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From Prey to Pattern: Integrating Faunal and Behavioural Evidence of Neanderthal Subsistence at Fumane Cave, Unit A9

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Abstract

This study presents a zooarchaeological and taphonomic analysis of the remaining portion of the Mousterian faunal assemblage from Unit A9 at Grotta di Fumane (northeastern Italy), offering refined insights into Neanderthal subsistence behaviour during Marine Isotope Stage 3. Building on the previously published analysis of the principal portion of the assemblage [1], the new data reaffirm a subsistence strategy focused on selective transport and intensive on-site processing of high-utility carcass components. The ungulate assemblage—dominated by *Cervus elaphus* and *Capreolus capreolus*, with additional contributions from *Rupicapra rupicapra* and *Capra ibex*—characterised by the dominance of hindlimb elements, moderate cranial representation, and a pronounced scarcity of axial remains. These patterns indicate that carcass reduction commenced at kill sites, where low-yield trunk segments were removed, while high-nutritional-value limb portions were preferentially transported to the cave for secondary processing. Taphonomic indicators, including abundant cut marks, percussion notches, and extensive bone fragmentation, demonstrate systematic defleshing, marrow extraction, and possible grease rendering within the cave, activities that were spatially associated with combustion features. Occasional cranial transport suggests targeted acquisition of high-fat tissues such as brains and tongue, behaviour consistent with cold-climate optimisation strategies documented in both ethnographic and experimental contexts. Collectively, the evidence indicates that Unit A9 served as a residential locus embedded within a logistically organised mobility system, where carcass processing, resource exploitation, and lithic activities were closely integrated. These findings reinforce the broader picture of late Neanderthals as adaptable and behaviourally sophisticated foragers capable of strategic planning and efficient exploitation of ungulate prey within the dynamic environments of northern Italy.

Keywords: zooarchaeology; taphonomy; ungulates; subsistence behaviour; middle palaeolithic; MIS 3

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1. Introduction

This study presents a new bone assemblage from Grotta di Fumane, the Mousterian unit A9, where discoid manufacturing lithic industries are extensively reported [2,3]. The aim of this research is to provide a complete picture of the faunal assemblage by thoroughly examine the substantial bone assemblage recovered from the innermost excavated area of the site, as this extensive collection has the potential to offer valuable insights into the subsistence strategies and foraging behaviours of the Neanderthal inhabitants.

The Grotta di Fumane, extensively investigated over two decades, provides a unique opportunity to explore Neanderthal foraging behaviour during the late Middle Palaeolithic period [4]. This time period is characterised by extensive cultural replacements, as indicated by diverse archaeological signatures, such as technological innovations that are the product of adaptive strategies and changes in dietary habits [5–7]. The Mousterian unit A9 preserves a well-defined cultural layer [8,9] that can provide additional insights and contribute to the understanding of these topics, through the study of its faunal assemblage. The zooarchaeological and taphonomic framework is used to examine the associated aspects of Neanderthal behaviour.

Human occupation at Fumane unit A9, is attested by numerous faunal remains, lithics artefacts and combustion features [4,10] contained in a 15–20 cm thick stratigraphic complex characterised by overlapping thin layers and lenses. The composition includes frost-shattered stones, aeolian silt and sands, and dark sediments, all extensively distributed due to intense human activities. Topographical mapping has identified intact or fragmented bones, teeth, and determinable fragments ≥ 5 cm, while smaller fragments, micromammal and small avifaunal bones were recovered through wet sieving [1].

2. Materials and Methods

Zooarchaeological and Taphonomical Frame of Reference

The faunal material discussed here represents the portion of the A9 assemblage that remains unexamined, while the rest has already been analysed and published in 2014 [1,11]. Zooarchaeological analysis was conducted on the entire faunal assemblage recovered from 1m^2 squares 137, 147, 157, 158, 167, and 168, totalling 6m^2 excavated in the innermost explored area beyond the cave entrance. To determine anatomical and taxonomical classifications, first the assemblage was classified following the same dimensional division method used in the previous study. Additionally, burned and calcined bones were segregated from unburned specimens. Taxonomic and anatomical identifications in this study was based on established zooarchaeological comparative alpine and archaeological collection of the University of Ferrara and at Laboratory of Prehistory and Zooarchaeology of MUSE, the Museum of Science, and a series of reputable publications [12–16]. Microscopic analyses of bone surfaces were aided by a Leica S6D Greenough stereomicroscope with 0.75-70x magnification range. The studied material was recorded in a database specifically catered for the study's aims.

Both identified remains and those deemed unidentifiable based on morphological or size characteristics were categorised into three mammal body-size classes, following the methodology of Bunn *et al.* [17]: I - small (i.e., *Lepus* sp. and other lagomorphs, Mustelidae, *Vulpes vulpes*); II - Medium (i.e., *Capreolus capreolus, Rupicapra rupicapra, Capra ibex, Canis lupus*); III- Large (i.e., *Cervus elaphus, Ursidae, Megaloceros giganteus, Bovinae*). This categorisation is deemed more useful for evaluating the faunal assemblage of these sites, emphasising the disparity in body size between red deer and giant deer/bovids. When species determination is indeterminable, specimens were identified to their family (e.g., Cervidae, Caprinae) or genus (e.g., Capra/Cervus, Rupicapra/Capreolus, Bos/Bison sp.) level.

According to modern animal birth criteria, the age at death and the state of epiphysis fusion were determined using tooth eruption, replacement sequences, and dental wear. Priority was given to ungulates, such as *Capreolus capreolus* [18], *Cervus elaphus* [19–21], and bovids [22–24].

All taxonomically identified specimens, including shaft fragments, were considered in the analysis of skeletal part profiles. NISP (Number of Identified Specimens) [25] and MNI (Minimum Number of Individuals) [26], indexes were used in order to evaluate species abundance. MNI were estimated considering all skeletal elements, including both bones and teeth, with a particular emphasis on the tibia for ungulates and teeth for carnivores (if any). MNE (Minimum Number of Elements) was calculated by selecting the zone with the highest representation of >50%, which was further combined with side and fusion data for each specific element.

The identification of taphonomic alterations, whether organic (microorganism, animal, plant, etc.) or inorganic and mechanical (manganese strains, weathering, water circulation or sediment mobilisation, sediment compaction, etc.), were reliant upon data presented in published materials [14,27–37]. The evidence of anthropic modification was based on examining the position, type, and their orientation of cutmarks. Incisions and scraping marks were identified as types of cutmarks [30,32,38–40]. A concise analysis of cutmarks were conducted in order to infer possible actions carried out on the bone, such as skinning, disarticulation, defleshing, tendons removal and periosteum removal [41]. The analysis considered the number of striations, their location and distribution, and orientation. Furthermore, the presence of chop marks was given attention. Chop marks refer to broad and relatively short linear depressions with a V-shaped cross section [14,31]. Anthropic traces resulting from bone breakage for extracting marrow were traced and categorised into two types: percussion marks and impact flakes. Percussion marks take the form of semi-circular cavities located on the fracture edges, with corresponding negative flake scars. Impact flakes, on the other hand, are positive flakes of the percussion notches that result from breaking the diaphysis [34,35,42–44]. Deliberate bone fracturing to reach marrow was identified by analysing the form of the shattered extremities of the shafts themselves [31,36,45–48]. Every anatomical element (over 3 cm long) was examined both macroscopically and microscopically to identify surface alterations. The degree of combustion was evaluated by the methodology developed by Stiner *et al.* [49]. Assessing the skeletal representation of various species and the survival rates of bones was based on fragmentation indices methodologies developed by Binford [32], Brain [33], and Lyman [14].

