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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. Additionally, 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 ($38^{\circ}32'55''$ N, $-8^{\circ}8'18''$ 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 $\sim 12 \times 15$ 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

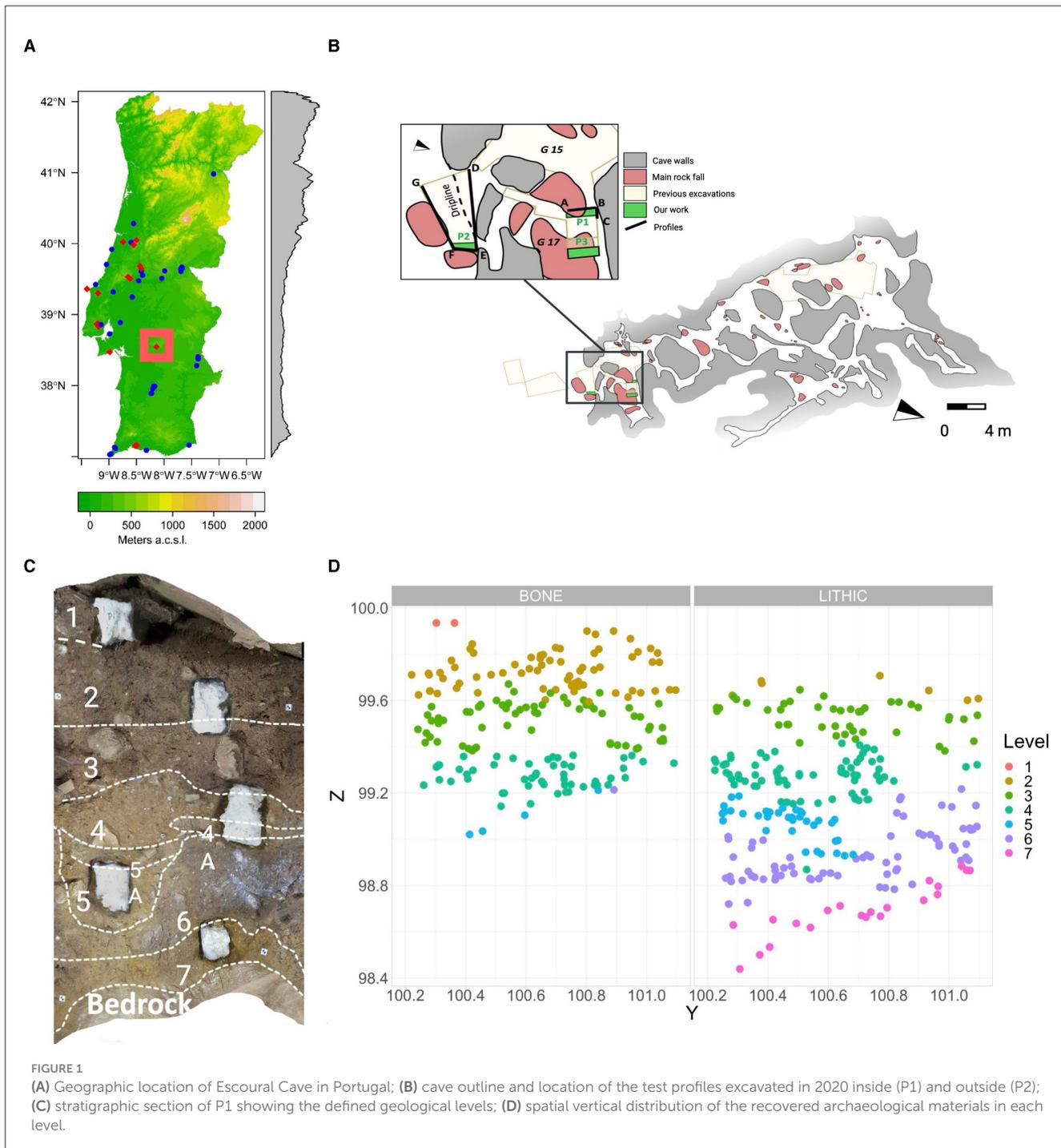
reported identified assemblage represents 27.8% of the total, increasing to 73.4% when including rabbit remains. Despite being very fragmented, the assemblage showed good preservation. The macrofaunal collection is dominated by several species of equids and cervids but also includes a diverse taxonomic 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



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 \times . 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 rrttools 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 biostratigraphic 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

