

Subsistence strategies in the early upper Paleolithic of central Iberia: Evidence from Abrigo de la Malia

Edgar Téllez ^{a,*}, Antonio Rodríguez-Hidalgo ^{b,c}, Manuel Rodríguez-Almagro ^a, Carmen Núñez-Lahuerta ^{d,c}, Andion Arteaga-Brieba ^{a,c}, Adrián Pablos ^{e,a}, Nohemi Sala ^a

^a Centro Nacional de Investigación sobre Evolución Humana (CENIEH), P. ° Sierra de Atapuerca, 3, 09002, Burgos, Spain

^b Instituto de Arqueología-Mérida, Consejo Superior de Investigaciones Científicas (CSIC-Junta de Extremadura), Plaza de España 15, 06800, Mérida, Spain

^c Institut Català de Paleoeccologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4 - Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain

^d Departamento de Geología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea UPV/EHU, Barrio Sarriena s/n, 48940, Leioa, Spain

^e Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Madrid, Spain

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ABSTRACT

Knowledge of early Anatomically Modern Humans settlements in the interior of the Iberian Peninsula remains limited. Traditional perspectives have long assumed that this region, known as the Iberian Plateau, was abandoned after the disappearance of Neanderthals and remained largely uninhabited until the end of the Last Glacial. In contrast, coastal areas have so far been the primary focus of archaeological studies, as they are where the majority of known sites are located and where the most research has been conducted on subsistence practices. The recent discovery of the Abrigo de la Malia rock shelter site (Tamajón, Guadalajara) has challenged this paradigm, providing evidence of occupation in Central Iberia during the Aurignacian and Gravettian periods (36,200–26,260 cal BP). This work is focused on the zooarchaeological and taphonomic analysis of the Paleolithic faunal assemblage from the Malia rock shelter, aiming to reconstruct the subsistence strategies of the earliest Anatomically Modern Humans inhabiting central Iberia during the early Upper Paleolithic. The results indicate anthropogenic activities focused on the processing of medium- and large-sized ungulates, with carnivores either playing a marginal role. The combined data suggest that the Malia rock shelter was used for short but recurrent occupations, likely by small groups engaged in hunting expeditions. This study highlights the adaptability of these populations who inhabited this region during MIS-3 as they faced severe climatic conditions while exploiting the available environmental resources.

1. Introduction

The lack of information about archaeological sites from the early stages of the Upper Paleolithic in the interior of the Iberian Peninsula, whether due to an actual absence or insufficient research in this field (Yravedra et al., 2016; Alcaraz-Castaño et al., 2021), directly impacts our understanding of the adaptation and occupation models of Anatomically Modern Humans (AMH) in this region. This period represents the final phase of the Marine Isotopic Stage (MIS) 3 (around 60–27 ka), marked by a cooling trend that resulted in expanded open landscapes and several arid episodes (Alcaraz-Castaño et al., 2017; Vidal-Cordasco et al., 2022; Álvarez-Alonso et al., 2024; Sala et al., 2024). The traditional assumption argues that early Upper Paleolithic

human groups lacked the necessary traits that would have allowed them to adapt to the climatic conditions of this region, suggesting a complete or almost complete depopulation of the Iberian Plateau until the Late Glacial (Alcaraz-Castaño et al., 2017, 2021; Straus, 2015). This scarce number of archaeological sites on the Iberian Plateau stands in sharp contrast to the extensive evidence found in other parts of the peninsula, such as the Cantabrian range (e.g., Arrizabalaga and Altuna, 2000; Yravedra, 2001; Straus, 2005; Fano Martínez and coord, 2007; Cabrera Valdés et al., 2007; Yravedra and Gómez-Castanedo, 2011; de la Rasilla et al., 2020; Lombera-Hermida et al., 2021; Arenas-Sorriquetta et al., 2023; Luret et al., 2020; Sanz-Royo et al., 2023, 2024), the Iberian Mediterranean range (e.g., Davidson, 1989; Yravedra, 2001; Aura-Tortosa et al., 2002a, 2010; Cortes-Sánchez et al., 2008; Soler and

* Corresponding author. Centro Nacional de Investigación sobre Evolución Humana-CENIEH, Paseo de la Sierra de Atapuerca, 3, 09002, Burgos, Spain.
E-mail address: edgartpvilvi@gmail.com (E. Téllez).

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Soler, 2016; Villaverde et al., 2021; Real and Villaverde, 2022; Sanchis et al., 2023), or the Central and Southern Portugal (e.g., Valente, 2004; Bicho and Haws, 2008; Bicho et al., 2010; Zilhão et al., 2010; Haws et al., 2020).

These assemblages have been studied extensively, though knowledge of these groups' subsistence strategies remains limited in certain aspects. During the early Upper Paleolithic, subsistence patterns largely continued from the Middle Paleolithic, with a strong reliance on hunting deer or medium-sized ungulates, complemented with other large mammals such as horse and aurochs (Marín-Arroyo and Sanz-Royo, 2021; Vidal-Cordasco et al., 2022). Evidence suggests that humans selectively hunted these animals, while smaller ungulates like ibex and chamois were primarily introduced to sites by carnivores rather than human hunters (Sánchez-Romero et al., 2020). This pattern indicates that human occupations were relatively short, allowing alternating use of sites between humans and carnivores (Arribas-Herrera et al., 2004; Valente, 2004; Yravedra, 2013).

The strategies of the first AMH inhabiting the Iberian Peninsula's coast ranges during the Aurignacian and Gravettian periods are generally described as diversified, predominantly hunting medium and large-sized adult ungulates (primarily red deer, and to a lesser extent, horses and large bovids) as well as leporids (p.e. Arrizabalaga and Altuna, 2000; Yravedra and Gómez-Castanedo, 2011; Villaverde et al., 2021; de la Rasilla et al., 2020; Lombera-Hermida et al., 2021; Real and Villaverde, 2022; Sanchis et al., 2023; Sanz-Royo et al., 2023). In some assemblages, there is evidence of a preference for specific taxa, such as *Cervus elaphus* (Yravedra et al., 2016; Arenas-Sorriquetta et al., 2023), or in mountainous environments, the exploitation of taxa typical of these biotopes, such as Iberian ibex (*Capra pyrenica*) and chamois (*Rupicapra rupicapra*) (de la Rasilla et al., 2020; Lombera-Hermida et al., 2021; Arenas-Sorriquetta et al., 2023; Sanchis et al., 2023). Several authors suggest regional variability in the subsistence behavior (Pike-Tay et al., 1999; Yravedra, 2001; Marín-Arroyo, 2010; Jones, 2015). While in the Cantabrian region subsistence would focus on the exploitation of red deer and Iberian ibex, in the Mediterranean area and Portugal, rabbits would be a fundamental part of the diet (Hockett and Bicho, 2000; Fa et al., 2013; Lloveras et al., 2016). The reasons put forward to explain this variation have focused on different causes, such as mobility and settlement patterns, climatic and environmental, and models based on optimal foraging theories (Stiner et al., 2000; Hockett and Haws, 2002; Aura-Tortosa et al., 2002b; Stiner and Munrom, 2002).

Occupations from this period are typically long-term residential camps (Arrizabalaga and Altuna, 2000; Soler and Soler, 2016; Villaverde et al., 2021; de la Rasilla et al., 2020; Real and Villaverde, 2022), with even occasional evidence of hut structures as in Cueva Morín (Maflo-Fernández et al., 2014). From a taphonomic perspective, there is evidence of primary access and intense carcass exploitation by humans, as well as differential transport of remains; carnivores typically have secondary access to the remains during periods of abandonment. This type of occupation has been described at sites such as Labeo Koba VII (Arrizabalaga and Altuna, 2000), Aurignacian and Gravettian levels of Cueva Morín (Yravedra and Gómez-Castanedo, 2011), the Aurignacian levels of La Viña (de la Rasilla et al., 2020), level G of Cova de L'Arbreda (Soler and Soler, 2016), level D of Cova del Reclau Viver (Soler and Soler, 2016), Cova de les Cendres XVIIA (Villaverde et al., 2021; Real and Villaverde, 2022), or level GR of Cova de les Malladetes (Sanchis et al., 2023). However, there are also cases of short-term occupation by small groups who carried out sporadic, specialized, and low-intensity occupations, such as Labeo Koba VI (Arrizabalaga and Altuna, 2000), levels X and IX of La Viña (Arenas-Sorriquetta et al., 2023), level 2 of Cova Eirós (Lombera-Hermida et al., 2021), Cova de les Cendres XVIC and XVID (Villaverde et al., 2021), level AU of Cova de les Malladetes (Sanchis et al., 2023) or level II of Pego do Diabolo (Valente, 2004). In some instances, these human occupations alternate with the use of the same spaces by carnivores, such as hyenas, as documented at Cueva de Nerja (Arribas-Herrera et al., 2004). The predominance of medium-sized

adults characterises these occupations, followed in distance by large-sized adults and, to a lesser extent, subadult ungulates, with a low MNI and specific variability, although in some cases, a single taxon dominates due to specialized hunting. The skeletal profiles, characterized by a predominance of cranial and appendicular elements, suggest differential carcass transport based on size and weight; however, this pattern is also influenced by post-depositional attrition, which leads to the underrepresentation of less dense axial elements, and by transport decisions shaped by the catchment area and distance to the site (Marín-Arroyo, 2009). Anthropogenic activity varies depending on the intensity of occupation, while carnivores have a marginal presence, except in sites they occupy during periods of human absence, which leads to distinct anatomical and taxonomic profiles.