Ecological characteristics of the ungulate assemblage is proportional to two habitat types [50,51]. Ungulates such as moose (*Alces alces*), giant deer (*Megaloceros giganteus*), red deer (*Cervus elaphus*), roedeer (*Capreolus capreolus*), and wild-boar (*Sus scrofa*) represents a mixed habitat, such as, grasslands, wetlands and forests of the lower elevations, while mountainous habitats were preferred by ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*), in higher elevations than the former.

3. Results

3.1. Zooarchaeology and Taphonomy

Out of a total of 5825 bone fragments chosen for analysis (>1 cm), 692 (11.9%) were sufficiently preserved to allow morphological assessment. Of these, 424 specimens (61.3%) were successfully identified to species or genus level (Table 1). Natural modifications in the assemblage are primarily marked by manganese stains (44.8%), followed by root marks (32.5%). Weathering-related micro fissures (5.5%) and trampling (6.5%) are comparatively low, while other modifications, including exfoliations (1.9%), carbonate concentrations (0.8%), carnivore marks (2.1%), rodent gnawing marks (1.4%), and corrosion (0.3%), each account for less than 3% of the total. Burned fragments accounts for 2.3% of the total, while calcined fragments make up to approximately 2% of the total assemblage (Figure 1). Carnivore and rodent contribution to the accumulation is minimal, collectively does not exceed 5% of the total assemblage, suggesting that carnivores may had secondary access to the assemblage, but did not make a huge impact to the bone accumulation.

Table 1. Taxonomical determinations of the assemblage followed by NISP and MNI.

Taxa	NISP	*NISP%*	MNI
Rodentia indet.	4	*0.9*	1
Tot. *Rodentia*	**4**	***0.9***	**1**
Aves	1	*0.2*	1
Tot. *Aves*	**1**	***0.2***	**1**
Vulpes vulpes	1	*0.2*	1
Ursus arctos	3	*0.7*	3
Ursus spelaeus	2	*0.5*	2
Ursus sp.	3	*0.7*	3

Meles meles	2	*0.5*	1
Carnivora indet	1	*0.2*	
Tot. *Carnivora*	**12**	***2.8***	**10**
Megaloceros giganteus	1	0.2	1
Alces alces	2	*0.5*	1
Cervus elaphus	92	*21.7*	8
Capreolus capreolus	30	*7.1*	3
Large *Cervidae*	3	*0.7*	2
Cervidae indet.	12	*2.8*	5
Caprine	6	*1.4*	1
Capra ibex	8	*1.9*	3
Rupicapra rupicapra	18	*4.2*	2
Ungulata indet.	235	*55.4*	
Tot. *Ungulata*	**407**	***96***	**26**
TOT. NISP	**424**	***100.00***	**38**
Undetermined Specimens			
Small size mammals	1	*0.1*	
Medium size mammals	18	*2.6*	
Medium-Big size mammals	27	*3.9*	
Big size mammals	8	*1.2*	
Undetermined	214	*30.9*	
TOT. UNDETERMINED	**268**	***38.7***	
TOT. NR	**692**	***100.00***	

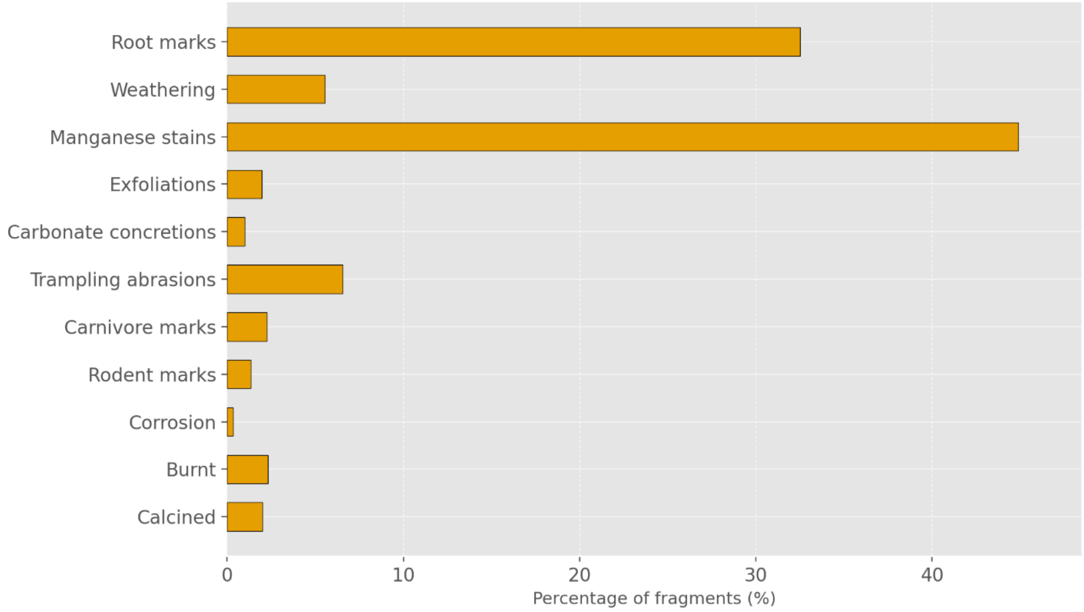

Figure 1. Natural modifications observed in the assemblage.

The ungulates represent nearly 96% of the total assemblage, primarily through their limb bones (Figure 2). Red deer and roe deer are the most common species, indicating a sparse forest environment. Thought the relatively low presence of giant deer and moose is an indicative cold-temperate environment with occasional access to open grazing areas. These ecological conditions are consistent with those found in the vicinity of the site, which could also serve as a refuge for species such as chamois and ibex. The high frequency of cervids aligns with faunal records from Mousterian contexts globally [52–56]. In the preceding layers (A11-10) at Fumane, there is a noticeable increase in these species, with a corresponding decline in those adapted to open environments [1].

