming that bone fragments from Amud are significantly smaller in size and more affected by exposure to fire than those from Kebara.

Although the surface area of the Kebara specimens is, on average, generally larger than that of the Amud specimens, both samples display similar numbers of cut-marks per specimen. This results in a much higher cut-mark density on the small bone fragments from Amud and a more clustered appearance of cut-marks, which tend to be placed close to each other and intersect more often than on the cut-marked specimens from Kebara. In addition, a smaller proportion of the observed cut-marks were found to be linear on the bones from Amud, giving an overall impression of clutter in comparison to the specimens from Kebara. Cut-marks from Kebara tend to be significantly longer (see below) and more variable in their depth than those from Amud. Otherwise, the microscopic characteristics of the cut-marks in the detailed samples from the two sites are relatively similar, with comparable values of floor radius, opening angle and width at the surface, which

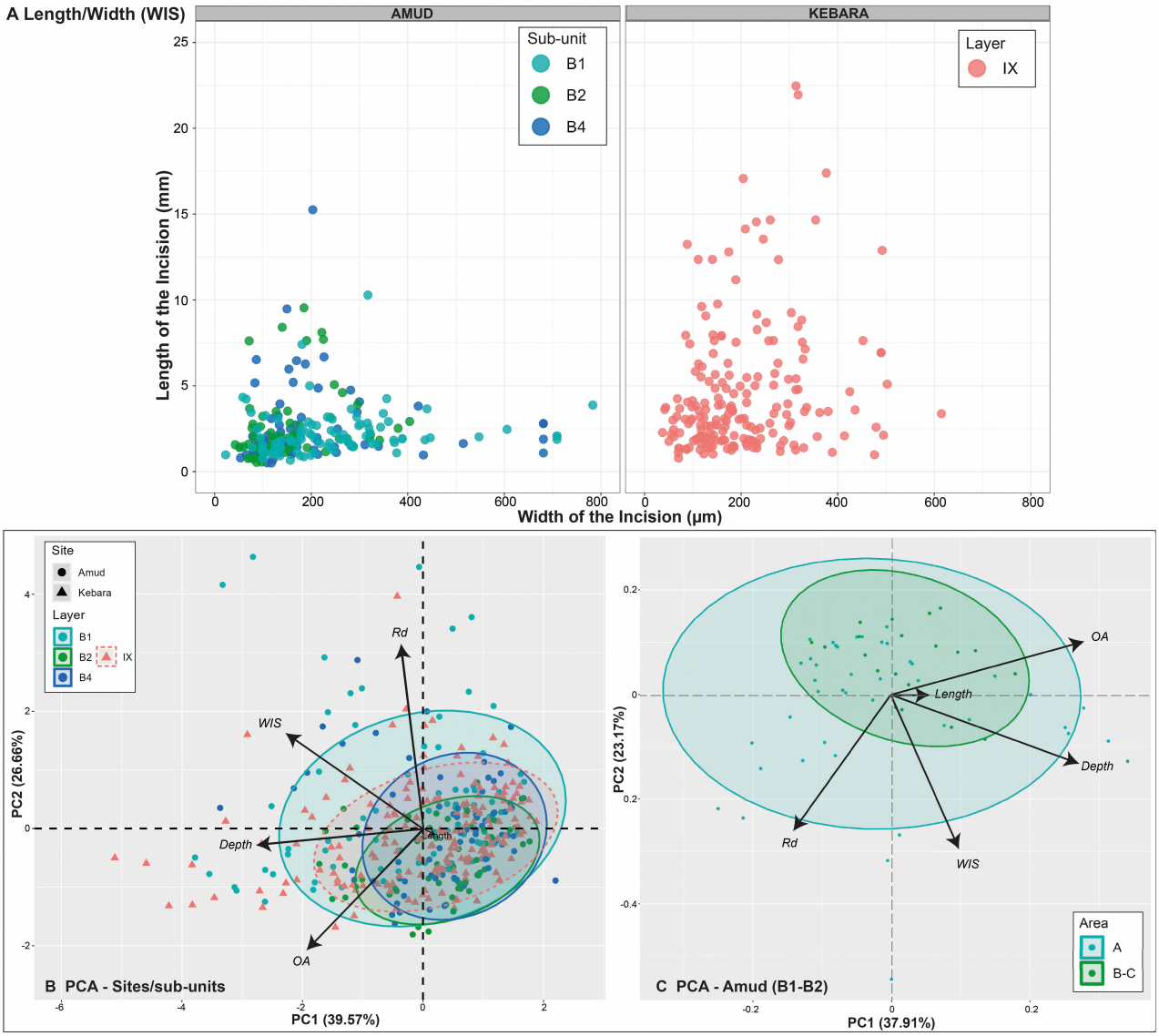

FIGURE 5
Micro-morphometric measurements for the Amud and Kebara samples (as shown in Figure 2). Variation in measurements across site and Sub-units is shown through **(A)** the length and width at the surface of the incisions (WIS). **(B, C)** present outputs from Principal Component Analyses (PCA) performed on the dataset using all variables (length, WIS, depth, OA, and floor radius) to assess the overall variation of cut-marks micro-morphometrics across time and space, for **(B)** the two sites and all sampled Sub-units, and **(C)** within the Amud B1–B2 sub-sample to compare spatial patterns between the main occupation Areas (A vs. B–C; see Supplementary Figure 6 for boxplots for each variable, and Supplementary Table 5 for PCA results and variable loadings).

further confirms the use of similar tool implements at the two sites (Bello et al., 2009).

In the following sections, we will delve into a detailed discussion of these results, examining the extent to which taphonomic factors or broader site-related differences can account for these patterns, and identifying aspects that likely reflect distinct human behaviors.