During Gravettian and Solutrean chronologies, occupations in Central Iberia have been documented in sites at Los Enebrales (Álvarez-Alonso et al., 2024) and Peña Capón (Alcaraz-Castaño et al., 2021). The Gravettian site of Los Enebrales has a limited archeological assemblage and has not provided data that allows for subsistence interpretations. In contrast, some inferences have been made into the Solutrean site of Peña Capón, which describes the exploitation of deer, horses, Iberian ibex, and leporids by human groups, although the type of occupation at the site remains unknown (Yravedra et al., 2016). Therefore, the identification of these early assemblages has not allowed for in-depth exploration of the subsistence strategies or occupation and mobility patterns of the first AMH in the region. Recently, a new site has been added to the map of early Upper Paleolithic sites in the Iberian Plateau: the Abrigo de la Malia rock shelter (herein Malia). With sediments dated to the early Upper Paleolithic (Lithostratigraphic Unit LU-V) and middle Upper Paleolithic (LU-IV) chronologies, this site represents the oldest documented AMH occupation to date in inland Iberia (Sala et al., 2024) and is key to studying the behavior of these groups.

Sedimentological studies, microvertebrate analyses, paleobotanical research, and stable isotope studies on ungulate fossils indicate the presence of a humid landscape with forested areas during the early Upper Paleolithic and a shift towards colder and more arid conditions during the middle Upper Paleolithic, with more open environments and reduced water availability (Sala et al., 2024). These findings align with broader ecological models that emphasize the role of climatic fluctuations in shaping human settlement patterns across Iberia. Specifically, regional variations in Net Primary Productivity appear to have influenced the availability of herbivore biomass, a critical resource for human subsistence. For example, a marked increase in resources availability around 35,000 cal BP in the so-called Submediterranean region (Vidal-Cordasco et al., 2022; Fig. 4), in which Malia is placed, may have facilitated human occupation of the area, suggesting that AMH were present at least during phases of climatic amelioration. More generally, recent modelling studies show that the arrival of *Homo sapiens* was associated with improved ecological conditions and a rise in herbivore carrying capacity (Vidal-Cordasco et al., 2022). These data support the hypothesis that the persistence and expansion of AMH groups were closely tied to ecological windows of opportunity driven by climate-induced resource fluctuations.

This study presents the zooarcheological and taphonomic analysis of the Pleistocene Lithostratigraphic Units (LU) from the Malia rock shelter. This site offers an unprecedented opportunity to study how the early AMH who occupied this territory adapted to climatic fluctuations. The hypothesis to be tested is whether the subsistence strategies developed by anatomically modern humans during the Early Upper Paleolithic on the Iberian Plateau were sufficiently stable and adaptable to allow the exploitation of available resources over a period of 10,000 years, despite evidence of increasingly rigorous climatic conditions.

2. The Abrigo de la Malia rock shelter

The Abrigo de la Malia site is located in Central Iberia in the village

of Tamajón (Guadalajara, Spain). The rock shelter rests amidst the eastern foothills of the Sistema Central Mountain range (Fig. 1A), between the Sorbe and Jarama rivers, at an altitude of 1100 m a.s.l. Discovered in 2017 during survey work in the Tamajón karst area (Fig. 1B), the site has been under continuous excavation since 2018, with the main excavation area of the Paleolithic units included in this work covering approximately 20 m² (Sala et al., 2024) (Fig. 1C).

The Malia sedimentary sequence is divided into five LU's (Fig. 1D), which span from the middle Holocene to the Late Pleistocene and have an average thickness of 110 cm based on the sequence excavated thus far, recently described by Sala et al. (2024). LU-I and LU-II, located at the top of the sequence, encompass Late Prehistory stratigraphic units with human-made negative structures like pits and silos with diverse sediment compositions. They include lithoclasts, pottery fragments, a mix of domestic and wild animal remains, and lithic industry. LU-II also shows evidence of channel morphology and fluvio-karstic reactivation during the Holocene, blending previous archaeological materials together. Both units display mixed artifacts with Paleolithic and Late Prehistoric origins. LU-III is partially eroded and has not yet yielded significant amounts of archaeological remains (Sala et al., 2024). At the sequence's base, LU-IV and LU-V house Late Pleistocene materials

examined in this study.

LU-IV is generally a sandy-silty unit with millimeter to centimeter-sized black shale lithoclasts, angular lithoclasts of autochthonous dolomite ranging from millimeters to meters, chronologically dated between 32,420 and 26,260 cal. BP (Sala et al., 2024). This unit has yielded the highest number of remains, including lithic artifacts, faunal remains, hearths, charcoals, and iron oxides (possibly pigments). Although the lithostratigraphic unit exhibits a uniform sedimentological composition, previous archaeo-stratigraphic analyses have identified two distinct horizons (LU-IVa and LU-IVb) based on material density and the presence of a thin sterile gap.

Directly beneath LU-IV lies LU-V, currently under excavation, which is more homogeneous in its matrix and composed of gravels, sands, and silts, similar to the previous LU. The sediment coloration varies from browner in the more sheltered areas of the shelter to more orange in the transition zones between LU-IV and LU-V. It is characterized by significant archaeological richness, composed of faunal remains, lithic, and bone industry. It is dated to 36,200–31,760 cal. BP (Sala et al., 2024). The lithic assemblage exhibits distinctive techno-typological features consistent with the Aurignacian technocomplex, specifically pointing to an Evolved Aurignacian. This is supported, for example, by the

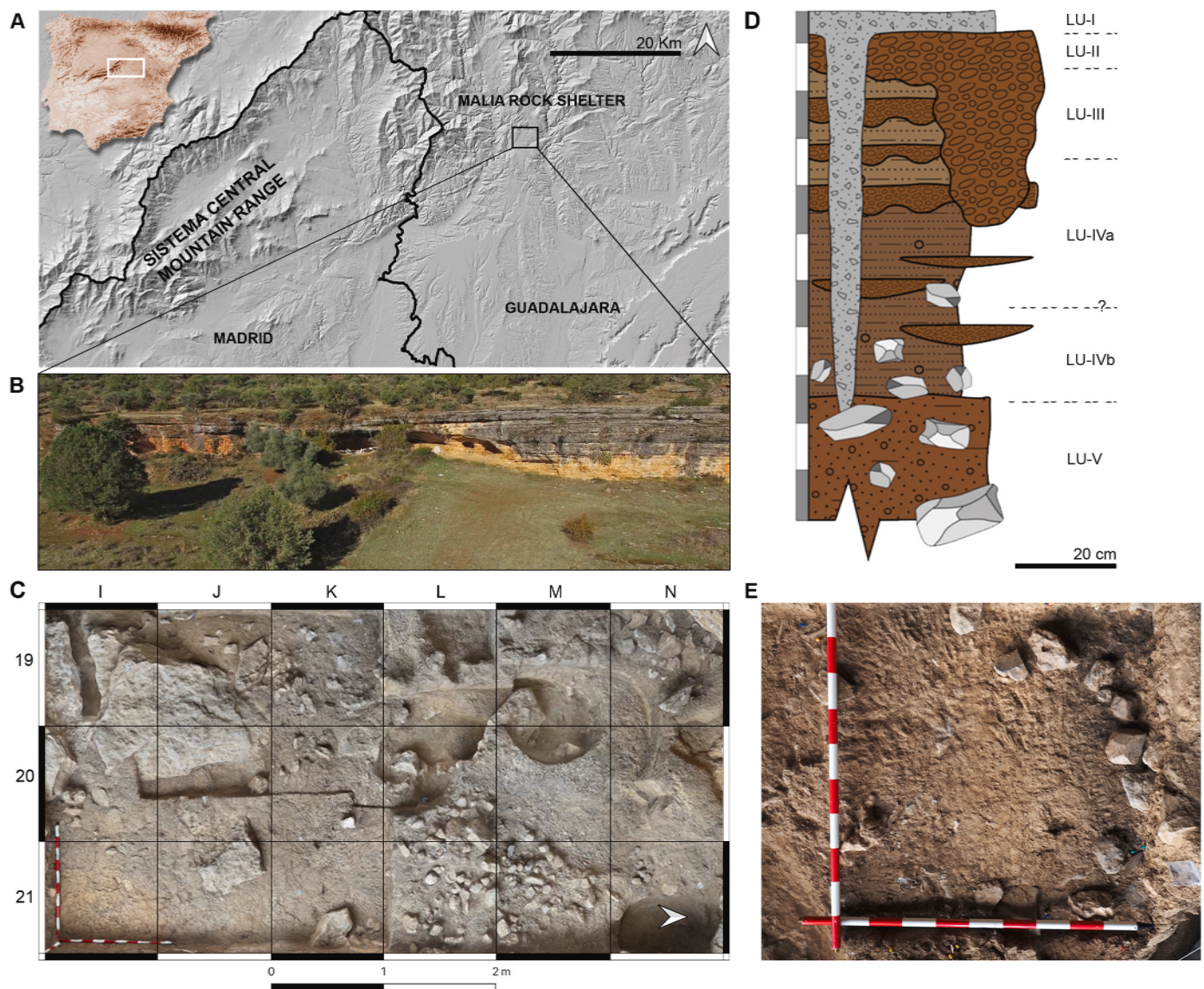


Fig. 1. A) Location map of the Malia rock shelter (Guadalajara, Spain) in the context of the Sistema Central Mountain range; B) View of the Tamajón karst area and the Malia rock shelter; C) Open-area excavation of the site; D) Stratigraphic column for the Malia rock shelter. E) Combustion structure identified in the LU-IVb.

production of bladelets, the presence of a carinated burin core, and an atypical nosed endscraper. Additionally, the presence of a single-beveled bone point further reinforces this attribution (Sala et al., 2024). In this sense, Malia represents the first unequivocal evidence to date of settlement in central Iberia during the early Upper Paleolithic, thus providing the earliest traces of *Homo sapiens* activity in the center of the Castillian plateau.