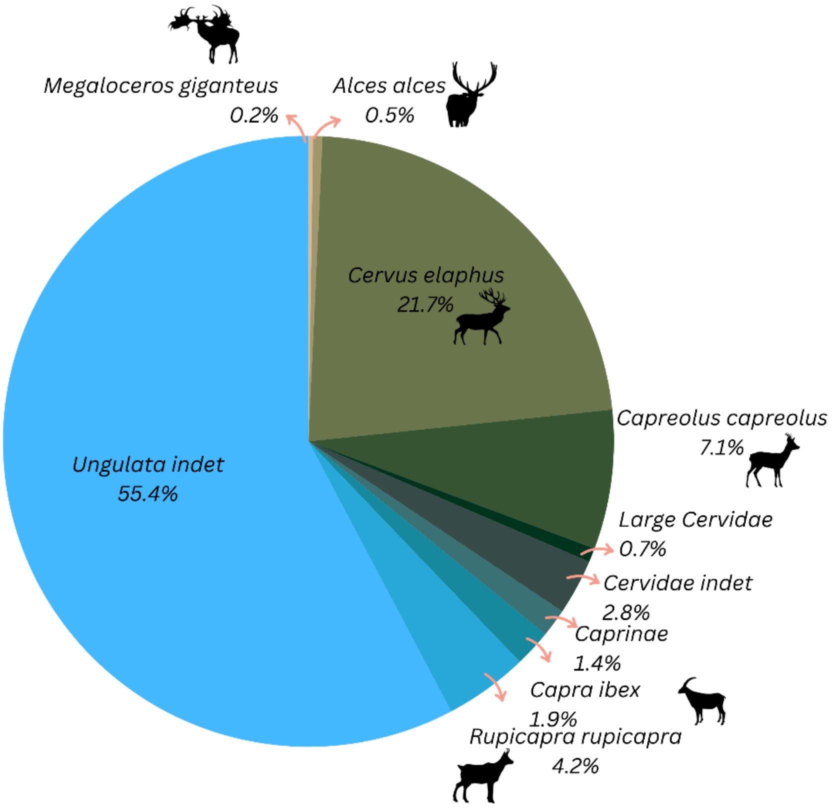

Figure 2. Ungulate distribution across the faunal assemblage.

Hunting and foraging practices appear to be biased towards forested environments, as reflected in the taxonomic composition of the assemblage. This suggests a focus on lowland areas and valley bottoms. Larger prey, such as moose and giant deer, likely had lower encounter and success rates compared to red deer and roe deer. However, these larger species may have been more successfully hunted than smaller prey in higher altitudes.

A range of species can be identified among the carnivore remains. The presence of the red fox (*Vulpes vulpes*) and ursids (genus *Ursus*) indicates a preference for forested habitats. A complete first phalanx of a brown bear (*Ursus arctos*) is the only human-induced modification found in the carnivore assemblage. The cut marks on this bone suggest skinning, possibly related to the removal of fur for utilitarian or subsistence purposes.

3.2. Exploitation of Carcasses

Anthropic marks, indicative of butchering activities, are observed on the surfaces and fresh fracture edges of bones from all types of ungulates (Table 2). The occurrence of cranial elements suggests that large ungulates, such as red deer, were processed differently from smaller prey species, including roe deer, chamois, and ibex. The presence of cranial elements suggests that whole carcasses were transported to the camp, rather than just the more economically advantageous meaty portions being brought to the site.

Cut marks made by lithic tools are abundant, with 111 marks found on ungulates (Table 2) and 86 on undetermined bone fragments. The majority of butchered specimens are red deer, with 33 specimens bearing cut marks and percussion marks (Table 3, Figures 4 and 5). Butchering marks on other commonly represented species, such as roe deer (n=11), chamois (n=5), and ibex (n=3), are relatively few. This can be partly explained by the relatively high number of undetermined ungulate remains bearing cut marks (n=65), suggesting that a larger proportion of these species were processed but cannot be precisely taxonomically identified.

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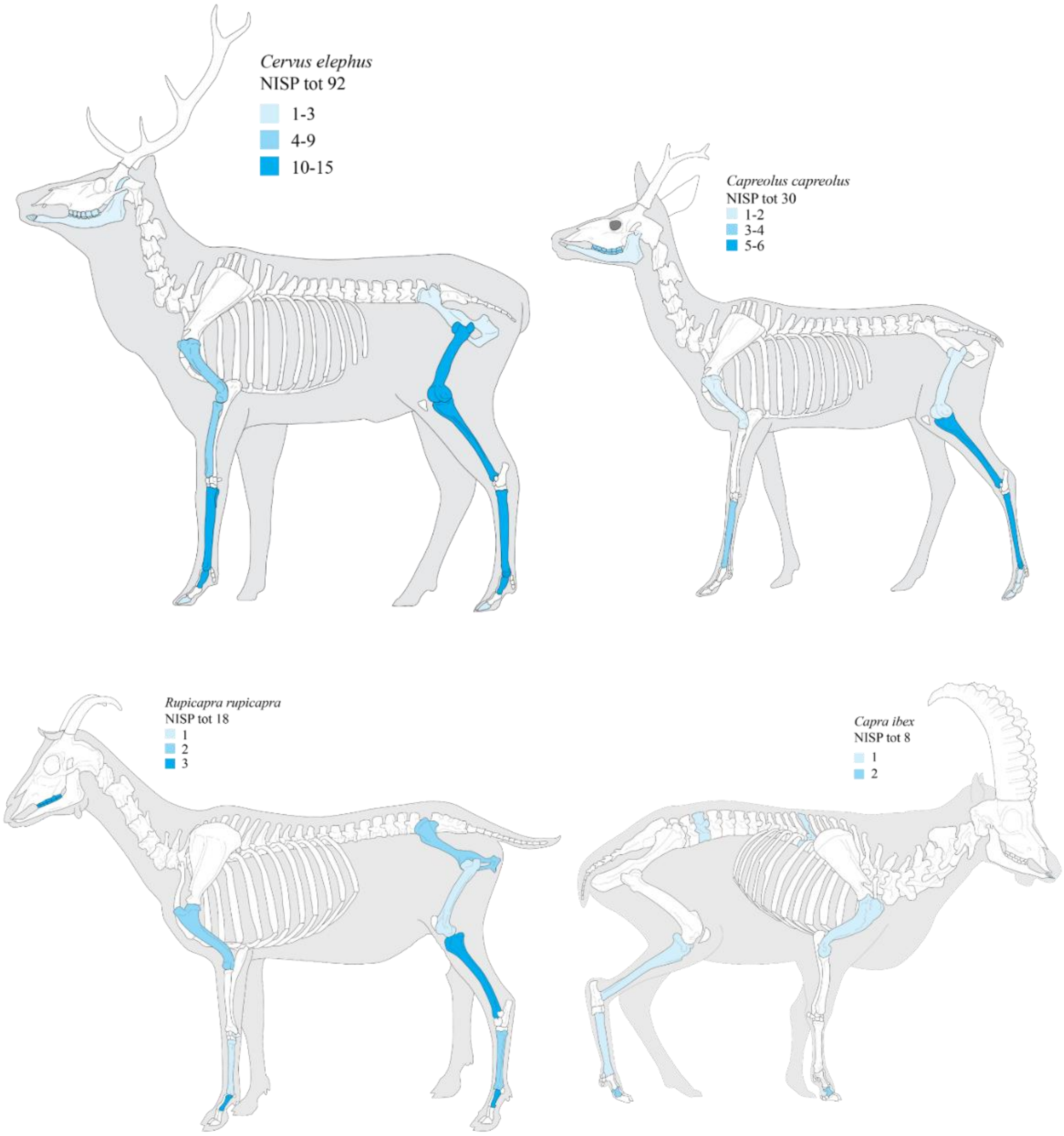

Figure 3. Representation of the frequence of anatomical elements for the main taxa of ungulates.

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Figure 4. Cut marks on ungulate diaphysis (A9-RF 264) (left) and Cut marks (skinning action) on *Cervus elaphus* diaphysis (A9-RF 155) (right).