5.1 Taphonomic alterations and their influence on butchery patterns

In the framework of the present study, the difference in fragment size between the two sites is significant, and it may have influenced several of the variables interpreted in the context of butchery behaviors. In particular, fragment size limits the ability to achieve taxonomic identifications and therefore to link butchery marks with prey choice. The strong difference in fragmentation of the two assemblages also likely distorted the comparison of the amounts of cut-marks present in each sample (see Abe et al., 2002; Domínguez-Rodrigo and Yravedra, 2009), despite the small difference observed between the two sites when evaluating the relative proportion of complete cut-marks observed in each sample. This potential bias was corrected in the present study by scaling the number of cut-marks per specimen relative to surface area, shifting the focus to the density of cut-marks per fragment, rather than cut-mark raw counts. Additionally, fragmentation affects the

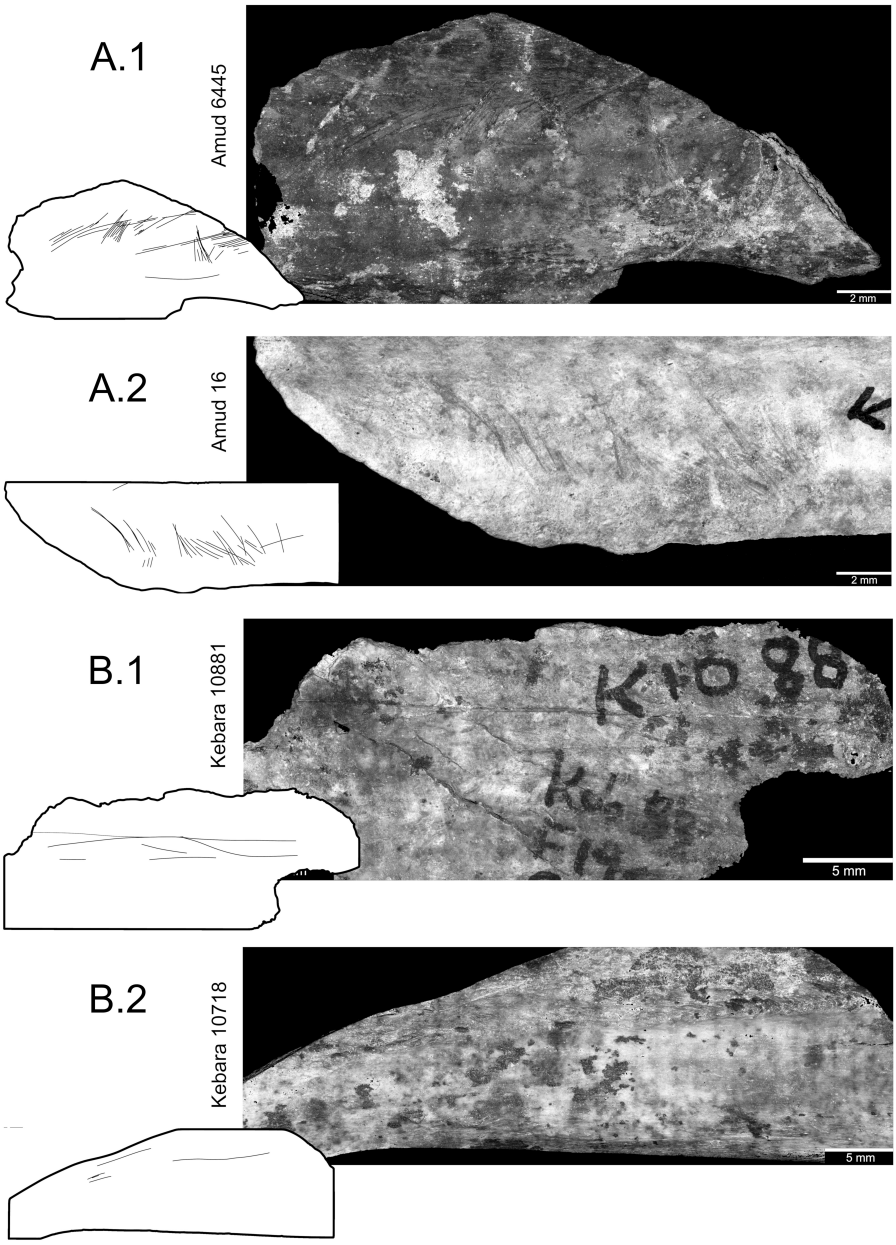

FIGURE 6
Alicona images (10× lens) and schematic sketches for cut-marked specimens from Amud **(A)** and Kebara **(B)** caves, illustrating the difference in cut-marks density between the two sites. In the sketches, thick borders represent the outer borders of the specimen, and the thin lines represent the observed cut-marks.

range of cut-mark lengths that could be measured in their entirety potentially leading to an underestimation of cut-mark length at Amud in comparison to Kebara, and thus explaining our results regarding this characteristic.

It might be tempting to argue that the difference in fragment size stems from different butchery strategies. Indeed, when comparing bone surface area in the two sites for only small ungulates (prey size 1), the two samples differ significantly, suggesting that the difference is not related to prey size. One could then argue that the smaller surface area of bone fragments in the Amud detailed sample and its lower size variability (Figure 4C) resulted from specialized butchery strategies meant to break bones into very small fragments. This interpretation, however, is not consistent with the limited amount of percussion damage observed at Amud relative to the size and number of fragments recovered. Another possible explanation is that the high frequency of burning at Amud (Section 4.1) led to its extreme bone fragmentation. Indeed, as suggested by previous studies, the bone fragments in Amud, burned in large proportions, would have been more friable and thus more susceptible to fragmentation due to post-depositional agents such as sediment compaction (Stiner et al., 1995; Rabinovich and Hovers, 2004; Reidsma, 2022). This topic would require further detailed study.

Despite the higher frequencies of burning, and potentially more post-depositional stresses on the bones of Amud in comparison to Kebara, it would seem that cut-mark morphology was preserved at both sites. At both sites, cut-marks outlines appeared pristine, with visible shoulder effects, internal microstriations and Hertzian cones visible in the SEM images (Supplementary Figure 5).

5.2 Faunal assemblage composition and stone tools: implications for the interpretation of butchery patterns

Cutting tools. One of the most prominent trends observed in the lithic assemblages of both open-air and cave sites in the late Middle Paleolithic in the Levant is the production of subtriangular short blanks, such as triangular flakes and points, often removed from unidirectional convergent Levallois cores. At Amud and Kebara, this similarity in morphology is obtained through slightly different site-specific knapping procedures (Meignen, 1995, 2019; Hovers and Belfer-Cohen, 2013; Krakovsky, 2017). Still, flint was the main raw material used for tool production at both sites. The two lithic assemblages are generally similar also in the preponderance of Levallois flaking strategies and in the production of flakes including points and triangular flakes and the low frequencies of retouched items (Goder-Goldberger, 1997; Hovers, 1998, 2004; Alperson-Afil and Hovers, 2005; Ekshtain et al., 2017; Meignen, 2019 and references therein). The general overlap in cut-mark micro-morphometrics across the two detailed samples (in particular the width and opening angle of the cut) is therefore not surprising when considering the broad similarities of the lithic assemblages (Section 2.1). The similarities in raw material used and in toolkit is a plausible explanation of the inter-assemblage similarities in micro-morphometric characteristics of the cut-marks.