3. Materials and methods

For this study, a total of 1176 faunal remains from the Malia rock shelter were analyzed using zooarcheological and taphonomic methods. The faunal remains belong to the Late Pleistocene Lithostratigraphic Units: LU-IVa (NSP = 271), LU-IVb (NSP = 644) and LU-V (NSP = 261). All identifiable and unidentifiable coordinated and recovered remains (from 2018 until 2023) were subjected to analysis. This corresponds to any faunal remain that has a major axis measuring longer than 20 mm. During the fieldwork, the uncoordinated remains (<20 mm) were grouped by LU, square and date, called “level bags”. These level bags were subjected to a process of identification and individualization and were then analyzed in the same way as the remains coordinated in the field.

3.1. Taxonomic analyses

Osteometric measurements taken on macromammal bones and teeth were taken following the standards of von den Driesch (1976) and Arceredillo-Alonso (2015), and have been used to draw inferences related to the specific identification and age of the individuals. All measurements were taken using standard digital calipers. Bivariate plots were made with R (R Core Team, 2025). A total of 23 specimens were employed for the taxonomic identification of macromammals and birds. For horse identification, dental series were used (P3–M2, p3–m2, and P2). In the case of deer, the talus and proximal phalanges were employed. Chamois identification was based on teeth (p3, p4, and m1), as well as the talus and intermediate and proximal phalanges. Bison was identified using the malleolus, while bird identification relied on various long bones (see Section 4.1). The age of death of the individuals was established based on the degree of ossification (Schmid, 1972; Barone, 1976) as well as dental eruption and wear sequence (Hillson, 1996; Bunn and Pickering, 2010; Marín et al., 2017), identifying three groups: Young, Adult and Old.

Anatomic and taxonomic identification was carried out using the atlases compiled by Pales and Lambert (1971), Barone (1976) and Varela and Rodríguez (2004), as well as compared with the anatomical referential collection from *Institut Català de Paleocologia Humana i Evolució Social* (IPHES-CERCA) in Tarragona and *Centro Nacional de Investigación sobre la Evolución Humana* (CENIEH) in Burgos.

In order to differentiate between different genera or species some prior studies were referenced: *Bos* and *Bison* were distinguished using Lehmann (1949), Sala (1986) and Sala et al. (2010); *Cervus*, *Dama* and *Capreolus* using Lister (1996) and data from several Iberian sites (Pérez-Ripoll, 1977; Buitrago, 1992; Altuna and Maríquezurrena, 2000; Castaños, 2014; Arceredillo-Alonso, 2015; Rodríguez-Almagro et al., 2021). The same archeological resources were referenced to distinguish between *Equus ferus* and *Equus hydruntinus* and *Rupicapra* cf. *pyrenaica* and *Capra pyrenaica*.

3.2. Taphonomic analyses of macromammals

Non-identified remains were grouped into bone type (long, flat, and articular) and weight-size categories by the time of death, which were established following what was proposed by Saladié et al. (2011): very small size (<10 kg), small (10–100 kg), medium (100–300 kg) and large (300–1000 kg). The estimation of the Number of Specimens (NSP), the Number of Identified Specimens (NIS), the Minimal Number of

Elements (MNE), the Minimal Number of Individuals (MNI) and the standardized Minimal Animal Units (%MAU) were calculated according to Brain (1981), Binford (1984), and Grayson (1984). The %MAU was correlated with mineral density to evaluate the integrity of the skeletal sample using Spearman's rho tests. Caprinae data were obtained from Lyman's work (1994) and from Lam et al. (1999) including from cervids, horses and large-sized bovids. The identification of *Cervus elaphus* and *Capreolus capreolus* at a taxonomic level were identified in few remains due to the assemblage's high rate of fragmentation. Consequently, all deer remains that could not be confidently attributed to either *C. elaphus* or *C. capreolus* have been classified as Cervidae.

To explore the fragmentation of macrovertebrate long bones we listed both shaft circumferences (FRS) and lengths (FRL) following Bunn's (1983) method, modified by Villa and Mahieu (1991). FRS refers to the percentage of the circumference that is preserved ($1 \leq 33\%$; $2 = 33\text{--}66\%$; $3 \geq 66\%$), whereas FRL refers to the percentage of the length that is preserved ($1 \leq 25\%$; $2 = 25\text{--}50\%$; $3 = 50\text{--}75\%$; $4 \geq 75\%$). The fractures edges of the long bones were analyzed according to the methods of Villa and Mahieu (1991).

The surfaces of bones, teeth and antlers were macroscopically and microscopically analyzed with a binocular microscope (OPTECH 120 Hz model with magnification between $7 \times$ to $40 \times$), HIROX KH-8700 3D Digital Microscope with an MXG-5000 REZ triple objective, and an Olympus OM-D camera with an OLYMPUS M. ZUIKO macro lens. Modifications produced by both hominins and carnivores were described according to the anatomical region and the portion where they were found. The anthropogenic modifications include: cut marks, differentiating between slices, chops, saws and scrapes (Binford, 1981; Domínguez-Rodrigo et al., 2009; Shipman, 1981; Shipman and Rose, 1983), percussion marks (Blumenshine and Selvaggio, 1988; Capaldo and Blumenshine, 1994), and burned bones (Téllez et al., 2022). Butchery activities were interpreted based on the features of the cut marks, using data provided by Binford (1978, 1981) and Nilssen (2000). Carnivore modifications were evidenced by the presence of tooth marks in the form of pits and scores (Blumenshine, 1994; Domínguez-Rodrigo and Barba, 2006; Shipman, 1981), in addition to modifications produced by gastric acids (digestion), crushing, furrowing, crenulated edges, spiral fractures or shaft cylinders (Haynes, 1980, 1983; Maguire et al., 1980; Binford, 1981; Brain, 1981; Blumenshine, 1994). Tooth marks with sharp outline were measured, in millimeters to two decimal places, using a digital caliper via observation through a binocular magnifier (OPTECH LFZ, up to 60). Regarding other taphonomic modifications, we also documented weathering and water abrasion based on the stages established by Behrensmeier (1978) and Cáceres (2002), respectively. Modifications such as trampling, the presence of manganese black stains, surface dissolution, and root-etching were described by their presence/absence following the descriptions of Brain (1981), Shipman (1981), Fernández-Jalvo (1992), and Lyman (1994).

3.3. Leporids analysis

The Number of Identified Specimens (NIS) and Relative Abundance were calculated. Relative abundance (%AR) that relates the observed MNE with the expected MNE based on the MNI was calculated (Dodson and Wexlar, 1979; Andrews, 1990). The proportions of the skeletal elements were also evaluated using several indices:

- PCRT/CR: postcranial (long elements, vertebrae and ribs) in relation to cranial (mandibles, maxillae and teeth);
- PCRLB/CR: postcranial long bones (humeri, radii, ulnae, femorae and tibiae) to cranial (mandibles and maxillae);
- AUT/ZE: autopodium elements (metapodials, carpals, tarsals and phalanges) to Zeugopodium and Stylopodium (tibiae, radii, ulnae, humeri, femora and patellae);
- Z/E: Zeugopodium (tibiae, radii and ulnae) to Stylopodium (femora and humeri);

- AN/PO: anterior elements (humeri, radii, ulnae and metacarpals) to posterior elements (femora, tibiae and metatarsals).

The %MAU of rabbits was correlated with mineral density to evaluate the integrity of the sample, following data from Pavao and Stahl (1999). Breakage patterns were described by the maximum length of all identified specimens. Different breakage categories were used depending on bone type following Rodríguez-Hidalgo et al., (2013, 2015): a) tarsals and ribs were considered complete or fragmented; b) phalanges were considered complete, proximal, distal or fragment; c) vertebrae were considered complete, vertebral body, vertebral epiphysis or spinous processes; d) breakage of teeth was calculated separately for isolated elements and for inside of the crania/mandible (Fernández-Jalvo and Andrews, 1992) and considered as complete or fragmented. Breakage categories used for the long bones, metapodials, mandibles, crania, scapulae and coxae are described following Lloveras et al. (2008a). Long bone cylinders (fragments of long bones with snapped ends as a result of consumption), their length in mm and V-shaped and helical fractures (Hockett, 1991; Hockett and Bicho, 2000; Rodríguez-Hidalgo et al., 2020) were counted as well.