Table 2. Ungulates with a list of butchering marks, thermal-alterations and carnivore marks. CM: cut marks; PM: percussion marks; CM + PM: cut marks + percussion marks; Tot. BM: Total butchering marks; % BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks.

Taxa	**NISP**	**CM**	**PM**	**CM+PM**	**Tot. BM**	**% BM**	**R**	**B**	**C**	**GM**
Megaloceros gigantieus	1									
Alces alces	2	1			1	50.00		1		
Cervus elaphus	92	28	4	1	33	35.87	1	3	3	7
Capreolus capreolus	30	9	1	1	11	36.67		1	1	
Large Cervidae	3									
Cervidae indet.	12	1			1	8.33				
Caprine	6	2	1	1	4	66.67				
Capra ibex	8	2	1		3	37.50				
Rupicapra rupicapra	18	3	1	1	5	27.78	1	2		
Ungulata indet.	235	65	2	2	69	29.36	2	6	8	5
TOTAL	**407**	**111**	**10**	**6**	**127**	**31.20**	**4**	**13**	**12**	**12**

Table 3. Number of anatomical elements of *Cervus elaphus* and with anthropic modifications and carnivore marks. CM: cut marks; PM: percussion marks; CM + PM: cut marks and percussion marks; IF: impact flakes; CM + IF: cut marks + impact flakes; Tot. BM: Total butchering marks; % BM: % butchering marks; R: retoucher; B: burned-black/brown bones; C: calcined-grey/white bones; GM: carnivore gnawing marks.

Anatomical Element	**NISP**	**CM**	**PM**	**CM+PM**	**Tot. BM**	**% BM**	**R**	**B**	**C**	**GM**
Cranium										
Hemimandible	5	1			1	20.0		1		1
Tooth	4									
Hyoid										
Total cranium	**9**	**1**			**1**	**11.1**				
Atlas-axis										
Vertebra										
Rib										
Total axial skeleton										
Scapula										
Humerus	6	2			2	33.3			1	1
Radius	5	3			3	60.0				
Ulna										
Metacarpal	14	4			4	28.6		1		2
Total forelimb	**25**	**9**			**9**	**36.0**				
Coxal	1									
Femur	12	3	3	1	7	58.3			1	
Tibia	13	4			4	30.8	1			2
Metatarsal	12	6			6	50.0		1	1	1
Total hindlimb	**38**	**13**	**3**	**1**	**17**	**44.7**				
Metapodials	6	2	1		3	50.0				
First phal.	7	2			2	28.6				
Second phal.										
Third phal.	2									
First phal. rudim.										
Second phal. rudim.	1									
Third phal. rudim.	1									

Sesamoid	2	1			1	50.0				
Diaphysis	1									
Total indet. Limb	*20*	*5*	*1*		*6*	*30.0*				
TOTAL	**92**	**28**	**4**	**1**	**33**	**35.9**	**1**	**3**	**3**	**7**

The number of bones bearing retouching impact marks is four (Figure 4): two from undetermined ungulates and one each from red deer and chamois. Stigmata-like punctiform impressions, linear impressions, retouch-induced striae, and notches can be explained by the fact that the bones were used as hammers to knap flint.

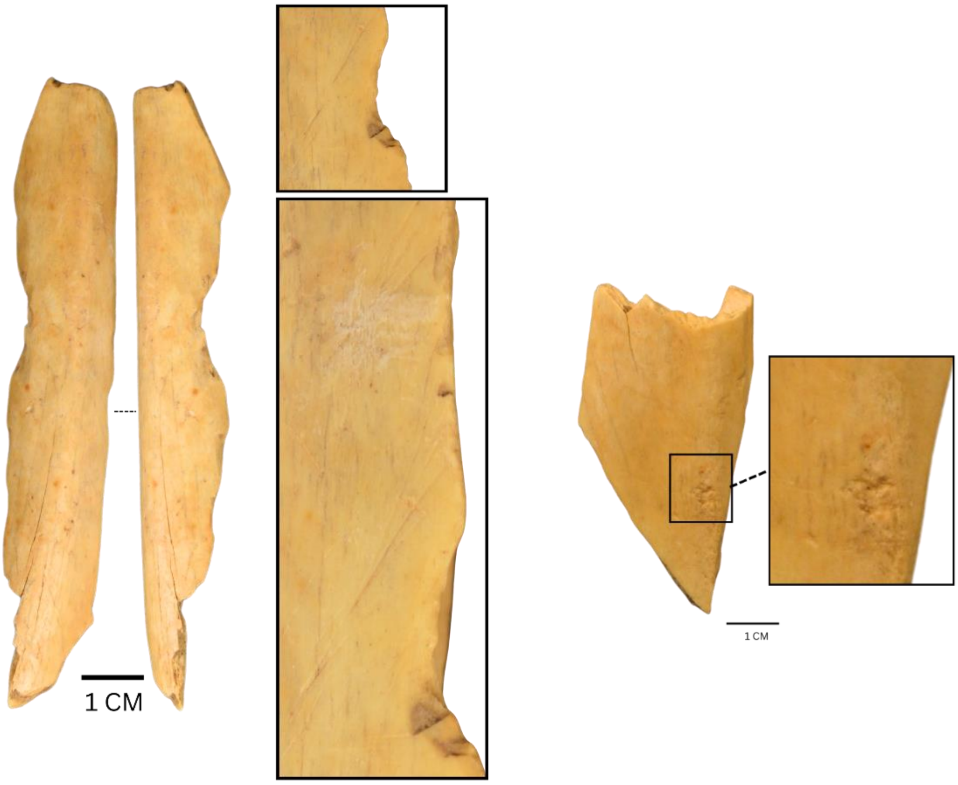

Figure 5. Percussion marks and cut marks on Caprine Tibia (RF 046) (left) and retouching marks on *Cervus elaphus* tibia (RF 002) (right) from Unit A9.

3.3. Carcass Representation Index

The anatomical composition of the A9 ungulate assemblage reveals a clear and structured pattern of skeletal-part representation that provides important insights into carcass transport and butchering practices carried out by Neanderthal groups at Fumane Cave. Cranial elements account for 13.2% of the identifiable remains, most of which consist of isolated teeth. This moderate proportion indicates occasional rather than systematic transport of heads, likely reflecting opportunistic acquisition of the high-fat resources contained within the cranium. Axial remains comprise only 2.7% of the assemblage, a figure consistent with the near absence of vertebrae and ribs throughout the layer. The scarcity of these bulky, low-utility elements strongly suggests that primary disarticulation occurred at kill sites, where axial portions were routinely discarded prior to transport.

Appendicular elements dominate the assemblage. Forelimb bones represent 18.5% of the total, whereas hindlimb elements form the largest category at 33.5%. The marked abundance of femora, tibiae, and metatarsals reflects their high flesh and marrow yield and corresponds to a transport strategy prioritising anatomical segments with the greatest caloric return. Autopodial elements—including metapodials, phalanges, and associated carpals and tarsals—comprise 21.5% of the assemblage (Figures 3 and 6). Their notable frequencies relate both to their intrinsic structural durability and to the regular transport of robust distal parts attached to major limb segments. This distribution closely parallels the pattern described for A9 by Romandini et al. [1], who likewise reported a dominance of hindlimb elements, moderate cranial representation, and minimal axial remains. Combined, the two datasets present a consistent behavioural signal: carcasses were initially reduced at kill locations, and only the nutritionally richest portions were transported to the cave. Intermediate frequencies of forelimb and cranial elements point to a flexible, yet consistently selective transport strategy designed to maximise caloric gain while minimising the labour involved in moving heavy, low-yield anatomical parts.