Faunal spectrum, body parts representation and butchering activities. Most of our Amud sample consists of fragments of long-bone diaphysis from small ungulates. These anatomical areas typically undergo a reduced range of butchery activities (e.g., fileting), which would result in a high number of small, clustered cut-marks (as shown in Figure 6; Soulier and Morin, 2016; Soulier and Costamagno, 2017). In contrast, given the higher proportion of medium-sized and large ungulates, as well as the wider range of skeletal elements represented in the Kebara sample, we would expect a wide range of butchering techniques in this sample (such as skinning, disarticulating, and fileting; Speth, 2012 and references therein; Gifford-Gonzalez, 2018). This may explain the greater variability observed in cut-marks length and depth (greater depth of cut as been associated with the cutting of larger muscles; Bello et al., 2009; Wallduck and Bello, 2018) at the two sites.

However, when comparing only small ungulates (prey size 1), we still observe a greater density of incisions, higher proportion of overlapping marks and lower proportion of linear marks in the Amud sample compared to Kebara (Sections 4.3.1). These macroscopic differences cannot be related to the presence of different prey sizes. Moreover, at both sites, prey size 1 includes nearly exclusively mountain gazelles. Thus, taxonomic variation within this group can be considered minimal and unlikely to account for the observed differences between assemblages. Therefore, these patterns may suggest behavioral differences in the processing of small ungulates (see Section 5.4).

5.3 Intra-site variation within Amud cave

The Amud sample in our study consists of three stratigraphic sub-units. Given their chronologies, we expected that if modes of faunal exploitation changed through time, B1 and B2 (both within MIS 3) would be more similar to one another and differ from the earlier B4 (dated to the end of MIS 4). However, the variations observed in the detailed sample across the various sub-units were contrary to our expectations, with some aspects of the B1 sample differing from the two other sub-units. Firstly, B1 fragments are larger, show a lower density of incisions and are less frequently burnt than in any of the other sub-units. Secondly, specimens from B1 are the most variable in terms of cut-mark micro-morphometrics, bearing generally wider cut-marks with a larger floor radius compared to specimens from B2 and B4. Interestingly, it also appears that within the Amud sample, the sub-sample from sub-unit B1 appears to be the most similar to the Kebara unit IX sample in its micro-morphometric measurements, as well as in terms of cut-marks density (Figure 4B).

It is important to note however that sub-unit B1 is only present in the peripheral area of the cave (Area A; Supplementary Figure 2). Hence the intra-site differences might not necessarily reflect chronological variation, but might instead relate to differential use of the space in each cave, with different butchery activities being carried out in the central occupation area (Areas B–C; represented in our sample by specimens attributed to sub-unit B2) compared to the peripheral area of the cave (Area A; represented in our sample by specimens attributed to sub-unit B1). Indeed, Alperson-Afil and Hovers (2005) suggested that in sub-unit B2, knapping and living activities were carried out in Area C, while Area A was used as a refuse area. This interpretation was further supported by archaeomagnetic data (Zeigen et al., 2019) documenting variable heating intensities in this area. Thus, the presence of relatively large bone fragments variably exposed to heat (based on bone coloration) in sub-unit B1 may be explained as the result of cleaning of the central area. Interestingly, previous publications have suggested that the concentrations of bones along the northern wall during accumulation of unit IX in Kebara likely represented a discard midden (Speth, 2019). It is therefore possible that the similarities between Kebara IX and Amud B1 stem from the similar use of the two areas as discard area. Still, we are unable to explain the differences in cut-mark densities within the Amud sample through this spatial functional perspective.

5.4 Potential cultural differences in carcass processing at Amud and Kebara sites

Experimental work combined with ethnographic and archeological case studies have shown that cut-marks may attest to behavioral variations. While the processes leading to these phenomena are not well-understood (Domínguez-Rodrigo et al., 2017), several authors noted behavioral variations related to

modes of exploitation and processing of the hunted fauna. For example, humans may opt for different timing and ways of obtaining meat off carcasses (i.e., preparing drying, boiled or rotten meat as opposed to fresh meat; e.g., Abe, 2005; Soulier and Morin, 2016; Soulier, 2021; Wallduck and Bello, 2018; Speth and Morin, 2022). Differences in group organization and social modes of food sharing were also suggested as underlying drivers of variation in the patterning of cut-marks (Stiner et al., 2009, 2011). Interestingly, experimental work on differences between expert vs. novice butchers suggested that skill cannot be correlated with the amount and morphologies of cut-marks (Pobiner et al., 2018; Soulier, 2021). For this reason, we consider that an interpretation suggesting that butchers were generally less skilled at Amud compared to butchers at Kebara does not sufficiently explain the higher density, clustered appearance and lower linearity of the cut-marks in Amud compared to Kebara.

Possibly, differences between cut-marks in the Amud and Kebara samples could stem from a more intensive exploitation of the carcasses at Amud cave. Such behavior could have resulted from a higher pressure on resources in a somewhat drier environment at Amud compared to Kebara (Section 1). Alternatively, more intensive occupations in Amud Cave, estimated through lithic frequencies per volume per duration (cf. Hovers, 2001, p. 133), could have necessitated a higher intensity of carcass use. However, experimental work has suggested that the frequencies of cut-marks are poorly correlated with the intensity of butchering activities (Egeland, 2003; Pobiner et al., 2018).

Another possible explanation for differences in cut-mark density and linearity between the two sites is that the butchering of meat in more advanced states of decomposition took place in Amud, but less frequently in Kebara. It has been shown that decaying carcasses tend to be more difficult to process, often resulting in the production of haphazard, deep, and sinuous cut-marks (Speth, 2017; Wallduck and Bello, 2018). The higher frequencies of non-linear marks in the Amud samples, compared to Kebara, could therefore suggest that the acquisition of meat off the prey was approached differently in the two sites, with, for example, decaying carcasses being processed more often at Amud Cave than at Kebara. Further experimental research and comparative work is needed to better assess the influence of these factors on cut-mark patterns. Additional variables, such as group organization (e.g., number of individuals involved simultaneously in butchering one carcass, see Egeland et al., 2014) and the types of gestures employed by the butcher(s) would also benefit from further investigation, which could help identifying the range of factors that could result in high frequencies of cut-marks.