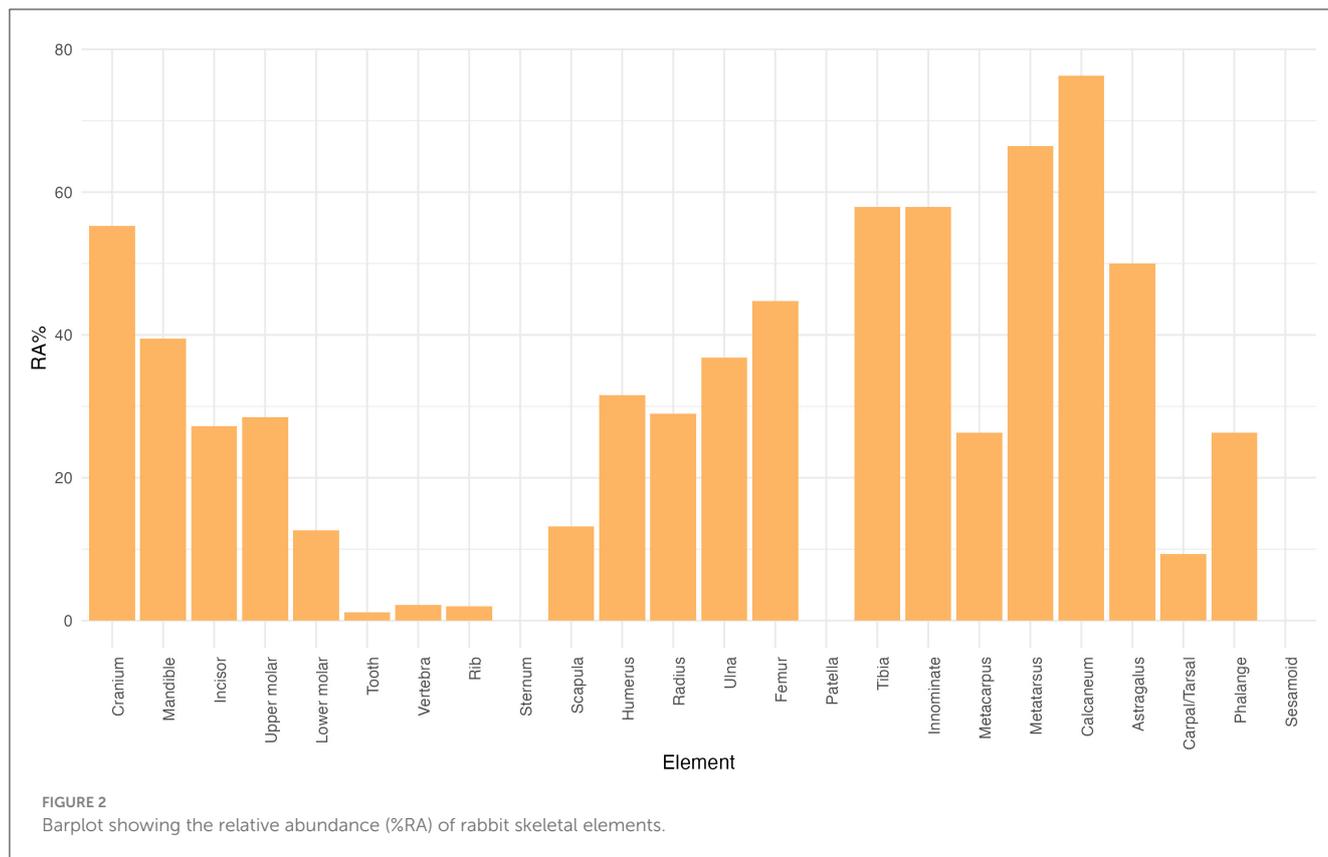
provides standardized and comparable values, unlike the indices of skeletal part representation calculated from NISP and MNE, and thus ensures more reliable outcomes. Assemblages were included in the reference dataset only if their minimum number of individuals (MNI) was higher than 9. The reference 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

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		

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



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

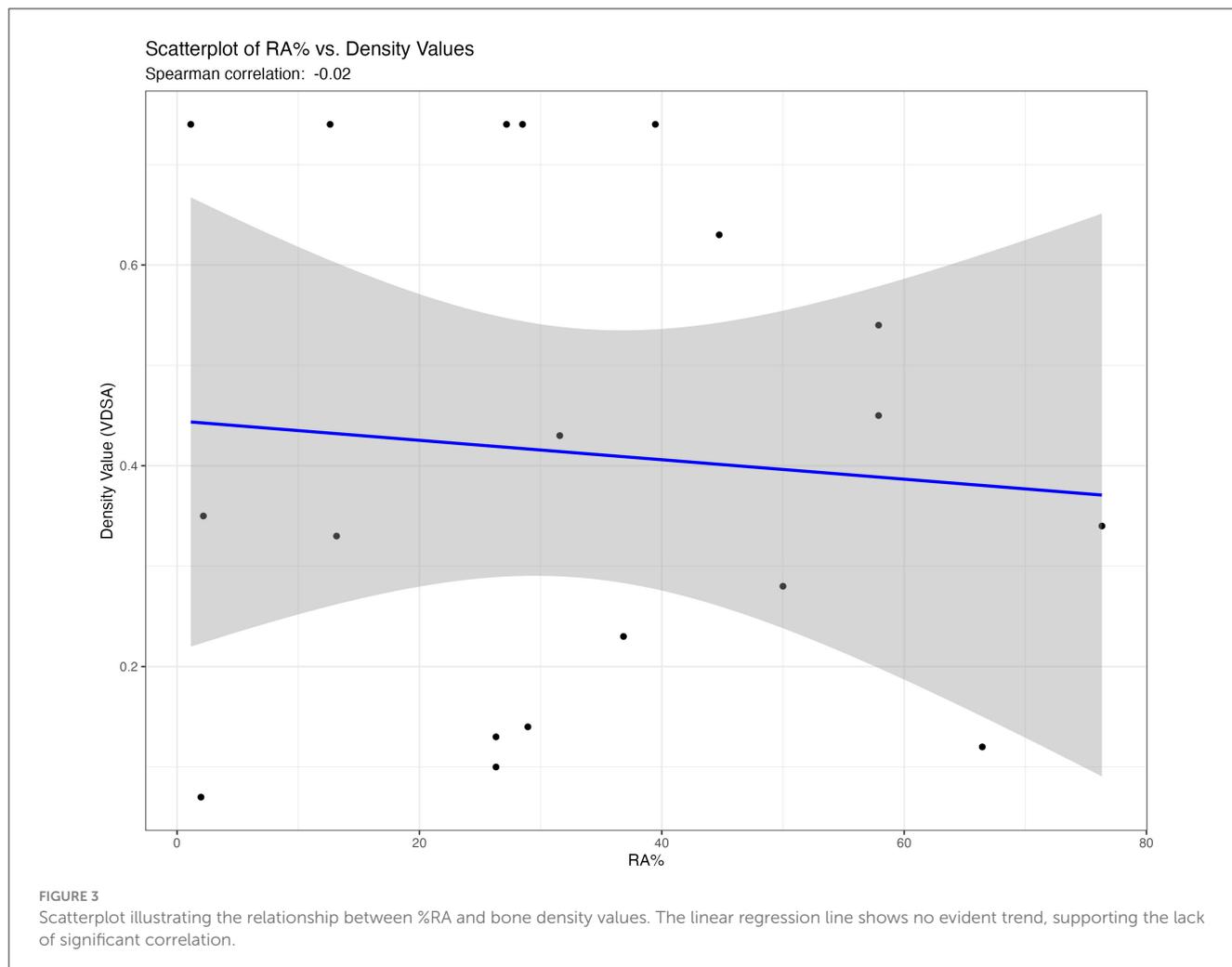
All identified bone specimens were classified into the breakage categories defined and described by Lloveras et al. (2008b). Breakage categories vary depending on bone element, and percentages are also recorded for complete elements and isolated and *in-situ* teeth. Long bones and metapodial breakage 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,