Bone surface modifications were examined following the same methods as those used for macromammals, while considering specific literature on rabbits (Lloveras et al., 2008a, 2008b, 2012; Rodríguez-Hidalgo et al., 2013, 2016).

3.4. Bird analysis

We followed the analytical methodology applied by Lloveras et al. (2008a, 2008b) for rabbits and then modified for birds' assemblages (Lloveras et al., 2014a, 2014b). NISP, MNE, MNI (Andrews, 1990; Lyman, 1994), and skeletal survival in the form of relative abundance (%RA) (Dodson and Wexlar, 1979), were calculated and bone surface modifications were observed. The ratios used were the representation of wings vs legs; we used the wing elements (humerus, ulna, carpometacarpus) divided by the sum of wings + leg elements (femur, tibiotarsus, tarsometatarsus). The presence of proximal and distal elements that were assessed refers to the division of the number of proximal elements (scapula, coracoid, humerus, femur, and tibiotarsus) by the sum of the proximal + distal fragments (ulna, radius, carpometacarpus, and tarsometatarsus). All ratios were calculated using MNE and expressed as a percentage (Lloveras et al., 2014a, 2014b).

4. Results

4.1. Taxonomic analyses

Of the 1176 remains analyzed, 379 (32.2 %) were taxonomically identified. The assemblage is composed predominantly of ungulates and leporids (Table 1). The remains were identified at the species level and when that was not possible, at the genus or family level. The identifications have been made primarily using dental elements and appendicular bones, as these were the only elements that allowed for metric and/or morphological study.

4.1.1. Order artiodactyla Owen, 1848

4.1.1.1. Family cervidae Goldfuss, 1820. In terms of macromammals, cervids are the dominant taxa in the site. All complete bones belonging to cervids were comparatively studied following the morphological criteria for distinguishing between *Cervus* and *Dama* (Lister, 1996). This includes three incisors, a radius, three proximal phalanges and two tali; however, just the proximal phalanges and the talus lend themselves to metrical comparison and provide results with respect to genus and species.

Genus *Cervus* Linnaeus, 1758

Table 1

Quantification of the remains that were recovered from Abrigo de la Malia form different Pleistocene LU's. When possible, identified non-taxonomic remains were included in weight-size categories (NISP/MNE/MNI).

Taxa	LU-IVa	LU-IVb	LU-V
<i>Cervus elaphus</i>	1/1/1	1/1/1	1/1/1
<i>Capreolus capreolus</i>	–/–/–	1/1/1	–/–/–
<i>Cervidae</i> medium-sized	48/21/2	85/29/1	30/15/1
<i>Equus ferus</i>	24/9/2	22/9/2	10/5/1
<i>Bison</i> cf. <i>priscus</i>	–/–/–	1/1/1	–/–/–
<i>Bovidae</i> large-sized	1/1/1	8/5/–	4/3/1
<i>Rupicapra</i> cf. <i>pyrenaica</i>	–/–/–	–/–/–	8/8/1
<i>Bovidae</i> small-sized	1/1/1	3/2/1	3/3/1
<i>Galliformes</i> indet.	–/–/–	–/–/–	1/1/1
<i>Columbiformes</i> ?	–/–/–	1/1/1	–/–/–
<i>Pyrhacorax graculus</i>	–/–/–	1/1/1	1/1/1
<i>Pyrhacorax</i> sp.	–/–/–	2/2/–	2/2/–
<i>Aves</i> indet.	–/–/–	6/6/2	2/2/1
<i>Leporidae</i>	10/8/2	62/47/4	42/33/3
Total NISP/MNE/MNI	85/41/9	193/105/15	101/71/12
Large Sized	28/–/–	77/–/–	25/–/–
Medium Sized	85/–/–	163/–/–	46/–/–
Small Sized	–/–/–	8/–/–	8/–/–
Very small	–/–/–	–/–/–	5/–/–
Total Weight	113/–/–	248/–/–	84/–/–
Indeterminable	73/–/–	203/–/–	76/–/–
Total NSP	271	644	261

Cervus elaphus Linnaeus, 1758

A talus and three proximal phalanges were classified as *C. elaphus*, belonging to a MNI = 3, one from each assemblage (LU-IVa, LU-IVb and LU-V). The phalanges recovered in the Malia rock shelter present a straight edge on the distal end of the condyles, a characteristic described in Arcercedillo-Alonso (2015) for *C. elaphus*; metrically, these phalanges fall well within the *C. elaphus* range of variation identified in several Iberian sites (Fig. 2A; 3A)

Regarding the talus, Arcercedillo-Alonso (2015) describes common features for *C. elaphus* and *C. capreolus*, mainly the presence of a marked groove on the proximal trochlea, the pronounced protrusions of the proximal condyles on the plantar side, and the fact that the surface articulating with the calcaneus is separated from the proximal trochlea by a continuous mediolateral depression. The two tali recovered in the Malia rock shelter exhibit this morphology, and the main difference between them is their size. As can be observed in Figs. 2B and 3A, the dimensions of the larger of these remains fall well within the *C. elaphus* range of variation identified in several Iberian sites.

Genus *Capreolus* Gray, 1821

Capreolus capreolus Linnaeus, 1758

A single talus from LU-IVb was classified as *C. capreolus*. Morphologically, it is similar to the element described above. Metrically, it is smaller than those attributed to *C. elaphus* in Malia and Iberian sites and falls within the range of *C. capreolus* (Figs. 2B and 3B).

4.1.1.2. Family bovidae Gray, 1821. Genus *Bison* Smith, 1827.

Bison cf. *priscus* Bojanus, 1827.

The anatomical differences between bovines are limited, thus posing a challenge in distinguishing between *Bos* and *Bison*. According to Sala (1986), in genus *Bison*, the tibia articulations are nearly separated, whereas in genus *Bos*, they are fused. While no Bovini distal tibiae were found in Malia, there is a malleolus that allows us to make inferences in this regard. As summarized by Sala and colleagues (2010), the superficial area of the malleolus interrupts the articular surface of the tibia in *Bison*, forming a sharp edge in this area. In the genus *Bos*, on the other hand, the malleolar surface is not interrupted and the edge between it and the articular surface for the talus is less pronounced (Lehmann, 1949; Altuna, 1972). In other words, in *Bos*, the articular facets for the malleolus are joined together by a rather narrow border, whereas in *Bison*, these facets are totally isolated (Buitrago, 1992). The anterior