6 Conclusion

The Amud samples show a number of patterns that are repeated over time and, despite observed intra-site variations, differ from Kebara IX. We discussed the similarities and differences in cut-marks patterns observed between the Amud and Kebara samples, from environmental, functional, and site-use perspectives. While we cannot fully untangle the various factors that resulted in the cut-mark patterns reported in this study, our results do suggest that the broadly contemporaneous groups of Neanderthals that occupied Amud and Kebara caves exploited similar communities of ungulates in nuancedly different ways. Our study suggests that animal exploitation can leave archeological evidence that reflects group-specific butchering strategies. Thus, detailed analysis of butchery marks can provide useful information to our understanding of group-specific action choices. This hypothesis can be tested by future comparative studies to reveal potential underlying patterns of socially-transmitted traditions—as it is the case with lithic technology.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

AJ: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. LC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. SB: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing. EH: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing. RR: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, 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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fearc.2025.1575572/full#supplementary-material

References

Abadi, I., Bar-Yosef, O., and Belfer-Cohen, A. (2020). Kebara V-A contribution for the study of the middle-upper paleolithic transition in the levant. *PaleoAnthropology* 2020, 1–28. doi: 10.4207/PA.2020.ART139

Abe, Y. (2005). *Hunting and butchering patterns of the Evenki in the Northern Transbaikalia, Russia* (PhD dissertation). Stony Brook University, Stony Brook, NY, United States.

Abe, Y., Marean, C. W., Nilssen, P. J., Assefa, Z., and Stone, E. C. (2002). The analysis of cutmarks on archaeofauna: a review and critique of quantification procedures, and a new image-analysis GIS approach. *Am. Antiq.* 67, 643–663. doi: 10.2307/1593796

Albert, R. M., Bar-Yosef, O., and Weiner, S. (2007). "Use of plant materials in Kebara Cave: phytoliths and mineralogical analyses," in *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archaeology*, Part I, eds. O. Bar-Yosef and L. Meignen, American School of Prehistoric Research Bulletin 49 (Cambridge: Peabody Museum of Archaeology and Ethnology, Harvard University), 147–164.

Alperson-Afil, N., and Hovers, E. (2005). Differential use of space in the Neandertal site of Amud Cave, Israel. *Eurasian Prehistory* 3, 3–22.

Andrews, P. (1995). Experiments in taphonomy. *J. Archaeol. Sci.* 22, 147–153. doi: 10.1006/jasc.1995.0016

Asouti, E., Kabukcu, C., White, C. E., Kuijt, I., Finlayson, B., and Makarewicz, C. (2015). Early Holocene woodland vegetation and human impacts in the arid zone of the southern Levant. *Holocene* 25, 1565–1580. doi: 10.1177/0959683615580199

Bar-Yosef, O., and Meignen, L. (2007). *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archaeology*, Part I, 352p. Cambridge: American School of Prehistoric Research, Peabody Museum, Harvard University Press.

Bar-Yosef, O., Vandermeersch, B., Arensburg, B., Belfer-Cohen, A., Goldberg, P., Laville, H., et al. (1992). The excavations in Kebara Cave, Mt. Carmel [and comments and replies]. *Curr. Anthropol.* 33, 497–550. doi: 10.1086/204112

Behrensmeyer, A. K., Gordon, K. D., and Yanagi, G. T. (1986). Trampling as a cause of bone surface damage and pseudo-cutmarks. *Nature* 319, 768–771. doi: 10.1038/319768a0

Bello, S. M. (2011). New results from the examination of cut-marks using three-dimensional imaging. *Dev. Quat. Sci.* 14, 249–262. doi: 10.1016/B978-0-444-53597-9.00013-3

Bello, S. M., De Groote, I., and Delbarre, G. (2013). Application of 3-dimensional microscopy and micro-CT scanning to the analysis of Magdalenian portable art on bone and antler. *J. Archaeol. Sci.* 40, 2464–2476. doi: 10.1016/j.jas.2012.12.016

Bello, S. M., and Galway-Witham, J. (2019). Bone taphonomy inside and out: application of 3-dimensional microscopy, scanning electron microscopy and micro-computed tomography to the study of humanly modified faunal assemblages. *Quat. Inter.* 517, 16–32. doi: 10.1016/j.quaint.2019.02.035

Bello, S. M., Parfitt, S. A., and Stringer, C. (2009). Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. *J. Archaeol. Sci.* 36, 1869–1880. doi: 10.1016/j.jas.2009.04.014

Bello, S. M., and Soligo, C. (2008). A new method for the quantitative analysis of cutmark micromorphology. *J. Archaeol. Sci.* 35, 1542–1552. doi: 10.1016/j.jas.2007.10.018

Binford, L. R. (1978). Dimensional analysis of behavior and site structure: learning from an Eskimo hunting stand. *Am. Antiq.* 43, 330–361. doi: 10.2307/279390

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths*. New York, NY: Academic Press.

Blasco, R., Rosell, J., Peris, J. F., Arsuaga, J. L., Bermúdez de Castro, J. M., and Carbonell, E. (2013). Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quat. Sci. Rev.* 70, 124–144. doi: 10.1016/j.quascirev.2013.03.008

Blasco, R., Rosell, J., Peris, J. F., Cáceres, I., and Vergès, J. M. (2008). A new element of trampling: an experimental application on the Level XII faunal record of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 1605–1618. doi: 10.1016/j.jas.2007.11.007

Blasco, R., Rosell, J., Smith, K. T., Maul, L. C., Sañudo, P., Barkai, R., et al. (2016). Tortoises as a dietary supplement: a view from the Middle Pleistocene site of Qesem Cave, Israel. *Quat. Sci. Rev.* 133, 165–182. doi: 10.1016/j.quascirev.2015.12.006

Blumenschine, R. J., Cavallo, J. A., and Capaldo, S. D. (1994). Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. *J. Hum. Evol.* 27, 197–213. doi: 10.1006/jhev.1994.1042

Bunn, H. T. (1986). Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690. doi: 10.1016/S0047-2484(86)80004-5

Courtenay, L. A., Herranz-Rodrigo, D., Yravedra, J., Vázquez-Rodríguez, J. M., Huguet, R., Barja, I., et al. (2021). 3D insights into the effects of captivity on wolf mastication and their tooth marks; implications in ecological studies of both the past and present. *Animals* 11:2323. doi: 10.3390/ani11082323

Courtenay, L. A., Yravedra, J., Mate-González, M. Á., Aramendi, J., and González-Aguilera, D. (2019). 3D analysis of cut marks using a new geometric morphometric methodological approach. *Archaeol. Anthropol. Sci.* 11, 651–665. doi: 10.1007/s12520-017-0554-x

DeViva, J. C. (2014). Treatment utilization among OEF/OIF veterans referred for psychotherapy for PTSD. *Psychol. Serv.* 11, 179–184. doi: 10.1037/a0035077