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

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).



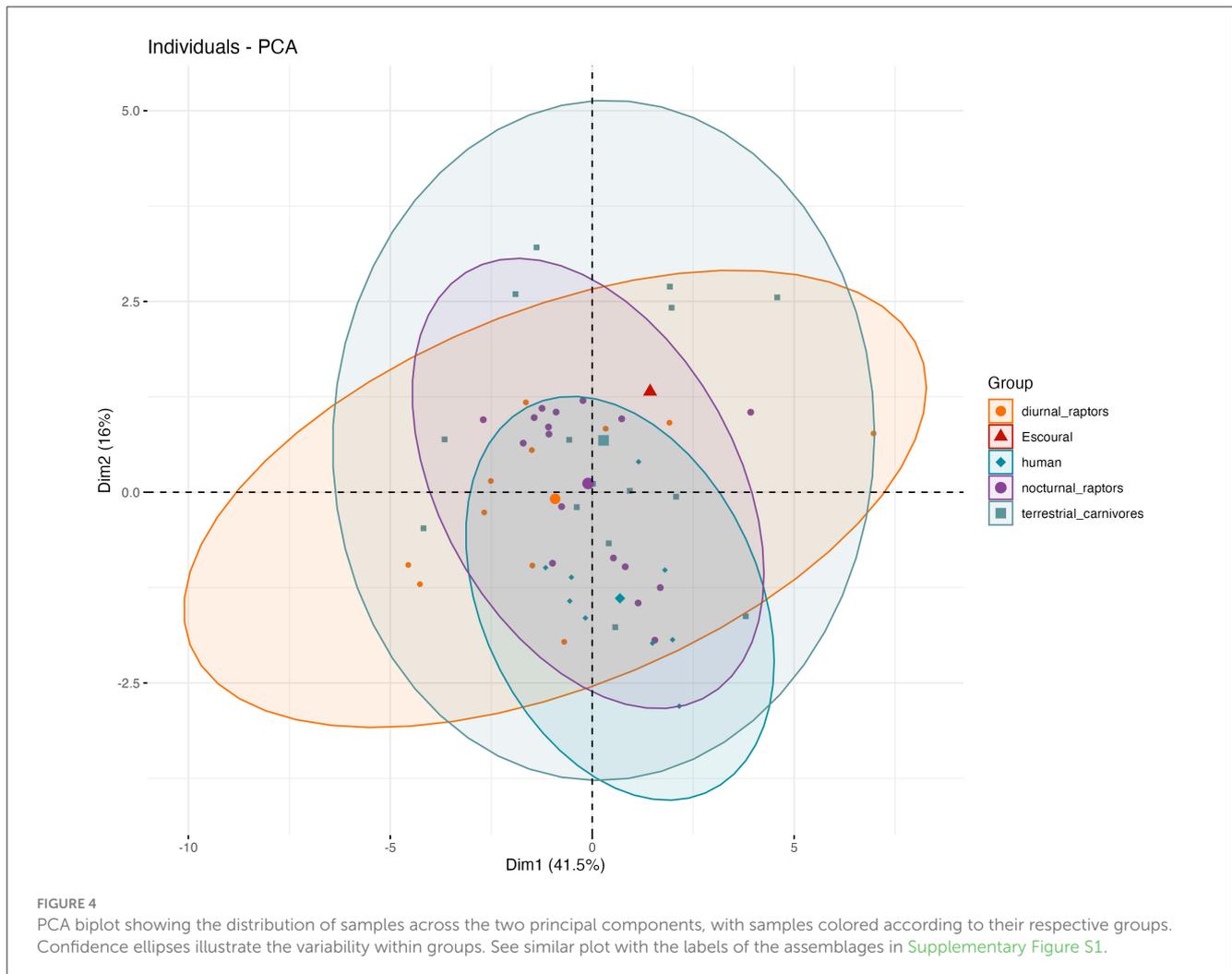
2.2.5 Bone surface modifications and digestion