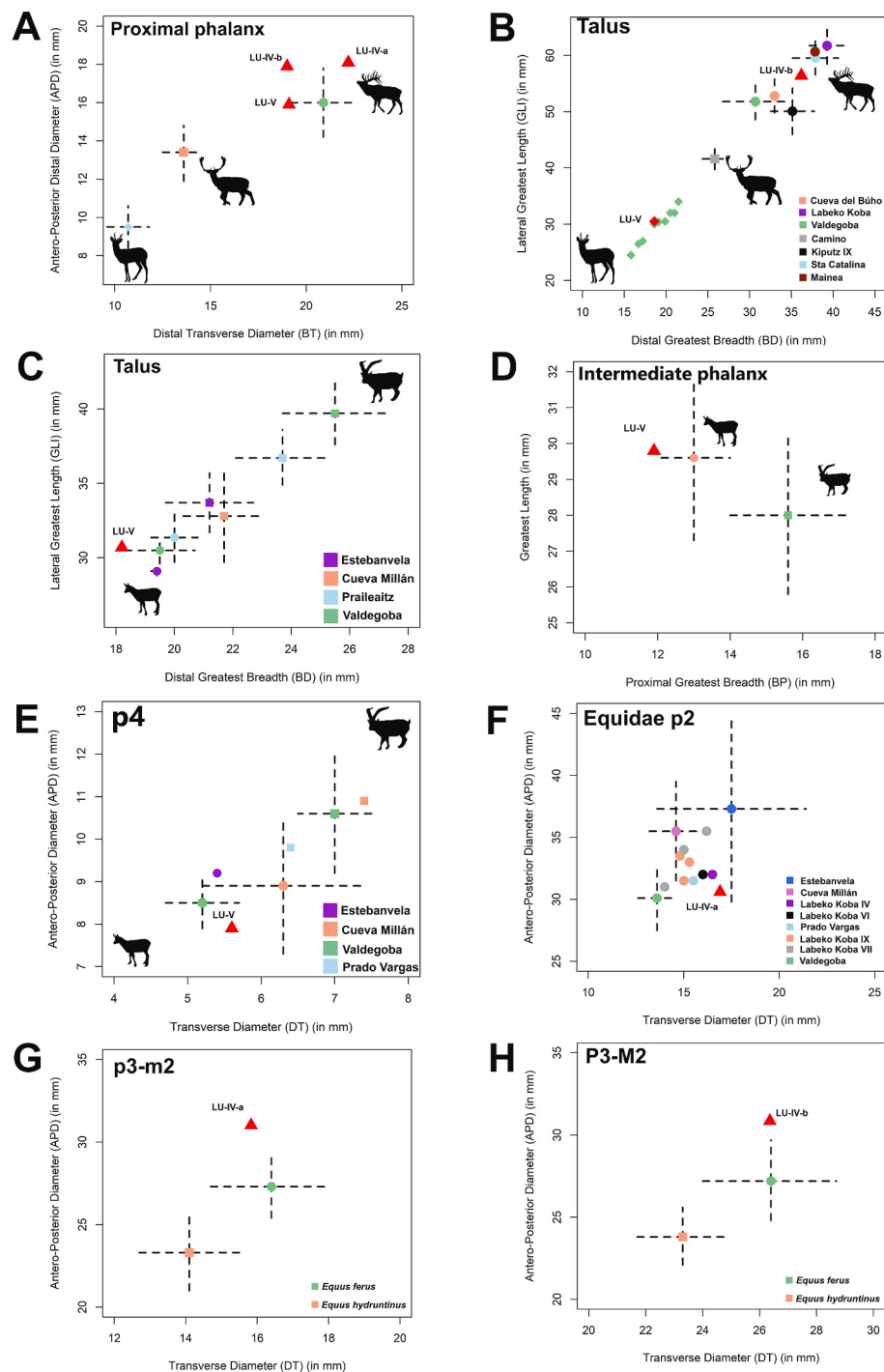


Fig. 2. Bivariate scatter plot of selected measurements of several ungulates from the Malia compared with samples from different Iberian sites represented by isolated remains or by means and standard deviations. Red triangles: Malia sample. Cervidae sample: Proximal phalanx (2A) of *Cervus elaphus* from LU-IVa, LU-IVb and LU-V and talus (2B) of *Cervus elaphus* from LU-IVb and a second talus of *Capreolus capreolus* from LU-V, compared with samples of *Cervus elaphus*, *Dama dama* and *Capreolus capreolus* from several Iberian sites. Bovidae sample: Talus (2C), intermediate phalanx (2D), and lower p4 (2F), p4 (2E) of *Rupicapra pyrenaica* from LU-V compared with samples of *Rupicapra pyrenaica* and *Capra pyrenaica* from several Iberian sites. Equidae sample: Lower p2 (2F), lower series p3-m2 (2G) and upper series P3-M2 (2H) of *Equus ferus* from LU-IVa and LU-IVb, compared with samples of *Equus ferus* and *Equus hydruntinus* from several Iberian sites. All metric data are available in Supplementary Tables S1-S5; S7; S9; S11. All graphic representations were executed using R (R Core Team, 2025).

facet of the malleolus recovered in Malia LU-IVb, belonging to an adult individual, is high, circular, and separated from the posterior facet, and thus can be morphologically ascribed to the genus *Bison* (Fig. 3C).

Genus *Rupicapra* Linnaeus, 1768

Rupicapra cf. *pyrenaica* Bonaparte, 1845.

A talus, a mandible (with p3, p4 and m1), two proximal phalanges

and an intermediate phalanx have been morphologically attributed to a small bovid. The main feature of the phalanges is that the distal trochlea is highly projected, unlike in cervids, where it is straight (Arcerillo-Alonso, 2015).

The phalanges were classified as *R. cf. pyrenaica*, as their dimensions fall well within the range of variability of this taxon compared with

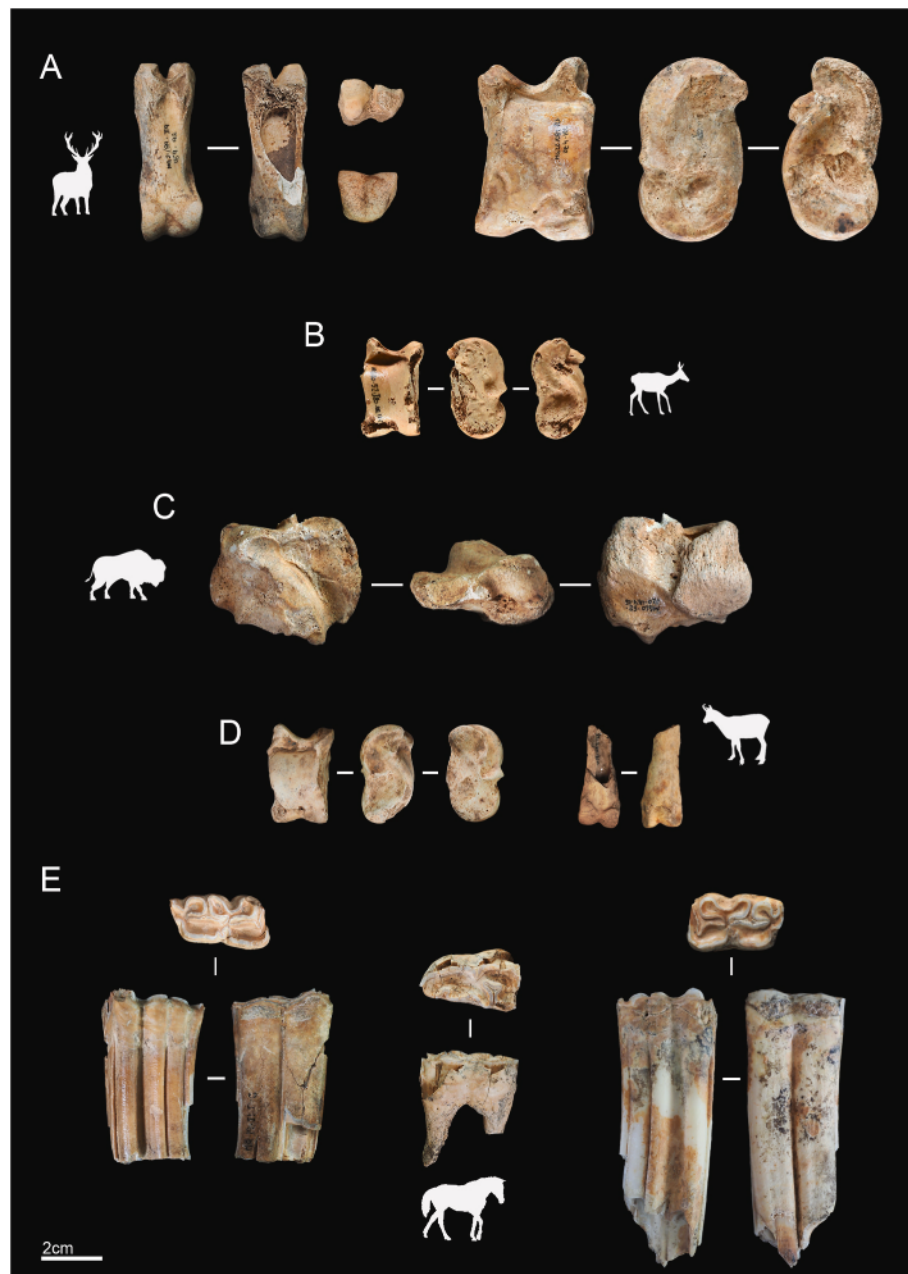


Fig. 3. Selected remains for identifying the representative taxa studied in Malia. A) Proximal phalange (J19-92-UE9) and talus (J21-100-UE4) of *Cervus elaphus*; B) Talus (J20-6-UE17) of *Capreolus capreolus*; C) Left malleolus (J20-15-UE4) of *Bison priscus*; D) Talus (I19-58-UE9) and proximal phalange (J19-18-UE9) of *Rupicapra pyrenaica*; E) From left to right, a lower molar/premolar (K19-85-UE4), a lower p2 (I19-189-UE4) and a lower molar/premolar (K20-28-UE4) of *Equus ferus*.

remains from other Iberian sites as opposed to those of *Capra pyrenaica* (Fig. 2D; 3D; Supp. Fig. 1A). Furthermore, the talus (Fig. 2C; Fig. 3D) and the lower dentition (Fig. 2E; Supp. Fig. 1B; 1C) also fall well within the range of variability exhibited by this taxon. These remains were documented in LU-V and belong to an adult individual.

4.1.2. Order perissodactyla Owen, 1848

4.1.2.1. Family equidae Gray, 1821. Genus *Equus* Linnaeus, 1758 *Equus ferus* Linnaeus, 1758

Five individuals were identified as horses in the different LU corresponding to three adults and two young. The fragmentation rate at the site is high, reason, which is why the taxonomical analysis was conducted on an identified lower second premolar (p2) and two unidentified specimens belonging to the P3-M2 and p3-m2 series. To

differentiate between equid species (*E. ferus* and *E. hydruntinus*), this study focuses on the metric and morphological criteria described in Eisenmann et al. (1988); Eisenmann and Baryshnikov (1995); Maldonado (1997); Sala et al., (2020), specifically in regard to these features: presence of longitudinal groove in the protocone, well-developed caballine folds in premolars, presence of grooves in the style of premolars in the upper dentition, and caballine-type double knot, U-shaped entoflexid, short-length ectoflexids or well developed plicostilid folds in the lower dentition. On the one hand, the biplot shows p2 within the range of variability for *E. ferus* samples from several Iberian sites (Fig. 2F). On the other hand, recovered specimens from the P3-M2 and p3-m2 series are closer to *E. ferus* samples from other Iberian sites rather than to *E. hydruntinus* (Fig. 2G; 2H; 3E). This identification is consistent with the analyses conducted on ancient equid DNA from the site (Lira et al., 2025). None of the remaining equid remains are anatomically complete