Domínguez-Rodrigo, M. (2019). Successful classification of experimental bone surface modifications (BSM) through machine learning algorithms: a solution to the controversial use of BSM in paleoanthropology?. *Archaeol. Anthropol. Sci.* 11, 2711–2725. doi: 10.1007/s12520-018-0684-9

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B., and Rodríguez, M. (2009). A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 12, 2643–2654. doi: 10.1016/j.jas.2009.07.017

Domínguez-Rodrigo, M., and Pickering, T. R. (2003). Early hominid hunting and scavenging: a zooarcheological review. *Evol. Anthropol.* 12, 275–282. doi: 10.1002/evan.10119

Domínguez-Rodrigo, M., Saladié, P., Cáceres, I., Huguet, R., Yravedra, J., Rodríguez-Hidalgo, A., et al. (2017). Use and abuse of cut mark analyses: the Rorschach effect. *J. Archaeol. Sci.* 86, 14–23. doi: 10.1016/j.jas.2017.08.001

Domínguez-Rodrigo, M., and Yravedra, J. (2009). Why are cut mark frequencies in archaeofaunal assemblages so variable? A multivariate analysis. *J. Archaeol. Sci.* 36, 884–894. doi: 10.1016/j.jas.2008.11.007

Egeland, C. P. (2003). Carcass processing intensity and cutmark creation: an experimental approach. *Plains Anthropol.* 48, 39–51. doi: 10.1080/2052546.2003.11949279

Egeland, C. P., Welch, K. R., and Nicholson, C. M. (2014). Experimental determinations of cutmark orientation and the reconstruction of prehistoric butchery behavior. *J. Archaeol. Sci.* 49, 126–133. doi: 10.1016/j.jas.2014.05.007

Ekshtain, R., Ilani, S., Segal, I., and Hovers, E. (2017). Local and nonlocal procurement of raw material in Amud Cave, Israel: the complex mobility of late Middle Paleolithic groups. *Geoarchaeology* 32, 189–214. doi: 10.1002/gea.21585

Faith, J. T., Domínguez-Rodrigo, M., and Gordon, A. D. (2009). Long-distance carcass transport at Olduvai Gorge? A quantitative examination of Bed I skeletal element abundances. *J. Hum. Evol.* 56, 247–256. doi: 10.1016/j.jhevol.2008.12.008

Fernández-Jalvo, Y., and Andrews, P. (2016). *Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification*. Cham: Springer. doi: 10.1007/978-94-017-7432-1

Fernández-Jalvo, Y., Andrews, P., Pesquero, D., Smith, C., Marín-Monfort, D., Sánchez, B., et al. (2010). Early bone diagenesis in temperate environments: Part I: Surface features and histology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 288, 62–81. doi: 10.1016/j.palaeo.2009.12.016

Galán, A. B., and Domínguez-Rodrigo, M. (2014). Testing the efficiency of simple flakes, retouched flakes and small handaxes during butchery. *Archaeometry* 56, 1054–1074. doi: 10.1111/arcm.12064

Gallo, G., Aldeias, V., and Stahlschmidt, M. (2025). Revisiting the thermal alteration of buried bone. *J. Archaeol. Sci. Rep.* 63:105080. doi: 10.1016/j.jasrep.2025.105080

Gifford-Gonzalez, D. (1998). Early pastoralists in East Africa: Ecological and social dimensions. *J. Anthropol. Archaeol.* 17, 166–200. doi: 10.1006/jaar.1998.0322

Gifford-Gonzalez, D. (2018). "Skeletal disarticulation, dispersal, dismemberment, selective transport," in *An Introduction to Zooarchaeology*, ed. D. Gifford-Gonzalez (Cham: Springer), 413–434. doi: 10.1007/978-3-319-65682-3_19

Goder-Goldberger, M. (1997). *Technological and typological aspects of Layer B1 in the Late Mousterian site at Amud Cave* (M.A. thesis). Hebrew University, Jerusalem, Israel.

Greenfield, H. J., Cheney, T., and Galili, E. (2013). "A taphonomic and technological analysis of the butchered animal bone remains from Atlit-Yam, a submerged PPNC site off the coast of Israel," in *Bones and Identity: Zooarchaeological Approaches to Reconstructing Social and Cultural Landscapes in Southwest Asia*, eds. N. Marom, R. Yeshuran, L. Weissbrod, and G. Bar-Oz (Oxford: Oxbow Books), 87–112. doi: 10.2307/j.ctvh1drw5.9

Hammer, Ø., Harper, D. A. T., and Ryan, P D. (2001). PAST–Palaeontological statistics. Software package for education and data analysis. ver. 1.34. *Palaeontol. Electron.* 4. Available online at: http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hovers, E. (1998). "The lithic assemblages of Amud Cave: implications for understanding the end of the Mousterian in the Levant," in Neandertals and Modern Humans in Western Asia, eds. T. Akazawa, K. Aoki, and O. Bar-Yosef (Boston, MA: Springer US), 143–163. doi: 10.1007/0-306-47153-1_10

Hovers, E. (2001). "Territorial behavior in the Middle Paleolithic of the Southern Levant," in *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age*, ed. N. Conard (Kerns Verlag, Tübingen), 123–152.

Hovers, E. (2004). "Cultural ecology at the Neandertal site of Amud Cave, Israel," in *Arkheologiya i paleoekologiya Evrasii (Archaeology and Paleoecology of Eurasia)*, eds. A. P. Derevianko, and T. I. Nokhrina (Novosibirsk: Institute of Archaeology and Ethnography SB RAS Press), 218–231.

Hovers, E. (2007). "The many faces of cores-on-flakes: a perspective from the Levantine Mousterian," in *Cores or Tools: Alternative Approaches to Stone Tools Analysis*, ed. S. McPherron (Newcastle: Cambridge Scholars), 42–74.

Hovers, E. (2009). *The Lithic Assemblages of Qafzeh Cave*. Oxford: Oxford University Press.

Hovers, E., and Belfer-Cohen, A. (2013). On variability and complexity: lessons from the levantine middle paleolithic record. *Curr. Anthropol.* 54, S337–357. doi: 10.1086/673880

Hovers, E., Kimbel, W. H., and Rak, Y. (2000). The Amud 7 skeleton—still a burial. Response to Gargett. *J. Hum. Evol.* 39, 253–260. doi: 10.1006/jhev.1999.0406

Hovers, E., Malinsky-Buller, A., Goder-Goldberger, M., and Ekshtain, R. (2011). "Capturing a moment: identifying short-lived activity locations in Amud Cave, Israel," in *The Lower and Middle Palaeolithic in the Middle East and Neighbouring Regions: Basel Symposium, May 8–10, 2008*, eds. J.-M. Le Tensorer, R. Jagher, and M. Otte, ERAUL, Vol. 126 (Liège: Université de Liège), 101–114.