Evidence for intensive on-site processing—including high levels of limb fragmentation and frequent cut and percussion marks on transported elements—indicates systematic defleshing and marrow extraction within the cave. These modifications support the interpretation of Unit A9 as a habitation area where carcass reduction was routinely completed. Overall, the anatomical and taphonomic data reflect a structured and efficient subsistence system in which Neanderthal groups employed cost-effective transport and processing behaviours, fully consistent with the broader A9 faunal patterns documented by Romandini et al. [1] .

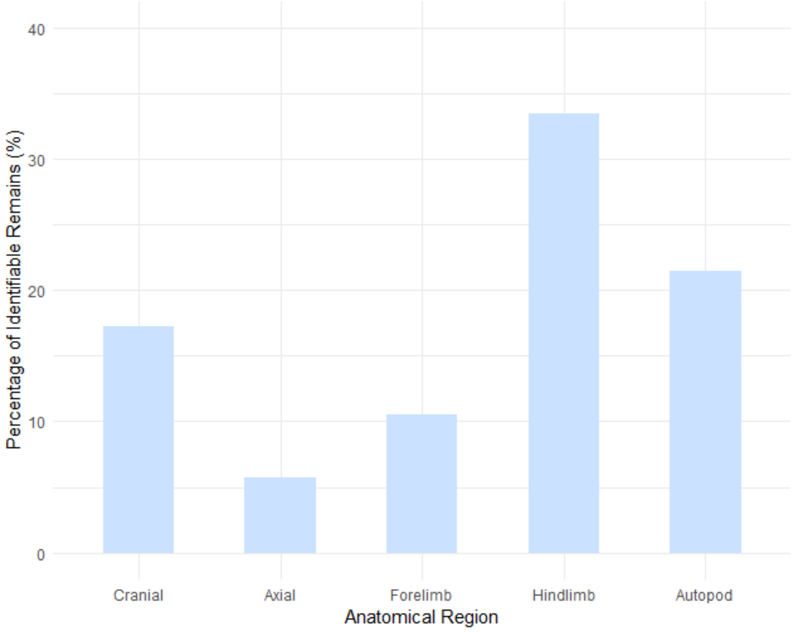

Figure 6. Carcass Representation Profile of Ungulates, Fumane Unit A9.

4. Discussion

The findings of this paper are consistent with those from the previously analysed section of the Fumane A9 unit [1]. The earlier analysis covered the majority of the faunal assemblage, and the present study examines the material that had not yet been analysed. With this analysis, the study of the faunal material from Fumane cave's A9 layer is now complete.

The zooarchaeological evidence offers a robust basis for reconstructing Neanderthal subsistence behaviour within the region. With regard to ecological context, the data are consistent with an environment characterised by sparse forest cover near open grazing zones. Such a mosaic landscape appears to have encouraged a flexible, opportunistic approach to hunting rather than a strategy targeting specific taxa. The diversity of species represented, coupled with the presence of individuals of varying ages, supports the interpretation of a generalist subsistence strategy adapted to the environmental heterogeneity of the Lessini plateau. Comparable behavioural plasticity has been documented in units A5–A6 at Fumane [57,58] and at other MIS 3 Mousterian sites in northern Italy, including Riparo Tagliente [59,60], Riparo Mezzena [61], and Grotta San Bernardino [62–64].

The skeletal-part representation of the A9 ungulate assemblage provides a coherent picture of carcass transport and processing practices during the late Middle Palaeolithic occupation of the site.

Hindlimb elements dominate the assemblage (33.5%), accompanied by substantial autopodial representation (21.5%), while axial remains are notably scarce (2.7%) and forelimb (18.5%) and cranial (13.2%) parts occur in more moderate proportions. This structured distribution mirrors the pattern reported in the earlier A9 study [1] and indicates consistent, economically rational transport strategies shaped by prey size, terrain, and logistical considerations.

Axial elements suggests that carcass processing typically began at kill locations, where bulky, low-utility components were discarded. This behaviour aligns with established models of transport optimisation [32,65,66], which predict that hunters negotiating complex topography, such as the Monti Lessini foothills, would prioritise the removal of high-yield, low-weight anatomical parts. The predominance of hindlimb elements—rich in flesh and marrow—supports this interpretation, as does the high frequency of anthropogenic modifications, including cut marks, percussion damage, and fragmentation indicative of marrow extraction. Taken together, the evidence points to the regular introduction of high-utility limb elements into the cave for intensive secondary processing.

Cranial representation (13.2%) reflects a more variable transport pattern. Occasional transport of skulls is consistent with the acquisition of nutritionally valuable resources such as brain, tongue, and facial musculature—packages particularly advantageous during colder climatic phases (biochemical basis: e.g., review of brain lipids; see [67,68]. Taphonomic evidence of cranial cut marks and percussion in Neanderthal contexts, including Goyet [69], as well as zooarchaeological studies documenting skull exploitation and selective transport [32,70] further supports this behaviour. However, the moderate frequency of cranial remains indicates that head transport was not systematic, reinforcing the interpretation that limb elements were preferentially transported over less predictable nutrient sources. This pattern parallels the earlier findings for A9 [1], which likewise suggested context-dependent decisions regarding head transport.

The relatively high proportion of autopodial elements (21.5%) merits particular attention. Although some of this representation can be attributed to the high density and consequent survivorship of distal limb bones, the recurrent presence of metapodials and phalanges suggests that entire limbs or large limb sections were frequently transported. Similar patterns have been documented at Middle Palaeolithic sites such as Bolomor Cave [71] where distal limb segments accompanied proximal ones due to natural anatomical attachment and their supplementary value for marrow, tendon, and hide processing. The A9 assemblage thus indicates that transported limb packages were not restricted solely to the most profitable components but often included a broader anatomical range.

Comparative data from other European Middle Palaeolithic contexts further situate the Fumane A9 findings. Selective limb transport at sites such as Abri du Maras (Rhône Valley) [72] and Combe-Grenal (France) [73], has been linked to mobility systems in which kill locations were spatially separated from residential hubs. The A9 anatomical profile conforms to this pattern, suggesting that Neanderthal groups hunted red deer and roe deer in nearby lowlands and transported high-utility body parts to the cave for processing. Combustion features and dense concentrations of fragmented limb bones at the cave entrance [1] reinforce the interpretation of A9 as a locus for regular food processing rather than short-term or task-specific use. Collectively, the anatomical representation, modification signatures, and inter-site comparisons indicate a subsistence system that maximised caloric return through coordinated transport and processing within a logistical mobility framework.