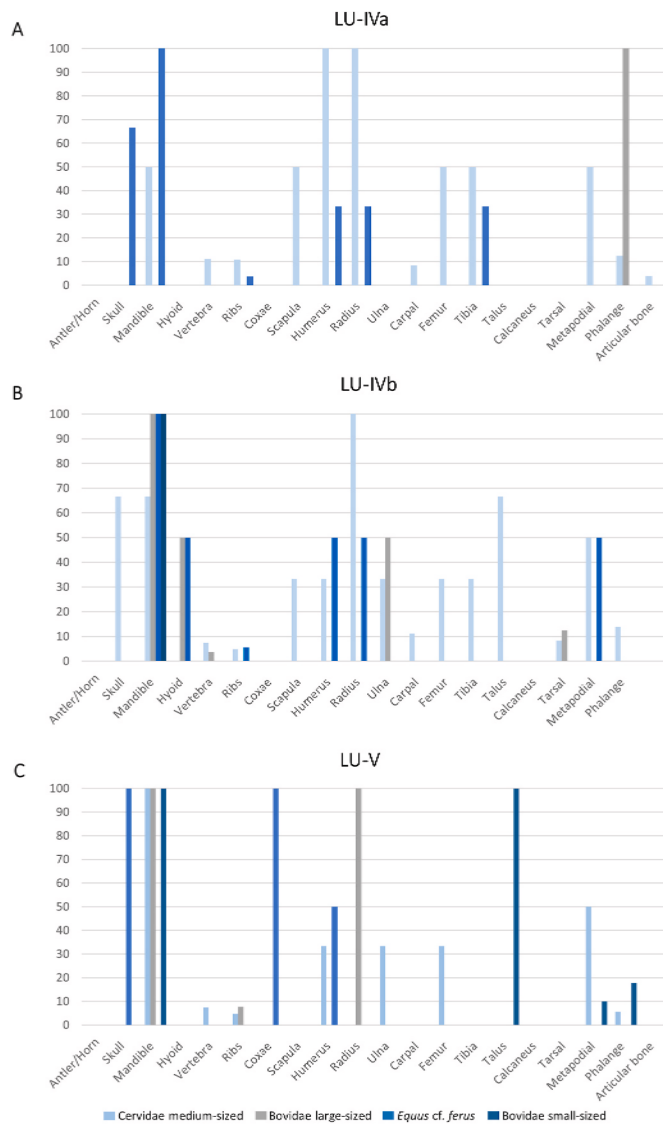


Fig. 4. %MAU of the different skeletal remains of ungulates of LU-IVa (A) LU-IVb (B) and LU-V (C).

enough for taxonomic evaluation. However, the large overall size of these specimens leads us to identify them as *E. ferus* instead of *E. hydruntinus*.

4.1.3. Order galliformes Temminck, 1820

A proximal left tarsometatarsus (proximal width 8 mm), with well-developed external and internal cotyles and characteristics compatible with the Galliformes anatomy, such as the shape of the tendinal canal in the mesial hypotarsal ridge (Gilbert et al., 1985). The proximal width corresponds to several Perdicinae and Tetraoninae taxa, such as *Lagopus* or *Alectoris* (Kraft, 1972). The conservation of the remain hinders its further identification.

4.1.4. Order columbiformes? Latham, 1790

Small sized left proximal carpometacarpus. The *spatium intermetacarpalis* is the same height as the *trochlea carpalis*, which is characteristic of Columbiformes (Gilbert et al., 1985). However, the remain is fractured and the proximal epiphysis cannot be analyzed, thus it cannot be definitively assigned to Columbiformes.

4.1.5. Order passeriformes linnaeus, 1758

4.1.5.1. Family corvidae Vigors, 1825. Genus *Pyrrhonorax* Tunstall, 1771

Pyrrhonorax graculus Linnaeus, 1766

The shape of these bones corresponds to a Corvidae. The size of the left distal humerus (distal width 11 mm) is on par with several small and middle-sized Corvidae, such as *Pica pica*, *Nucifraga caryocatactes*, *Pyrrhonorax* or *Corvus monedula*. The remain can be identified as *P. graculus* due to the shape of the *processus supracondylaris dorsalis apex*, which has the same height, a characteristic typical of *Pyrrhonorax*. Within the *Pyrrhonorax* species, it can be identified as *P. graculus* thanks to the height of the *processus supracondylaris dorsalis* (5.6 mm), which is smaller than *P. pyrrhonorax* (Tomek and Bochenski, 2000). The distal left tarsometatarsus also corresponds to several middle and small-sized Corvidae. The presence of two openings in the plantar surface of the bone and the presence of a groove in the plantar side of the trochlea metatarsi II, together with the size of the bone (minimum thickness of the shaft 1.5 mm), leads to its assignment to *P. graculus* (Tomek and Bochenski, 2000).

Pyrrhonorax sp.

Several fragments from both LU-IV and LU-V correspond in shape and size to medium-sized corvids, specifically with the genus *Pyrrhonorax*. The measurements, however, fall within the variability of both sister taxa: *P. pyrrhonorax* and *P. graculus*, and thus, these remains were assigned to the genus *Pyrrhonorax*.

4.2. Taphonomic analyses

4.2.1. LU-IV

A total of 915 faunal remains were analyzed in the LU-IV, 271 of which belong to LU-IVa and 644 to LU-IVb (Table 1). In both units, the medium-sized cervid dominates the faunal representation, followed by *E. ferus* and Leporidae. In contrast, remains of large bovids, *R. cf. pyrenaica*, and birds are not as abundant. The documentation of a talus from *C. capreolus* in LU-IVb, is noteworthy as this taxon is not documented in subunit LU-IVa. Bird remains have been documented in LU-IVb belonging to Columbiformes, *P. graculus*, *Pyrrhonorax* sp., and Aves indet.

For LU-IVa, the MNE amounts to 41 elements, and the %MAU representation by taxon allows us to make some inferences into skeletal representation (Fig. 4A and Supp. Table S12), although the low MNE (<50) means that such inferences should be treated with caution. Cranial and appendicular elements have the highest values in both medium-sized cervids and horses, while the rest of the elements are completely or nearly absent. The MNI reveals nine individuals (five adults and four young). For LU-IVb, the MNE amounts to 105 elements. The estimation of %MAU (Fig. 4B and Supp. Table S12) also shows a predominance of appendicular and cranial elements for large-sized bovids, medium-sized cervids and *E. ferus*. The MNI reveals 15 individuals, 11 of which belong to mammals (seven adults and four young) and four birds.

The correlation between %MAU and the mineral density of the sample yields values slightly above 0 for all taxa in both LU (Supp. Fig. 2A and Supp. Fig. 2B), although the *p*-value is higher than 0.05 in almost all cases, indicating that the correlations are not statistically significant and no meaningful statistical relationships can be inferred.

Regarding the postdepositional taphonomic modifications, a common pattern was observed in both LU-IVa and LU-IVb (Table 2). The most documented are black staining produced by manganese oxide/dioxide, followed by root etching and moisture cracking. Moreover, these modifications are associated with humid environments.

If we direct our attention the fragmentation of the macromammal long bones (Fig. 5A and B) a similar pattern is also observed in both subunits. With respect their size, the majority include less than 1/3 of their shaft cylinder and 1/4 of their length, which implies a high

Table 2

Non-anthropogenic taphonomic modifications documented at different Pleistocene LU's.

	LU-IVa		LU-IVb		LU-V	
	n	%	n	%	n	%
Root Etching	71	26.3	174	27	41	16.3
Trampling	10	3.7	31	4.8	10	4
Chemical corrosion	1	0.4	–	–	3	1.2
Dissolution	1	0.4	1	0.2	3	1.2
Black stains	129	47.8	248	38.5	57	22.7
Orange stains	1	0.4	10	1.6	5	2
Gnawing	2	0.8	3	0.5	3	1.2
Fissures pressure	3	1.1	9	1.5	3	1.2
Fissures humidity	2	0.7	21	3.3	13	5.2
Fissured indet.	37	13.7	72	11.2	18	7.2
Biochemical marks	4	1.5	19	3	3	1.2
Rounding (R1)	1	0.4	1	0.2	1	0.4
Polishing (P1)	2	0.7	6	1	4	1.6
Weathering	W1	1	0.4	4	0.6	4
	W2	2	0.7	4	0.6	–
	W3	3	1.1	2	0.3	–

fragmentation rate of long bones. Additionally, with respect the fractured edges, the most commonly found are those with a longitudinal or curve delineation, oblique angle and smooth surface, features typically associated with green breakage, according to [Villa and Mahieu \(1991\)](#).

Modifications of anthropic origin are well represented in both subunits in the form of cut marks, breakage and thermoalteration. It is remarkable that this evidence is concentrated exclusively on the remains of macromammals, with no evidence of anthropization of the leporids and birds.