Hovers, E., Rak, Y., Lavi, R., and Kimbel, W. H. (1995). Hominid remains from Amud Cave in the context of the Levantine Middle Paleolithic. *Paléorient* 21, 47–61. doi: 10.3406/paleo.1995.4617

Jallon, A., Rivals, F., Hovers, E., and Rabinovich, R. (2025). Assessing seasonality and mobility from a fragmented faunal assemblage: the case of Amud Cave (Israel). *Archaeol. Anthropol. Sci.* 17, 1–20. doi: 10.1007/s12520-025-02231-5

Kassambara, A., and Mundt, F. (2017). *Package 'factoextra'. Extract and Visualize the Results of Multivariate Data Analyses*. Available online at: https://CRAN.R-project.org/package=factoextra (accessed March 15, 2024).

Krakovsky, M. (2017). *Technological traditions at the end of the Middle Palaeolithic in the southern Levant? Point reduction sequences from Amud and Kebara caves as a case study* (Unpublished M.A. thesis). Institute of Archaeology, The Hebrew University of Jerusalem, Jerusalem, Israel.

Lartet, M. E. (1860). On the coexistence of man with certain extinct quadrupeds, proved by fossil bones, from various Pleistocene deposits, bearing incisions made by sharp instruments. *Quart. J. Geol. Soc. London* 16, 471–479. doi: 10.1144/GSL.JGS.1860.016.01-02.63

Lorenzen, E. D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K. A., et al. (2011). Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479, 359–364. doi: 10.1038/nature10574

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9781139878302

Lyman, R. L. (1995). "A study of variation in the prehistoric butchery of large artiodactyls," in *Ancient Peoples and Landscapes*, ed. E. Johnson (Lubbock, TX: Texas Tech University Press), 233–253.

Mallol, C., Hernández, C. M., Cabanes, D., Sistiaga, A., Machado, J., Rodríguez, A., et al. (2013). The black layer of middle palaeolithic combustion structures. interpretation and archaeostratigraphic implications. *J. Archaeol. Sci.* 40, 2515–2537. doi: 10.1016/j.jas.2012.09.017

Martin, H. (1909). Désarticulations de quelques régions chez les ruminants et le cheval à l'époque moustérienne. *Bull. Soc. Prehist. Franç.* 6, 303–310. doi: 10.3406/bspf.1909.7919

Maté-González, M. Á., Aramendi, J., Yravedra, J., Blasco, R., Rosell, J., González-Aguilera, D., et al. (2017). Assessment of statistical agreement of three techniques for the study of cut marks: 3D digital microscope, laser scanning confocal microscopy and micro-photogrammetry. *J. Microsc.* 267, 356–370. doi: 10.1111/jmi.12575

Meignen, L. (1995). "Levallois lithic production systems in the Middle Paleolithic of the Near East: the case of the unidirectional method," in *The Definition and Interpretation of Levallois Technology*, Monographs in World Archaeology, No. 23, eds. H. L. Dibble and O. Bar-Yosef (Madison, WI: Prehistory Press), 31–380.

Meignen, L. (2019). "The Mousterian lithic assemblages from Kebara Cave," in *The Middle and Upper Paleolithic Archaeology*, Part II, eds. O. Bar-Yosef and L. Meignen (Cambridge, MA: Peabody Museum of Archaeology and Ethnology), 1–147.

Meignen, L., and Bar-Yosef, O. (2019). *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archaeology*, Part II. Cambridge: Harvard University Press.

Meignen, L., Bar-Yosef, O., Belfer-Cohen, A., Speth, J. D., and Vandermeersch, B. (2017). "Kebara Cave," in *Quaternary of the Levant: Environments, Climate Change, and Humans*, eds. Y. Enzel and O. Bar-Yosef (Cambridge: Cambridge University Press), 241–250. doi: 10.1017/9781316106754.027

Meignen, L., Bar-Yosef, O., Speth, J. D., and Stiner, M. C. (2006). "Middle Paleolithic settlement patterns in the Levant," in *Transitions Before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age*, eds. E. Hovers and S. L. Kuhn (New York, NY: Springer), 149–169. doi: 10.1007/0-387-24661-4_9

Metcalfe, D., and Barlow, K. R. (1992). A model for exploring the optimal trade-off between field processing and transport. *Am. Anthropol.* 94, 340–356. doi: 10.1525/aa.1992.94.2.02a00040

Monahan, C. M. (1998). The Hadza carcass transport debate revisited and its archaeological implications. *J. Archaeol. Sci.* 25, 405–424. doi: 10.1006/jasc.1997.0241

Moretti, E., Arrighi, S., Boschin, F., Crezzini, J., Aureli, D., and Ronchitelli, A. (2015). Using 3D microscopy to analyze experimental cut marks on animal bones produced with different stone tools. *Ethnobiol. Lett.* 6, 267–275. doi: 10.14237/ebl.6.2.2015.349

Morin, E., Speth, J. D., and Lee-Thorp, J. (2015). "Middle Palaeolithic diets," in *The Oxford Handbook of the Archaeology of Diet*, eds. J. Lee-Thorp and M. Van der Veen (Oxford: Oxford University Press), 251–267. doi: 10.1093/oxfordhb/9780199694013.013.24

O'Connell, J. F., Hawkes, K., and Jones, N. B. (1988). Hadza hunting, butchering, and bone transport and their archaeological implications. *J. Anthropol. Res.* 44, 113–161. doi: 10.1086/jar.44.2.3630053

O'Connell, J. F., Hawkes, K., and Jones, N. B. (1990). Reanalysis of large mammal body part transport among the Hadza. *J. Archaeol. Sci.* 17, 301–316. doi: 10.1016/0305-4403(90)90025-Z

Orbach, M., and Yeshurun, R. (2021). The hunters or the hunters: human and hyena prey choice divergence in the Late Pleistocene Levant. *J. Hum. Evol.* 160:102572. doi: 10.1016/j.jhevol.2019.01.005

Otárola-Castillo, E., Torquato, M. G., Hawkins, H. C., James, E., Harris, J. A., Marean, C. W., et al. (2018). Differentiating between cutting actions on bone using

3D geometric morphometrics and Bayesian analyses with implications to human evolution. *J. Archaeol. Sci.* 89, 56–67. doi: 10.1016/j.jas.2017.10.004

Pérez, L., Sanchis, A., Hernández, C. M., Galván, B., Sala, R., and Mallol, C. (2017). Hearths and bones: an experimental study to explore temporality in archaeological contexts based on taphonomical changes in burnt bones. *J. Archaeol. Sci. Rep.* 11 287–309. doi: 10.1016/j.jasrep.2016.11.036

Pobiner, B. L., Higson, C. P., Kovarovic, K., Kaplan, R. S., Rogers, J., and Schindler, W. (2018). Experimental butchery study investigating the influence of timing of access and butcher expertise on cut mark variables. *Int. J. Osteoarchaeol.* 28, 377–387. doi: 10.1002/oa.2661

Pokines, J. T., L'Abbe, E. N., and Symes, S. A. (Eds.). (2021). *Manual of Forensic Taphonomy*. CRC press.