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: MicroCopiaDigital 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



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%

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			

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 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	<i>"in situ"</i>					
	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.

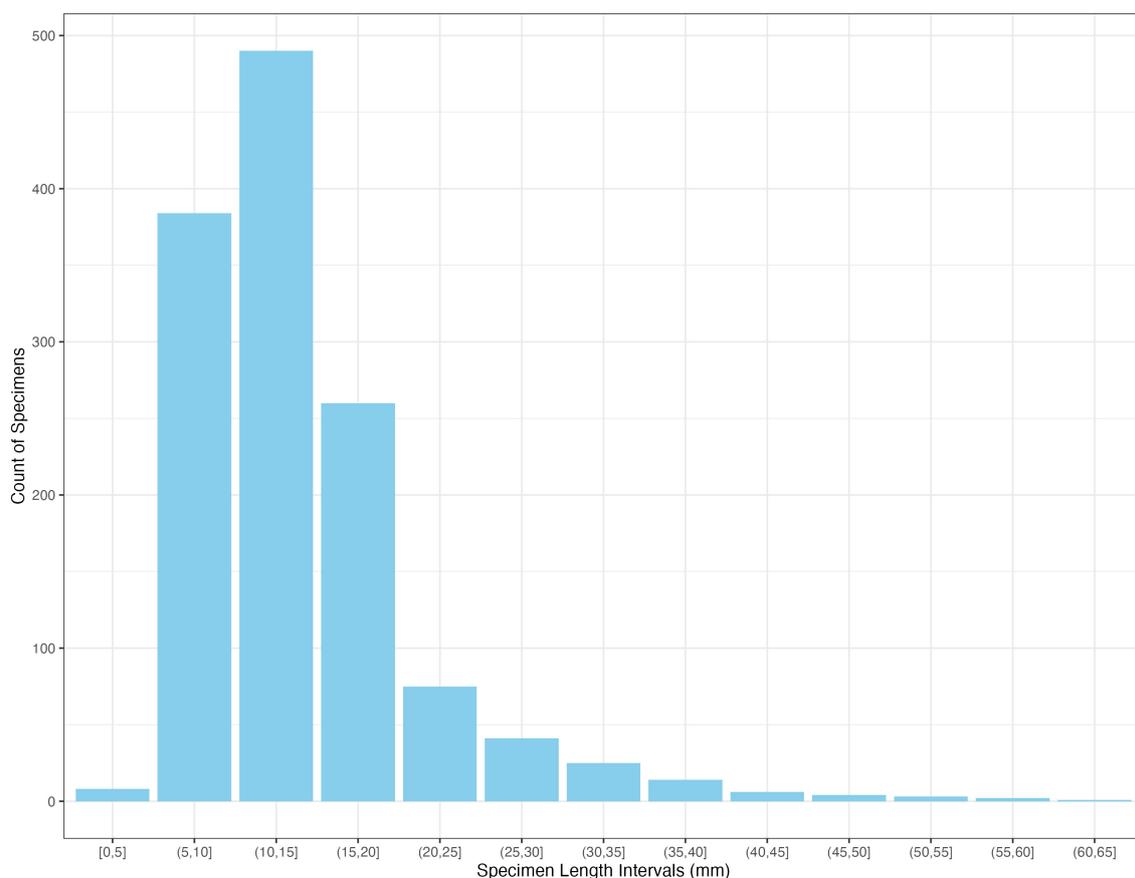


FIGURE 5 Specimen length distribution of the recovered rabbit remains.

Innominate 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

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.

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).