The cut marks analysis in LU-IVa ($n = 49$; 17.7 %) is focused on medium-sized cervids and horses, as well as medium and large sized bones ([Fig. 6](#)). In general, the highest amount of cut marks is concentrated on limb bone fragments, mostly on the shaft and to a lesser extent on the shaft ends, on ribs, and other flat bone fragments ([Table 3](#)). According to the morphology, the most abundant type of marks are slices followed by scrapes and chops. Some butchery activities can be inferred through this evidence: most of the marks have been linked to defleshing of the bones, although the cut marks on a medium-sized cervid metapodial could be indicative of skinning. Anthropic breakage was identified in 23 (8.5 % of the NSP) bones. Almost all of the anthropic breakage evidence is concentrated in the long bones, which have a higher medullary content. The taxonomic analysis, once again focuses on medium-sized cervid and horse remains, as well as on medium-sized bones, and present notches, adhered and conchoidal flakes, cortical extractions, percussion impacts and signs of abrasion. The evidence of breaking indicates that the exploitation of the carcasses must have been intensive and included access to the bone marrow. Finally, thermoaltered bones display a predominance of high degrees of colors (types 3 to 5), which would imply exposure to high temperatures ([Table 4](#)).

Regarding anthropic modifications in LU-IVb, the pattern observed is similar to that described in LU-IVa, where cut marks ($n = 98$; 15.2 %) predominantly appear on cervid and horse bones. These marks are found mainly on medium and large-sized bones and are concentrated in limb bones and ribs ([Table 5](#)). The cut marks are predominantly observed in the form of slices, but there are also scrapes, chops, and saw marks. The butchering activities documented in LU-IVb follow a comparable pattern to that described in LU-IVa, with a predominance of marks related to defleshing, although cut marks on medium-sized cervid and horse metapodials were also documented, once again indicative of skin removal.

Furthermore, breakage evidence in LU-IVb is documented in 49 (7.6 %) remains. Percussion marks, cortical extractions, and notches are among this evidence, most of them in indeterminate bones, humerus, ribs, and radius. An opposite notch, as a result of percussion on an anvil, was documented on a large-sized humerus fragment. Once more, the

fractures suggest access to the bone marrow and, consequently, exploitation of medullary resources. Thermoaltered bones are infrequent (5.3 %) and there is a predominance of types 2.2, 3, and 4 ([Table 4](#)). In LU-IVa, archeological remains are scattered across the entire excavation surface with no evident spatial distribution pattern, though a higher concentration of burnt bones can be noted in the densest area of remains, associated with three pieces of charcoal ([Fig. 7A](#)). In LU-IVb, it is noteworthy that two combustion structures were identified during fieldwork in the K19 Square, close to which an accumulation of medium- and large-sized remains with cut marks was documented ([Fig. 7B](#)), potentially suggesting the existence of a faunal processing area nearby.

Evidence of carnivore activity on macromammals is scarce in both units: three remains show tooth marks in LU-IVa (1.1 %) and four in LU-IVb (0.6 %). Likewise, in LU-IVa tooth marks are documented on two medium-sized rib fragments, which also display cut marks. One large-sized ulna displays depressions as well. In LU-IVb these marks are documented in one medium-sized cervid phalanx, a long bone, a rib of a medium-sized carcass, and one indeterminate fragment.

4.2.1.1. Leporids and birds. [Table 6](#) shows the anatomical composition of leporids elements identified in LU's IVa and IVb. In LU-IVa, 10 remains belong to eight elements and two individuals; thus, few elements were recovered and they are limited to one cranium, scapula, humerus, radius, and ulna, in addition to three vertebrae. The relative abundance index (%RA) reveals a low representation of all the elements, especially for vertebrae. To the contrary, in LU-IVb, where 62 remains belong to at least 47 elements and four individuals, there is a high representation of the different skeletal elements.

Regarding the relative proportions between the anatomical elements, values are generally low. In LU-IVa, the cranial elements are scarcer than the post-cranial ones (PCRT/CR = 0.7; PCRLB/CR = 3). There is a total absence of autopodium (AUT/ZE = 0), whereas zeugopodium is more represented than stylopodium (Z/E = 2). The total absence of posterior elements is the reason why there is no value in the AN/PO ratio. In LU-IVb, cranial elements are represented below the postcranial ones (PCRT/CR = 6.8; PCRLB/CR = 1.8). Autopodium are more represented than zeugopodium and stylopodium (AUT/ZE = 1.5); among the latter two zeugopodia are the most represented (Z/E = 1.2). Furthermore, we found more anterior than posterior elements (AN/PO = 1.1).

The correlation between %MAU and the mineral density of the leporids ([Supp. Fig. 2A](#) and [Supp. Fig. 2B](#)) yields positive values in both LU but only in LU-IVb is the p -value < 0.05 , thus indicating a positive tendency and statistically significant rate of preservation of the densest elements in that level.

[Tables 7 and 8](#) show the breakage patterns in LU-IVa and LU-IVb respectively. In LU-IVa no complete leporid remains were found. We documented shaft fragments of long bones (PES and SDE), as well as fragments of mandibles, scapulae, and vertebrae bodies. In LU-IVb, metapodials, calcaneum and phalanges are mostly complete. This is not the case, however, for the rest of the long and flat bones, which are diversely fragmented.

[Table 9](#) shows the anatomical composition of bird elements identified in LU-IVb. There are 10 remains belonging to at least 10 elements and to four individuals: one Columbiformes, one *P. graculus* and two indeterminate birds. These elements include a cranium, a mandible, two humeri, three carpal-metacarpals, and three limb bone shaft fragments. The %RA shows that we have 25 % of the expected values for the skull, mandible, and humerus and 37.5 % for the carpal-metacarpals.

There is no documentation of anthropic activity in either of the subunits, but there is evidence of carnivore activity on birds, and mainly on leporids. For leporids, punctures in two coxae were identified in addition to scores in a metatarsal, innominate, scapula and ulna; a shaft cylinder in a humerus and light evidence of digestion in a mandible, more evidence in the case of a radius; crenulated edges in a femur,

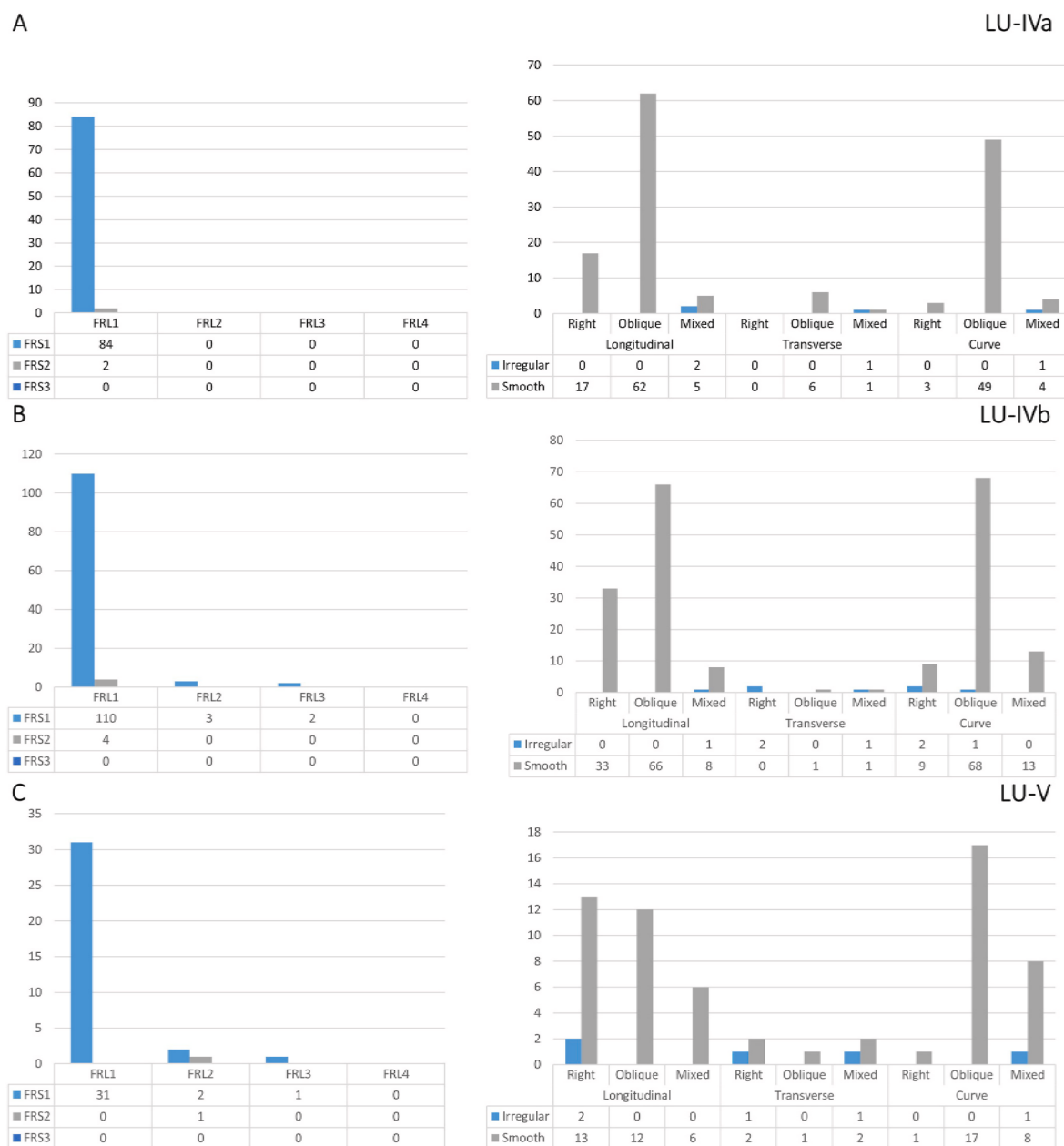


Fig. 5. Analysis of fragmentation patterns (left) and fracture edges (right) of the limb bones of LU-IVa (A) LU-IVb (B) and LU-V (C).

innominate, scapula and ulna, and spiral fractures in a humerus were also recorded. Scratching has been identified in 10 remains. In terms of birds, a tarsometatarsus and a carpometacarpus of a corvid, have pits and scores (Fig. 8).