Posit Team (2022). *RStudio: Integrated Development Environment for R*. Boston, MA: Posit Software, PBC. Available online at: http://www.posit.co/ (accessed March 15, 2024).

Potts, R., and Shipman, P. (1981). Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 291, 577–580. doi: 10.1038/291577a0

Rabinovich, R., Gaudzinski-Windheuser, S., Kindler, L., and Goren-Inbar, N. (2012). "Materials and methodology," in *The Acheulian Site of Gesher Benot Ya'aqov*. Vol. III, ed. N. Goren-Inbar (Dordrecht: Springer), 25–42. doi: 10.1007/978-94-007-2159-3

Rabinovich, R., and Hovers, E. (2004). Faunal analysis from Amud Cave: preliminary results and interpretations. *Int. J. Osteoarchaeol.* 14, 287–306. doi: 10.1002/oa.762

Rebollo, N. R., Weiner, S., Brock, F., Meignen, L., Goldberg, P., Belfer-Cohen, A., et al. (2011). New radiocarbon dating of the transition from the Middle to the Upper Paleolithic in Kebara Cave, Israel. *J. Archaeol. Sci.* 38, 2424–2433. doi: 10.1016/j.jas.2011.05.010

Reidsma, F. H. (2022). Laboratory-based experimental research into the effect of diagenesis on heated bone: implications and improved tools for the characterisation of ancient fire. *Sci. Rep.* 12:17544. doi: 10.1038/s41598-022-21622-5

Rendu, W. (2022). "Selection versus opportunism: a view from Neanderthal subsistence strategies," in *Updating Neanderthals*, eds. E. Camarós and J. Rosell (Cambridge, MA: Academic Press), 109–122. doi: 10.1016/B978-0-12-821428-2.00013-5

Rendu, W., and Speth, J. D. (2019). "Seasonnality of Kebara's Middle Paleolithic occupations: a cementum increment analysis," in *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archeology*, Part II, eds. L. Meignen and O. Bar-Yosef (Cambridge: Harvard University Press), 237–255.

Rink, W. J., Schwarcz, H. P., Lee, H. K., Rees-Jones, J., Rabinovich, R., and Hovers, E. (2001). Electron spin resonance (ESR) and thermal ionization mass spectrometric (TIMS) 230Th/234U dating of teeth in Middle Paleolithic layers at Amud Cave, Israel. *Geoarchaeology* 16, 701–717. doi: 10.1002/gea.1017

Rivals, F., Bocherens, H., Camarós, E., and Rosell, J. (2022). "Diet and ecological interactions in the Middle and Late Pleistocene," in *Updating Neanderthals*, eds. E. Camarós and J. Rosell (Cambridge, MA: Academic Press), 39–54. doi: 10.1016/B978-0-12-821428-2.00003-2

Romagnoli, F., Rivals, F., and Benazzi, S. (2022). *Updating Neanderthals*. London: Academic Press.

Schoville, B. J., and Otárola-Castillo, E. (2014). A model of hunter-gatherer skeletal element transport: the effect of prey body size, carriers, and distance. *J. Hum. Evol.* 73, 1–14. doi: 10.1016/j.jhevol.2014.06.004

Shahack-Gross, R., Ayalon, A., Goldberg, P., Goren, Y., Ofek, B., Rabinovich, R., et al. (2008). Formation processes of cemented features in karstic cave sites revealed using stable oxygen and carbon isotopic analyses: a case study at Middle Paleolithic Amud Cave, Israel. *Geoarchaeology* 23, 43–62. doi: 10.1002/gea.20203

Sharpe, D. (2015). Your chi-square test is statistically significant: now what?. *Practi. Assess. Res. Eval.* 20:n8.

Shipman, P., and Rose, J. (1983). Early hominid hunting, butchering, and carcass-processing behaviors: approaches to the fossil record. *J. Anthropol. Archaeol.* 2, 57–98. doi: 10.1016/0278-4165(83)90008-9

Soulier, M. C. (2021). Exploring meat processing in the past: insights from the Nunamiut people. *PLoS ONE* 16:e0245213. doi: 10.1371/journal.pone.0245213

Soulier, M. C., and Costamagno, S. (2017). Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. *J. Archaeol. Sci. Rep.* 11, 782–802. doi: 10.1016/j.jasrep.2016.12.033

Soulier, M. C., and Morin, E. (2016). Cutmark data and their implications for the planning depth of Late Pleistocene societies. *J. Hum. Evol.* 97, 37–57. doi: 10.1016/j.jhevol.2016.05.006

Speth, J., and Clark, J. (2006). Hunting and overhunting in the Levantine late Middle Palaeolithic. *Before Farm.* 2006, 1–42. doi: 10.3828/bfarm.2006.3.1

Speth, J. D. (2012). Middle Palaeolithic subsistence in the Near East: zooarchaeological perspectives–past, present and future. *Before Farm.* 2012, 1–45. doi: 10.3828/bfarm.2012.2.1

Speth, J. D. (2017). Putrid meat and fish in the Eurasian middle and upper paleolithic: Are we missing a key part of neanderthal and modern human diet?. *PaleoAnthropology* 2017, 44–72. doi: 10.4207/PA.2017.ART105

Speth, J. D. (2019). "Kebara as a Late Pleistocene settlement: insights from the ungulate remains," in *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archaeology*, Part II, eds. O. Bar-Yosef and L. Meignen (Cambridge, MA: Peabody Museum of Archaeology and Ethnology), 169–236.

Speth, J. D., and Morin, E. (2022). Putrid meat in the tropics: it wasn't just for Inuit. *PaleoAnthropology*. doi: 10.48738/2022.iss2.114

Speth, J. D., and Tchernov, E. (2001). "Neandertal hunting and meat-processing in the Near East: evidence from Kebara Cave (Israel)," in *Meat-eating and Human Evolution*, eds. C. B. Stanford and H. T. Bunn (Oxford: Oxford University Press), 52–72. doi: 10.1093/oso/9780195131390.003.0004

Speth, J. D., and Tchernov, E. (2007). "The Middle Paleolithic occupations at Kebara Cave: a faunal perspective," in *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic Archaeology*, Part I, eds. O. Bar-Yosef and L. Meignen (Cambridge, MA: Peabody Museum of Archaeology and Ethnology), 165–260.