3.4 Bone surface modifications and digestion

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

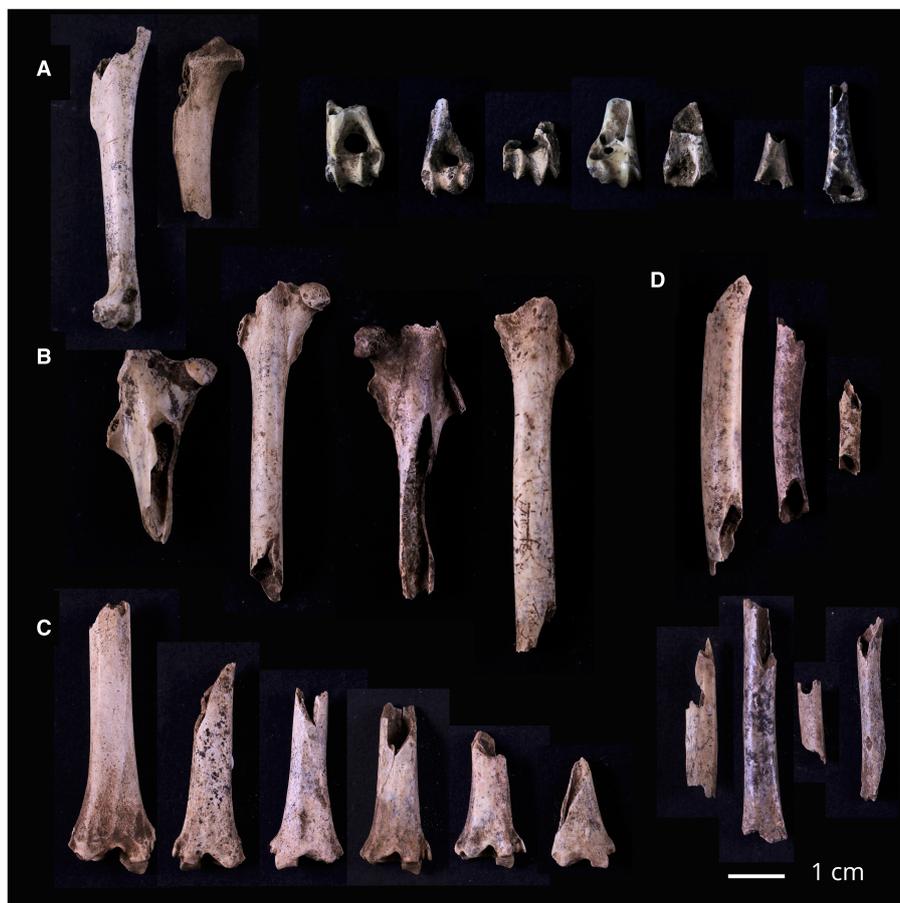


FIGURE 6

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.

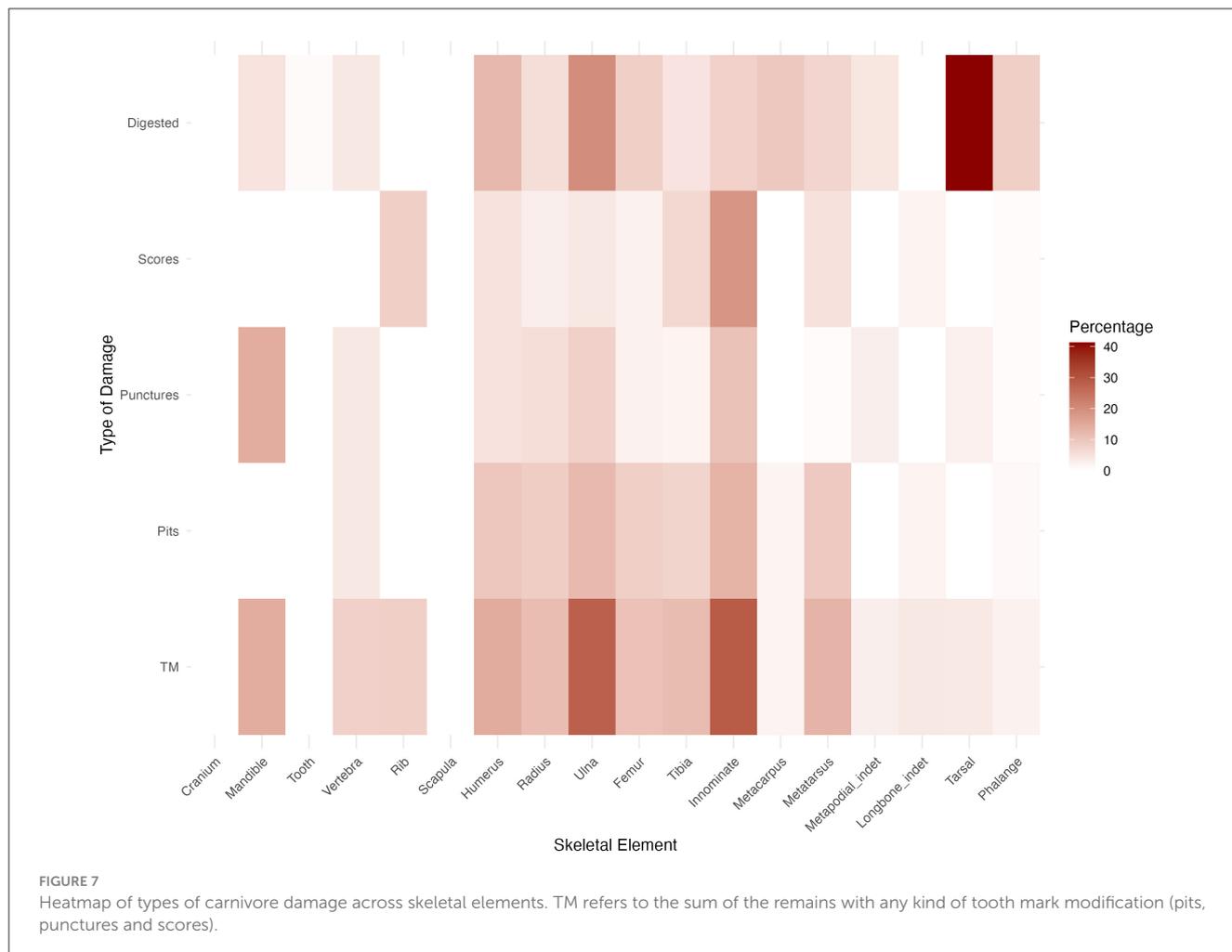
punctures, and scores) occur in relatively similar percentages across long bones.