The presence of a cut-marked bear bone, although limited in number, contributes to growing evidence for infrequent but meaningful Neanderthal exploitation of ursids in northern Italy. As noted by Romandini et al. [63], MIS 3 Mousterian sites such as Grotta San Bernardino and Grotta di Fumane preserve clear indicators of bear carcass processing. While sporadic, such evidence underscores the flexibility of Neanderthal foraging strategies and their willingness to exploit a wide array of available resources. taphonomic observations reveal minimal evidence of carnivore or rodent disturbance and low levels of weathering, confirming a predominantly anthropogenic accumulation. Burned and calcined remains, representing approximately 4% of the assemblage, attest to proximity to hearths [4,9] and the close association between faunal processing and combustion activities. The combined presence of cut marks, percussion damage, and retoucher use supports the interpretation of A9 as a residential and processing area rather than a secondary deposition zone. Balanced representation of axial and appendicular remains for larger ungulates, together with intensive butchery evidence, further suggests that primary carcass processing, marrow extraction, and possibly hide preparation occurred directly within the cave. These patterns are consistent with other structured on-site faunal exploitation documented in Italian Mousterian contexts, such as Grotta de Nadale [75,76].

Taken together, the faunal and statistical evidence highlights the behavioural sophistication of Neanderthal groups in the region. Subsistence practices at Fumane reflect logistical planning, broad-spectrum prey selection, and efficient utilisation of carcass resources, paralleling patterns observed in some Upper Palaeolithic contexts [77–79]. The integration of hunting, transport, butchery, and resource processing—supplemented by evidence for cranial exploitation, retoucher production, and controlled burning—demonstrates a high degree of cognitive flexibility and ecological awareness. Within the broader European context, the Fumane A9 assemblage aligns with an increasingly diversified Mousterian subsistence pattern during MIS 3, comparable to sites such as Teixoneres Cave (Spain) and Pié Lombard (France) [80]. Among northern Italian sites, Fumane stands out for its integrated faunal, lithic, and combustion evidence within a single stratigraphic unit, offering one of the clearest examples of a well-organised residential base from this period.

5. Conclusions

The faunal assemblage from Unit A9 at Grotta di Fumane provides a refined perspective on Neanderthal subsistence behaviour on the Lessini Plateau during MIS 3. Rather than reflecting purely opportunistic foraging, the anatomical distribution of ungulate remains indicates a structured and economically informed transport strategy. The strong predominance of hindlimb elements, combined with the near absence of axial remains and moderate cranial frequencies, suggests that carcass processing typically began at kill locations, where bulky, low-utility components were discarded. High-yield portions—particularly femora, tibiae, and metatarsals—were selectively transported to the cave for intensive secondary processing. This pattern mirrors that identified in the previously analysed A9 assemblage and aligns with broader Middle Palaeolithic evidence from sites such as Abri du Maras and Combe-Grenal, where selective limb transport has been interpreted as a key feature of logistically organised mobility systems.

The frequent occurrence of cut marks, percussion impacts, and extensive fragmentation further indicates that A9 functioned as a residential locus where carcass reduction and marrow extraction were routinely carried out. The presence of cranial elements, though at moderate levels, points to occasional skull transport for the acquisition of nutrient-rich tissues such as brain and tongue—behaviours consistent with ethnographic and experimental models of fat-oriented transport during cold climatic phases. Additional evidence, including cut-marked ursid remains, illustrates the behavioural flexibility of Neanderthal groups at Fumane, who maintained a consistent focus on cervids while opportunistically exploiting other taxa when encountered. Collectively, the faunal evidence from Unit A9 highlights the planning depth, transport optimisation, and ecological sensitivity that characterised Neanderthal lifeways in northern Italy. These results reinforce a growing understanding across European Middle Palaeolithic contexts: Neanderthal foragers were sophisticated, behaviourally complex hunter-gatherers who structured their subsistence systems around high-utility carcass components, landscape constraints, and the energetic demands of Pleistocene environments.

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References

1. Romandini, M.; Nannini, N.; Tagliacozzo, A.; Peresani, M. The ungulate assemblage from layer A9 at Grotta di Fumane, Italy: A zooarchaeological contribution to the reconstruction of Neanderthal ecology. *Quaternary International* 2014, 337, 11–27.
2. Delpiano, D.; Zupancich, A.; Peresani, M. Innovative Neanderthals: Results from an integrated analytical approach applied to backed stone tools. *Journal of Archaeological Science* 2019, 110, 105011.
3. Delpiano, D.; Heasley, K.; Peresani, M. Assessing Neanderthal land use and lithic raw material management in Discoid technology. *Journal of Anthropological Sciences* 2018, 96, 89–110.
4. Marcazzani, D.; Miller, C.E.; Ligouis, B.; Duches, R.; Conard, N.J.; Peresani, M. Middle and Upper Paleolithic occupations of Fumane Cave (Italy): A geoarchaeological investigation of the anthropogenic features. *Journal of Anthropological Sciences* 2023, 101, 37–62.
5. Delpiano, D.; Gravina, B.; Peresani, M. Back(s) to basics: The concept of backing in stone tool technologies for tracing hominin technical innovations. *Evolutionary Anthropology: Issues, News, and Reviews* 2024, 33.
6. Peresani, M. Inspecting human evolution from a cave. Late Neanderthals and early sapiens at Grotta di Fumane: present state and outlook. *Journal of Anthropological Sciences* 2022, 100, 71–107.
7. López-García, J.M.; dalla Valle, C.; Cremaschi, M.; Peresani, M. Reconstruction of the Neanderthal and Modern Human landscape and climate from the Fumane cave sequence using small-mammal assemblages. *Quaternary Science Reviews* 2015, 128, 1–13.
8. Kehl, M.; Marcazzan, D.; Miller, C.E.; Falcucci, A.; Duches, R.; Peresani, M. The Upper Sedimentary Sequence of Grotta di Fumane, Northern Italy: A Micromorphological Approach to Study Imprints of Human Occupation and Paleoclimate Change. *Geoarchaeology* 2025, 40.
9. Sánchez-Romero, L.; Govoni, M.; Marcazzan, D.; Delpiano, D.; Nannini, N.; Martellotta, E.F.; Duches, R.; Peresani, M. Intra-site Organization of the Repeated Neanderthal Occupation of Unit A9, Grotta di Fumane. *Journal of Archaeological Method and Theory* 2025, 32, 45.
10. Benazzi, S.; Bailey, S.E.; Peresani, M.; Mannino, M.A.; Romandini, M.; Richards, M.P.; Hublin, J.-J. Middle Paleolithic and Uluzzian human remains from Fumane Cave, Italy. Journal of Human Evolution 2014, 70, 61–68.
11. Nannini, N. Studio archeozoologico del complesso faunistico delle unità musteriane A8 e A9. Approfondimenti tafonomici sulle modalità di sussistenza degli ultimi discoidi di Grotta di Fumane (VR). PhD Thesis, University of Ferrara, Italy, 2012.
12. France, D.L. *Human and Nonhuman Bone Identification: A Color Atlas*. CRC Press: New York, USA, 2009.
13. Davis, S.J.M. *The Archaeology of Animals*. Routledge Press: London, UK, 1987.
14. 14. Lyman, R.L. *Vertebrate Taphonomy*. Cambridge University Press: Cambridge, UK, 2014; pp. 1–524.
15. Broughton, J.M. *Zooarchaeology*. In International Encyclopedia of the Social & Behavioral Sciences, 2nd ed, 2015; pp. 849–853.
16. Reitz, E.J.; Wing, E.S. *Cambridge Manual of Zooarchaeology*. Cambridge University Press: Cambridge, UK, 2008.
17. Bunn, H.T.; Bartram, L.E.; Kroll, E.M. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. *Journal of Anthropological Archaeology* 1988, 7, 412–457.
18. Aitken, R.J. Delayed implantation in roe deer (Capreolus capreolus). *Reproduction* 1974, 39, 225–233.
19. Mariezkurrena, K. Contribución al conocimiento del desarrollo de la dentición y el esqueleto postcraneal de Cervus elaphus. *Munibe* 1983, 149–202.
20. D'Errico, F.; Vanhaeren, M. Criteria for identifying red deer (Cervus elaphus) age and sex from their canines. *Journal of Archaeological Science* 2002, 29, 211–232.
21. Hillson, S. *Teeth*. Cambridge University Press: Cambridge, UK, 2005.