Stiner, M. C., Barkai, R., and Gopher, A. (2009). Cooperative hunting and meat sharing 400–200 kya at Qesem Cave, Israel. *Proc. Natl. Acad. Sci. U.S.A.* 106, 13207–13212. doi: 10.1073/pnas.0900564106

Stiner, M. C., Gopher, A., and Barkai, R. (2011). Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *J. Hum. Evol.* 60, 213–233. doi: 10.1016/j.jhevol.2010.10.006

Stiner, M. C., Kuhn, S. L., Weiner, S., and Bar-Yosef, O. (1995). Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* 22, 223–237. doi: 10.1006/jasc.1995.0024

Suzuki, H., and Takai, F. (1970). *The Amud Man and his Cave Site*. Tokyo: University of Tokyo Press.

Valladas, H., Joron, J. L., Valladas, G., Arensburg, B., Bar-Yosef, O., Belfer-Cohen, A., et al. (1987). Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel. *Nature* 330, 159–160. doi: 10.1038/330159a0

Valladas, H., Mercier, N., Froget, L., Hovers, E., Joron, J. L., Kimbel, W. H., et al. (1999). TL dates for the Neanderthal site of the Amud Cave, Israel. *J. Archaeol. Sci.* 26, 259–268. doi: 10.1006/jasc.1998.0334

Valtierra, N., Courtenay, L. A., Yravedra, J., and López-Polín, L. (2024). Cumulative effect of high-resolution silicone moulds on the morphology of cut marks. *Archaeometry* 66, 665–682. doi: 10.1111/arcm.12938

Vettese, D., Blasco, R., Cáceres, I., Gaudzinski-Windheuser, S., Moncel, M. H., Hohenstein, U. T., et al. (2020). Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeol. Anthropol. Sci.* 12, 1–19. doi: 10.1007/s12520-019-00972-8

Vettese, D., Borel, A., Blasco, R., Chevillard, L., Stavrova, T., Thun Hohenstein, U., et al. (2022). New evidence of Neandertal butchery traditions through the marrow extraction in southwestern Europe (MIS 5–3). *PLoS ONE* 17:e0271816. doi: 10.1371/journal.pone.0271816

Vigne, J. (2006). Découpe du cerf (*Cervus elaphus*) au Mésolithique moyen, à Noyen-sur-Seine (Seine-et-Marne): analyses tracéologique et expérimentale. *Revue Paléobiologie* 24:69.

Walker, P. L. (1978). Butchering and stone tool function. *Am. Antiq.* 43, 710–715. doi: 10.2307/279502

Wallduck, R., and Bello, S. M. (2018). Cut mark micro-morphometrics associated with the stage of carcass decay: a pilot study using three-dimensional microscopy. *J. Archaeol. Sci. Rep.* 18, 174–185. doi: 10.1016/j.jasrep.2018.01.005

Weiner, S., Berna, F., Cohen, I., Shahack-Gross, R., Albert, R. M., Karkanas, P., et al. (2007). "Mineral distributions in Kebara Cave: diagenesis and its effect on the archaeological record," in *Kebara Cave, Mt. Carmel, Israel: The Middle and Upper Paleolithic*, Part I, eds. O. Bar-Yosef and L. Meignen (Cambridge, MA: Peabody Museum of Archaeology and Ethnology), 131–146.

Weiner, S., Goldberg, P., and Bar-Yosef, O. (1993). Bone preservation in Kebara Cave, Israel using on-site Fourier transform infrared spectrometry. *J. Archaeol. Sci.* 20, 613–627. doi: 10.1006/jasc.1993.1037

White, T. E. (1952). Observations on the butchering technique of some aboriginal peoples: I. *Am. Antiq.* 17, 337–338. doi: 10.2307/276520

Wickham, H. (2006). An introduction to *ggplot*: an implementation of the grammar of graphics in R. *Statistics* 1, 1–8.

Yravedra, J., Maté-González, M. Á., Palomeque-González, J. F., Aramendi, J., Estaca-Gómez, V., San Juan Blazquez, M., et al. (2017). A new approach to raw material use in the exploitation of animal carcasses at BK (Upper Bed II, Olduvai Gorge, Tanzania): a micro-photogrammetric and geometric morphometric analysis of fossil cut marks. *Boreas* 46, 860–873. doi: 10.1111/bor.12224

Zeigen, C., Shaar, R., Ebert, Y., and Hovers, E. (2019). Archaeomagnetism of burnt cherts and hearths from Middle Palaeolithic Amud Cave, Israel: tools for reconstructing site formation processes and occupation history. *J. Archaeol. Sci.* 107, 71–86. doi: 10.1016/j.jas.2019.05.001

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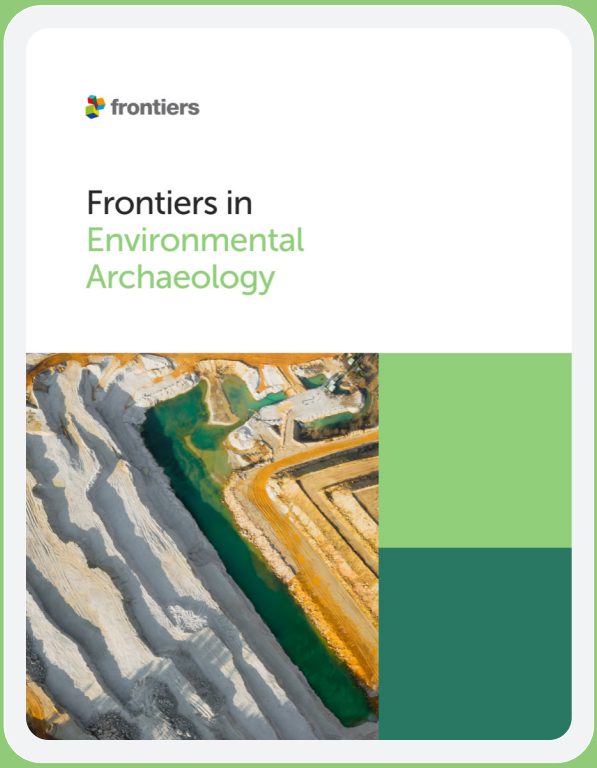

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