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 Navalmaillo 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



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 Navalmaillo, 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 ([Cocharde 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](#); [Télez et al., 2022](#)). This indicates that Neanderthals may have focused on other food sources or different subsistence strategies during their occupation of the site.

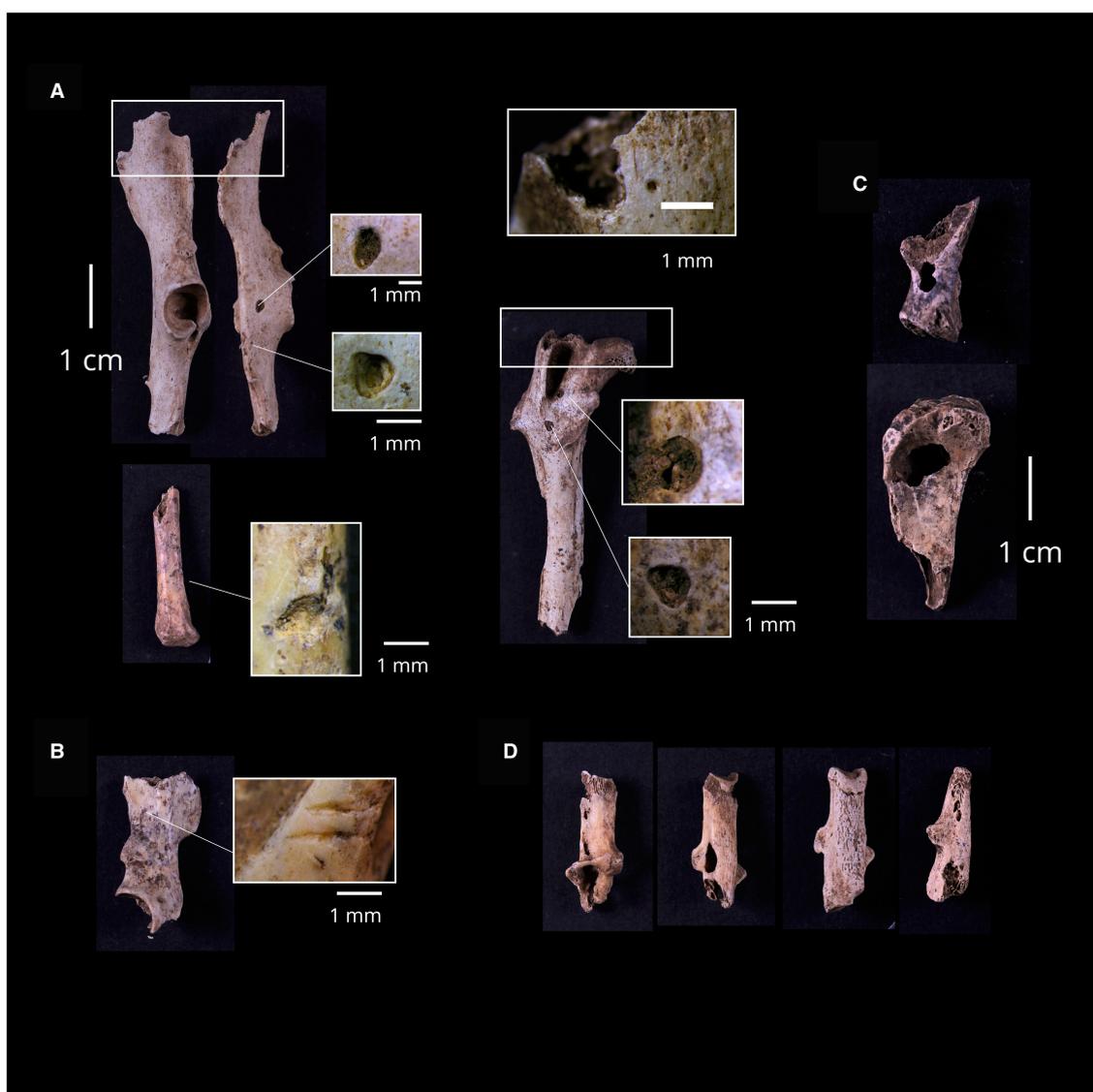


FIGURE 8
 Examples of tooth marked and digested specimens. **(A)** Specimens showing pits and crenulated edges, **(B)** pelvis fragment with carnivore scores, **(C)** examples of punctured specimens, **(D)** several digested calcanei.