22. Silver, I. *The ageing of domestic animals*. In Science in Archaeology: A Survey of Progress and Research; Brothwell, D., Higgs, E., Clark, G., Eds.; Praeger Press: New York, USA, 1969; pp. 250–268.
23. Bunn, H.T.; Pickering, T.R. Methodological recommendations for ungulate mortality analyses in paleoanthropology. *Quaternary Research* 2010, 74, 388–394.
24. Habermehl, K.H. Die Altersbestimmung Bei Hausund Labortieren, 1975.
25. Grayson, D.K. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press: Orlando, USA, 1984.
26. Bökönyi, S. A New Method for the Determination of the Number of Individuals in Animal Bone Material. *American Journal of Archaeology* 1970, 74, 291–292.
27. Behrensmeyer, A.K. Taphonomic and ecologic information from bone weathering. *Paleobiology* 1978, 4, 150–162.
28. Fernandez-Jalvo, Y.; Andrews, P. *Atlas of Taphonomic Identifications*. Springer Netherlands: Dordrecht, Netherlands, 2016.
29. Brain, C.K. Bone weathering and the problem of bone pseudo-tools. *South African Journal of Science* 1967, 63, 97–99.
30. Shipman, P. *Life History of a Fossil: An Introduction to Taphonomy and Paleoecology*. Harvard University Press: Cambridge, USA, 1981.
31. Fisher, J.W. Bone surface modifications in zooarchaeology. *Journal of Archaeological Method and Theory* 1995, 2, 7–98.
32. Binford, L.R. *Bones: Ancient Men and Modern Myth*. Academic Press: New York, USA, 1981.
33. Brain, C.K. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press: Chicago, USA, 1981.
34. Blumenschine, R.J.; Selvaggio, M.M. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 1988, 333, 763–765.
35. Capaldo, S.D.; Blumenschine, R.J. A Quantitative Diagnosis of Notches Made by Hammerstone Percussion and Carnivore Gnawing on Bovid Long Bones. *American Antiquity* 1994, 59, 724–748.
36. Blumenschine, R.J. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 1995, 27, 197–213.
37. Domínguez-Rodrigo, M.; Piqueras, A. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science* 2003, 30, 1385–1391.
38. Potts, R.; Shipman, P. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 1981, 291, 577–580.
39. Shipman, P.; Rose, J. Early hominid hunting, butchering, and carcass-processing behaviors: Approaches to the fossil record. *Journal of Anthropological Archaeology* 1983, 2, 57–98.
40. Lyman, R.L. *Quantitative Paleozoology*. Cambridge University Press: Cambridge, UK, 2008.
41. Costamagno, S.; Soulier, M.-C.; Val, A.; Chong, S. The reference collection of cutmarks. *Palethnologie* 2019, 1, 1–93.
42. Blumenschine, R.J.; Selvaggio, M.M. On the marks of marrow bone processing by hammerstones and hyaenas: their anatomical patterning and archaeological implications. In *Cultural Beginnings: Approaches to Understanding Early Hominid Life-Ways in the African Savanna;* Clark, J.D., Ed.; Dr Rudolf Habelt GmbH: Bonn, Germany, 1991; pp. 17–32.
43. Blasco, R.; Rosell, J.; Domínguez-Rodrigo, M.; Lozano, S.; Pastó, I.; Riba, D.; Vaquero, M.; Peris, J.F.; Arsuaga, J.L.; de Castro, J.M.B.; Carbonell, E. Learning by Heart: Cultural patterns in the faunal processing sequence during the Middle Pleistocene. *PLoS ONE* 2013, 8, e55863.
44. Vettese, D.; Daujeard, C.; Blasco, R.; Borel, A.; Caceres, I.; Moncel, M.H. Neanderthal long bone breakage process: Standardized or random patterns? The example of Abri du Maras (Southeastern France, MIS 3). *Journal of Archaeological Science: Reports* 2017, 13, 151–163.
45. Villa, P.; Mahieu, E. Breakage patterns of human long bones. *Journal of Human Evolution* 1991, 21, 27–48.