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

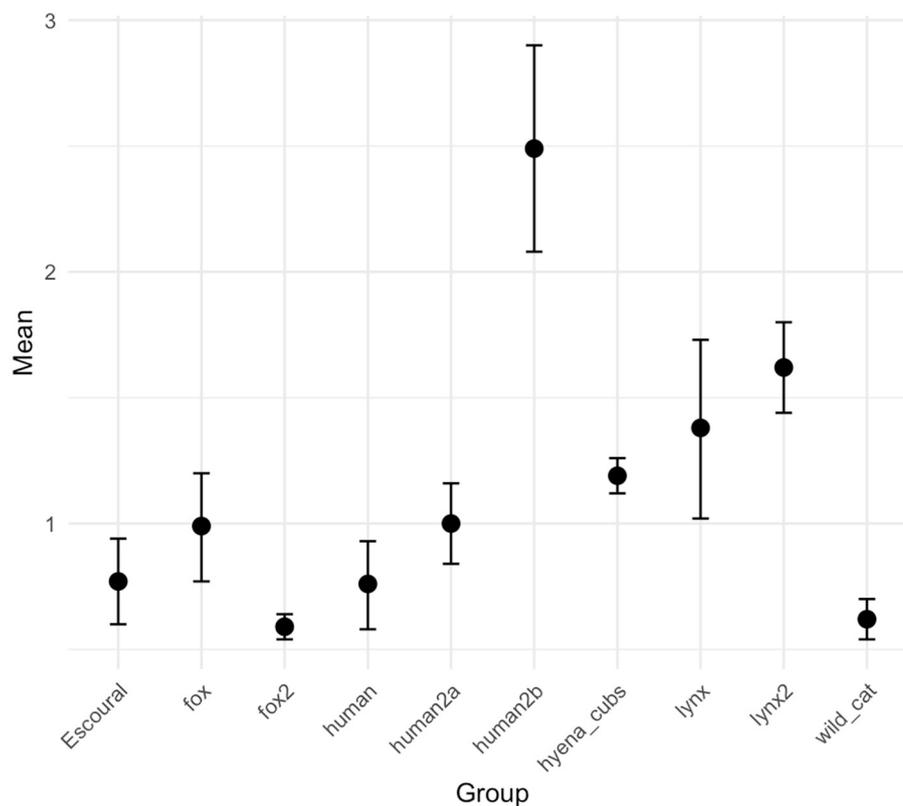


FIGURE 9

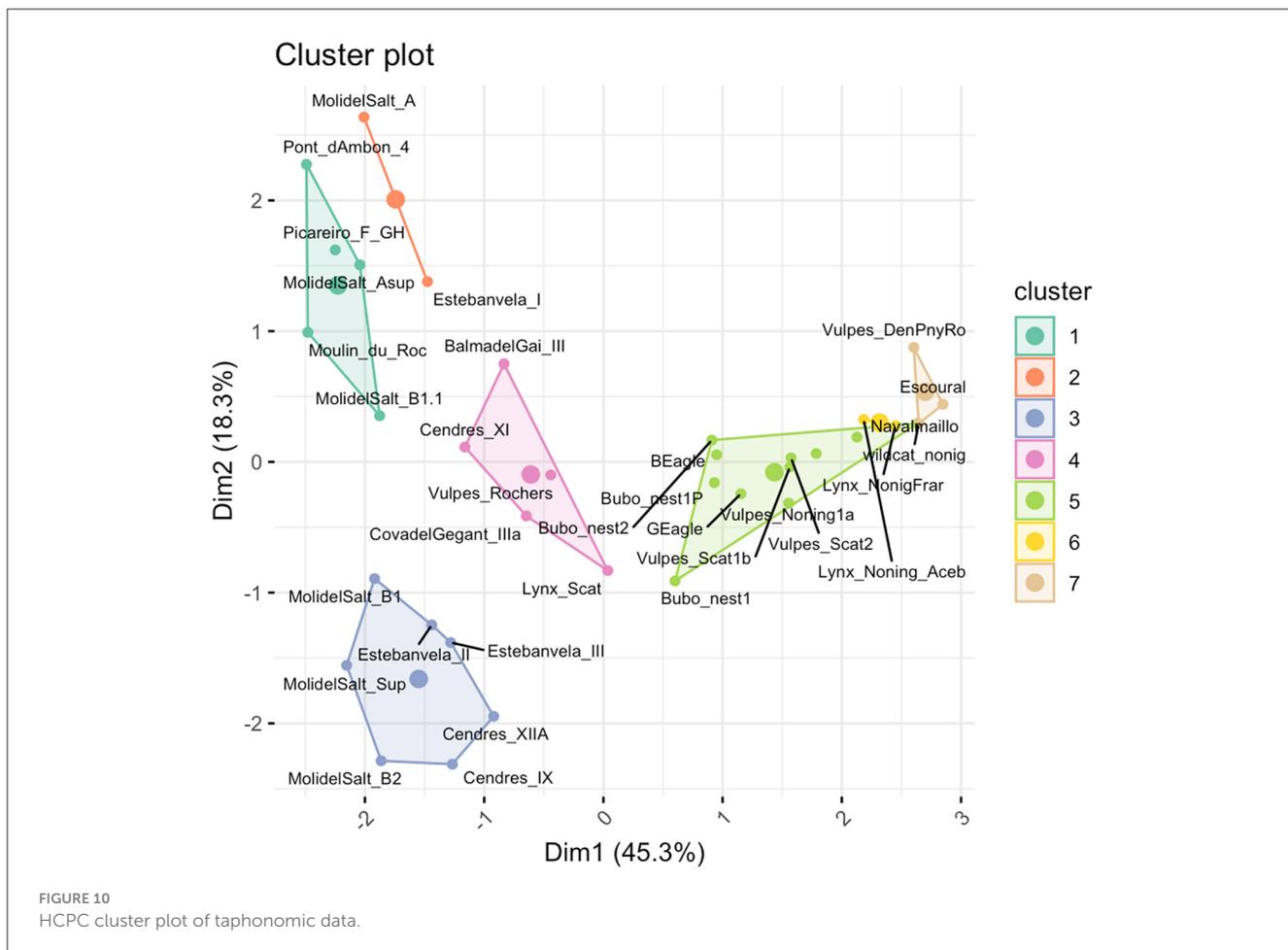
Mean values and 95% confidence intervals of tooth pit and puncture widths on cortical surfaces of long bone shafts on bone assemblages modified by fox, humans, hyena cubs, lynxes and wildcats. Comparative samples from [Andrés et al. \(2012\)](#), [Massigoge et al. \(2014\)](#), [Rodríguez-Hidalgo et 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.

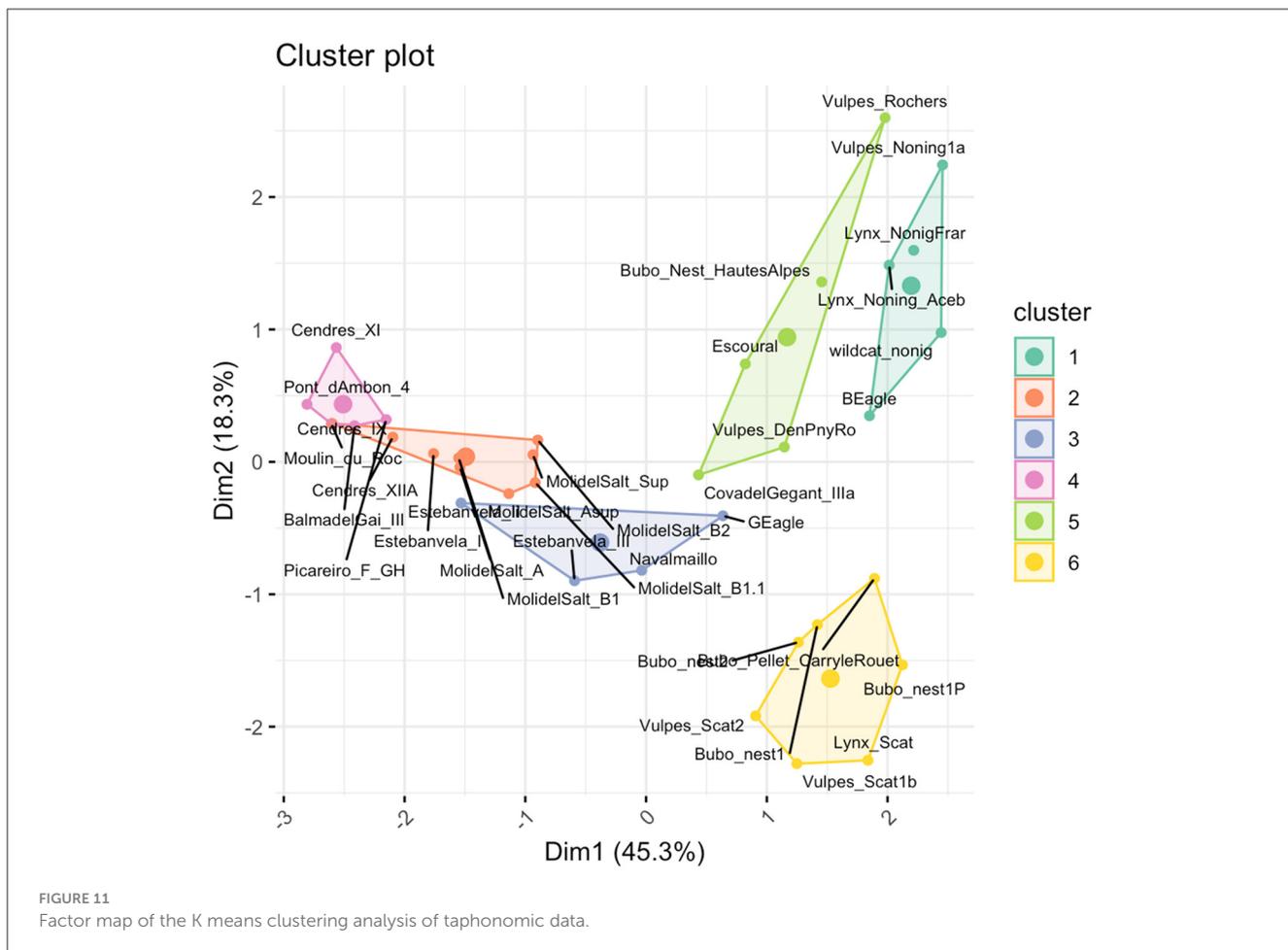
However, equifinality in rabbit assemblages complicates the identification of human activities. Studies have shown that even when cut marks and burning damage, which are exclusively attributed to humans, are considered, detecting human involvement as predators of rabbit assemblages remains challenging. 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,



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



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

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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.2024.1473266/full#supplementary-material>

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