46. Outram, A.K. A new approach to identifying bone marrow and grease exploitation: Why the "indeterminate" fragments should not be ignored. *Journal of Archaeological Science* 2001, 28, 401–410.
47. Grunwald, A.M. Analysis of fracture patterns from experimentally marrow-cracked frozen and thawed cattle bones. *Journal of Archaeological Science: Reports* 2016, 8, 356–365.
48. Coil, R.; Tappen, M.; Yezzi-Woodley, K. New analytical methods for comparing bone fracture angles: A controlled study of hammerstone and hyena (Crocuta crocuta) long bone breakage. *Archaeometry* 2017, 59, 900–917.
49. Stiner, M.C.; Kuhn, S.L.; Weiner, S.; Bar-Yosef, O. Differential burning, recrystallization, and fragmentation of archaeological bone. *Journal of Archaeological Science* 1995, 22, 223–237.
50. Miller, F.L. Caribou. In *Wild Mammals of North America: Biology, Management, and Conservation;* Feldhamer, G.A., Thompson, B.C., Chapman, J.A., Eds.; John Hopkins University Press: Baltimore, USA, 2003; pp. 965–997.
51. Mysterud, A. Diet overlap among ruminants in Fennoscandia. *Oecologia* 2000, 124, 130–137.
52. Yravedra, J.; Cobo-Sánchez, L. Neanderthal exploitation of ibex and chamois in southwestern Europe. *Journal of Human Evolution* 2015, 78, 12–32.
53. Carvalho, M.; Haws, J.A.; Jones, E.L. Late Neanderthal subsistence and foraging mobility at Lapa do Picareiro: a zooarchaeological and taphonomic analysis of Level JJ. *Frontiers in Environmental Archaeology* 2025, 4.
54. Rendu, W.; Costamagno, S.; Meignen, L.; Soulier, M.-C. Monospecific faunal spectra in Mousterian contexts: Implications for social behavior. *Quaternary International* 2012, 247, 50–58.
55. Bal-García, H.; Rey-Rodríguez, I.; de Lombera-Hermida, A.; Díaz-Rodríguez, M.; Fernández-Rodríguez, C.; Rodríguez-Álvarez, X.P.; Valcarce, R.F. Landscape and subsistence in NW Iberia during the Middle Palaeolithic (MIS3): Faunal analysis of Cova Eirós (Triacastela, Galicia, Spain). *Journal of Archaeological Science: Reports* 2025, 64, 105149.
56. Yravedra, J.; Estaca-Gómez, V.; Grandal-d'Anglade, A.; Pinto-Llona, A.C. Neanderthal subsistence strategies: new evidence from the Mousterian Level XV of the Sopeña rock shelter (Asturias, northern Spain). *Archaeological and Anthropological Sciences* 2024, 16, 6.
57. Peresani, M.; Chrzavzez, J.; Danti, A.; De March, M.; Duches, R.; Gurioli, F.; Muratori, S.; Romandini, M.; Trombino, L.; Tagliacozzo, A. Fire-places, frequentations and the environmental setting of the final Mousterian at Grotta di Fumane: a report from the 2006–2008 research. In *Quartär: International Yearbook for Ice Age and Stone Age Research*; Müller, W., Valentin Eriksen, B., Street, M., Weniger, G.-C., Eds.; Verlag Marie Leidorf GmbH: Rahden, Germany, 2011; pp. 131–151.
58. Romandini, M. Analisi archeozoologica, tafonomica, paleontologica e spaziale dei livelli Uluzziani e tardo-Musteriani della Grotta di Fumane (VR). Variazioni e continuità strategico-comportamentali umane in Italia Nord Orientale: i casi di Grotta del Col della Stria (VI) e Grotta del Rio Secco (PN). PhD Thesis, University of Ferarra, Italy, 2012.
59. Thun Hohenstein, U.; Caffarelli, L.; Arnetta, G.; Rivals, F.; Pozzobon, P.; Gialanella, S.; Delpiano, D.; Peresani, M. Taphonomy of the fauna and chert assemblages from the Middle Palaeolithic site of Vajo Salsone, Eastern Italian Alps. *Quaternary Science Advances* 2024, 14, 100183.
60. Modolo, M.; Rosell Ardèvol, J.; Blasco, R.; Turrini, M.; Hohenstein, U. Bone refits at Abric Romaní (Barcelona, Spain) and Riparo Tagliente (Verona, Italy): Testing Neanderthal use of space and post-depositional disturbances. In *Archaeological, Biological and Historical Approaches in Archaeozoological Research; Pişkin*, BAR Publishing: Oxford, UK, 2021.
61. Thun-Hohenstein, U.; Parere, V.; Sala, B.; Giunti, P.; Longo, L. Large mammals from Mezzena rockshelter: new biocronological and palaeoecological hypotheses and preliminary data on subsistence strategies. *Quaternary International* 2012, 259, 1–6.
62. Fiore, I.; Gala, M.; Romandini, M.; Cocca, E.; Tagliacozzo, A.; Peresani, M. From feathers to food: Reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane cave, unit A9. *Quaternary International* 2016, 421, 134–153.

63. Romandini, M.; Hohenstein, U.T.; Fiore, I.; Tagliacozzo, A.; Perez, A.; Lubrano, V.; Terlato, G.; Peresani, M. Late neandertals and the exploitation of small mammals in northern Italy: fortuity, necessity or hunting variability? *Quaternaire* 2018, 61–67.
64. Terlato, G.; Livraghi, A.; Romandini, M.; Peresani, M. Large bovids on the Neanderthal menu: Exploitation of Bison priscus and Bos primigenius in northeastern Italy. *Journal of Archaeological Science: Reports* 2019, 25, 129–143.
65. Binford, L.R. *Nunamiut Ethnoarchaeology*. Academic Press: New York, USA, 1978.
66. Binford, L.R. *In Pursuit of the Past: Decoding the Archaeological Record*. University of California Press: Berkeley, USA, 1983.
67. Chang, C.-Y.; Ke, D.-S.; Chen, J.-Y. Essential fatty acids and human brain. *Acta Neurologica Taiwanica* 2009, 18, 231–241.
68. Agam, A.; Barkai, R. Not the brain alone: The nutritional potential of elephant heads in Paleolithic sites. *Quaternary International* 2016, 406, 218–226.
69. Rougier, H.; Crevecoeur, I.; Beauval, C.; Posth, C.; Flas, D.; Wißing, C.; Furtwängler, A.; Germonpré, M.; Gómez-Olivencia, A.; Semal, P.; van der Plicht, J.; Bocherens, H.; Krause, J. Neandertal cannibalism and Neandertal bones used as tools in Northern Europe. *Scientific Reports* 2016, 6, 29005.
70. Domínguez-Rodrigo, M.; Pickering, T.R.; Semaw, S.; Rogers, M.J. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *Journal of Human Evolution* 2005, 48, 109–121.
71. Blasco, R.; Fernández Peris, J. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International* 2012, 252, 16–31.
72. Marín, J.; Daujeard, C.; Saladié, P.; Rodríguez-Hidalgo, A.; Vettese, D.; Rivals, F.; Boulbes, N.; Crégut-Bonnoure, E.; Lateur, N.; Gallotti, R.; Arbez, L.; Puaud, S.; Moncel, M.-H. Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). *Quaternary Science Reviews* 2020, 243, 106472.
73. Chase, P.G. *The Hunters of Combe-Grenal: Approaches to Middle Paleolithic Subsistence in Europe*. BAR International Series S286; British Archaeological Reports: Oxford, UK, 1986.
74. Romandini, M.; Terlato, G.; Nannini, N.; Tagliacozzo, A.; Benazzi, S.; Peresani, M. Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *Journal of Archaeological Science* 2018, 90, 71–91.
75. Livraghi, A.; Fanfarillo, G.; Colle, M.D.; Romandini, M.; Peresani, M. Neanderthal ecology and the exploitation of cervids and bovids at the onset of MIS4: A study on De Nadale cave, Italy. *Quaternary International* 2021, 586, 24–41.
76. Romandini, M.; Silvestrini, S.; Real, C.; Lugli, F.; Tassoni, L.; Carrera, L.; Badino, F.; Bortolini, E.; Marciani, G.; Delpiano, D.; Piperno, M.; Collina, C.; Peresani, M.; Benazzi, S. Late Neanderthal "menu" from northern to southern Italy: freshwater and terrestrial animal resources. *Quaternary Science Reviews* 2023, 315, 108233.
77. Gaudzinski, S. A matter of high resolution? The Eemian Interglacial (OIS 5e) in north-central Europe and Middle Palaeolithic subsistence. *International Journal of Osteoarchaeology* 2004, 14, 201–211.
78. Adler, D.S.; Bar-Oz, G.; Belfer-Cohen, A.; Bar-Yosef, O. Ahead of the Game. *Current Anthropology* 2006, 47, 89–118.
79. Stiner, M.C.; Munro, N.D.; Surovell, T.A. The Tortoise and the Hare: Small-Game Use, the Broad-Spectrum Revolution, and Paleolithic Demography. *Current Anthropology* 2000, 41, 39–79.
80. Uzunidis, A.; Blasco, R.; Brugal, J.-P.; Fourcade, T.; Ochando, J.; Rosell, J.; Roussel, A.; Rufà, A.; Sánchez Goñi, M.F.; Texier, P.-J.; Rivals, F. Neanderthal hunting grounds: The case of Teixoneres Cave (Spain) and Pié Lombard rockshelter (France). *Journal of Archaeological Science* 2024, 168, 106007.