4.2.2. LU-V

In the LU-V 261 remains were analyzed, and 101 of them could be identified anatomically and taxonomically (Table 1). Leporidae is the most represented, followed by medium-sized cervids, *E. ferus*, *R. cf. pyrenaica*, and large-sized bovids. One cervid remain was clearly attributed to *C. elaphus*. Bird remains were identified as Galliformes indet., *P. graculus*, *Pyrrhocorax* sp. and Aves indet. In LU-V, the MNE amounts to 71 elements: 33 elements correspond to leporids, 32 to macromammals, and six to birds. In general, the representation of % MAU (Fig. 4C and Supp. Table S12) suggests a predominance of limb bones and cranial elements for horses, medium-sized cervids and bovids, although once again, the low MNE should be interpreted with caution. In *R. cf. pyrenaica*, the talus and mandible represent the highest values. The

MNI reveals 12 individuals: nine mammals (six adults and three young) and three birds (Table 1)

The correlation between %MAU and the mineral density of the sample yields values slightly above 0 for all taxa in LU-V (Supp. Fig. 2C), although *p*-value is higher than 0.05 in almost all cases. The only exception is the medium-sized cervids, in which the *p*-value is < 0.05, which implies a positive and statistically significant trend suggesting greater preservation of the densest remains.

As for the postdepositional taphonomic modifications, in LU-V the most documented is black staining by manganese oxide/dioxide, closely followed by root etching (Table 2). Additionally, moisture cracking was also documented in the sample, linked to a humid environment while the other modifications are scarcely represented in this unit.

The fracture patterns of the ungulates from LU-V (Fig. 5C) follows the same pattern as in LUs IVa and IVb, where most of the limb bone sizes measure less than 1/3 of the shaft cylinder and 1/4 of its length, which implies a high fragmentation rate in the sample. Moreover, the most commonly documented fractured edges are longitudinal or curves,



Fig. 6. Evidence of anthropic activity on identified ungulate remains. From left to right, the images show percussion and fresh-breakage marks, evidence of incisions and scraping under microscopic view, and elements with signs of thermal alteration. A) Bone remains from LU-IVa (K20-45-UE4/K19-41-UE4/I19-34/UE4-9); Bone remains from LU-IVb (K19-24-UE4/K20-17-UE4/I19-30-UE4-9); C) Bone remains from LU-V (L20-1-UE19/I19-29-UE9/K20-30-UE4).

obliques and smooths edges, commonly associated with green breakage.

The most documented anthropic activity on bone surfaces in LU-V (Fig. 6) are cut marks, ($n = 22$; 8.4 %), mainly on cervids and medium-sized bone fragments (Table 10), though they were also documented in other taxa such as *E. ferus* or *R. cf. pyrenaica*. At an anatomical level, they were documented in cranial, axial, and appendicular elements, mainly in limb bones in the form of slices and scrapes.

Percussion marks were documented in 12 bone fragments (4.8 %), primarily in limb bones. Indeterminate long bones display parasitic flakes, notches, and abrasions. A medium-sized cervid metapodial has cortical extractions and notches, parasitic flakes, and opposite notches. The documented butchery activities in LU-V follow the same pattern as in LU-IV. The medium-sized cervids are noteworthy, as evidence is

documented across much of the skeleton and could be related to a complete processing of the carcasses. Notably, the only *R. cf. pyrenaica* remain, a proximal phalange, shows cut marks on its posterior side, correlated with skin removal. Furthermore, nine (3.6 %) remains were burned. In terms of the thermoaltered bones, the most documented color is type 4 (55.6 %), which is once again indicative of having reached high temperatures (Table 4).

Evidence of carnivore activity is scarce in ungulates ($n = 2$; 0.8 %), as it is only documented in medium-sized cervids: in a lower incisor and a rib fragment there are signs of heavy and light digestion, respectively.

4.2.2.1. Leporids and birds. 42 remains were recovered, belonging to at least 33 elements and three individuals (Table 6). The sample is

Table 3
Distribution of cut marks in the LU-IVa by anatomical element and taxon.

Element	Taxa/Weight size category					
	Cervidae médium-sized	<i>Equus ferus</i>	Large	Medium	Indeterminable	Total
Horn/Antler	1 (2.1 %)	–	–	–	–	1 (2.1 %)
Skull	–	1 (2.1 %)	–	–	–	1 (2.1 %)
Vertebra	1 (2.1 %)	–	–	–	–	1 (2.1 %)
Rib	5 (10.4 %)	3 (6.3 %)	1 (2.1 %)	6 (12.5 %)	–	15 (31.3 %)
Scapula	–	–	1 (2.1 %)	–	–	1 (2.1 %)
Humerus	–	1 (2.1 %)	–	1 (2.1 %)	–	2 (4.2 %)
Radius	2 (4.2 %)	–	–	–	–	2 (4.2 %)
Radius/Ulna	–	1 (2.1 %)	–	–	–	1 (2.1 %)
Ulna	–	–	1 (2.1 %)	–	–	1 (2.1 %)
Metapodial	1 (2.1 %)	–	–	–	–	1 (2.1 %)
Limb	1 (2.1 %)	–	3 (6.3 %)	6 (12.5 %)	–	10 (20.8 %)
Flat	–	–	3 (6.3 %)	2 (4.2 %)	3 (6.3 %)	8 (16.7 %)
Indeterminate	–	–	–	–	4 (8.3 %)	4 (8.3 %)
Total	11 (22.9 %)	6 (12.5 %)	9 (18.8 %)	15 (31.3 %)	7 (14.6 %)	48 (100 %)

Table 4
Distribution of colors by cremation in LU's.

Color types	LU-IVa	LU-IVb	LU-V
1.1. Brown + not burned	1 (6.3 %)	1 (2.9 %)	–
1.2. Homogeneous brown	1 (6.3 %)	2 (5.9 %)	–
2.1. Not burned + brown + black	–	3 (8.8 %)	1 (11.1 %)
2.2. Brown + black	3 (18.8 %)	10 (29.4 %)	2 (22.2 %)
3. Black	7 (43.8 %)	9 (26.5 %)	1 (11.1 %)
4. Black + White/Grey/Blue	2 (12.5 %)	7 (20.6 %)	5 (55.6 %)
5. White/Grey/Blue	2 (12.5 %)	1 (2.9 %)	–
6. Not burned + Brown + Black + White/Grey/Blue	–	1 (2.9 %)	–
Total	16 (100 %)	34 (100 %)	9 (100 %)

characterized by humerus, radius, ulna, and tibia remains which have a %RA that amounts to 50 %.

Regarding the relative proportions between the anatomical elements in LU-V, cranial elements are less represented than the postcranial (PCRT/CR = 10; PCRLB/CR = 4.7). Autopodium are less represented than zeugopodium and stylopodium (AUT/ZE = 0.5). Moreover, with respect to the latter, zeugopodiums are the most represented (Z/E = 1.8). Lastly, more anterior elements were found than posterior (AN/PO = 2).

The correlation between %MAU and the mineral density of the leporids (Supp. Fig. 2C) yields a positive and statistically significant value,

indicating a higher rate of preservation for the densest elements.

Regarding breakage of leporids in LU-V (Table 11), although the long bones are mostly fragmented, one in three is complete. There is documentation of complete phalanges, while flat and articular bones are mostly diversely fragmented. No signs of anthropic processing were documented, but carnivore activity. An ulna shows furrowing on its proximal epiphysis and a calcaneus shows signs of digestion. A radius shows signs of scratching as well (Fig. 8).

Table 9 shows the anatomical composition of bird elements identified in LU-V. There are six remains belonging to at least six elements and three individuals: one Galliformes indet., one *P. graculus*, and one indeterminate bird. Those elements include two ulnae, one tibiotarsal, two tarsal-metatarsals, and one limb bone shaft fragment. The %RA suggest that we have 33.3 % of what is expected for ulna and tarsal-metatarsals and 16.7 % for tibiotarsals.

5. Discussion

5.1. Subsistence strategies during the LU-V formation

The meso- and macro-mammal assemblage from LU-V reflects a varied ecological landscape, featuring a mix of open areas, forests, and mountain areas. Leporids are the most common taxa, but ungulates of different sizes, including horse (*E. ferus*), chamois (*R. cf. pyrenaica*), large-sized bovid, and red deer (*C. elaphus*) are present as well, indicating a diverse habitat. This diversity aligns with evidence from charcoal and microvertebrate remains at LU-V (Sala et al., 2024), suggesting an environment of relatively humid meadows. Microvertebrates include the snow vole (*Chionomys nivalis*) and various *Microtus* species that thrive in moist grassy areas, together with woodland species like *Eliomys*

Table 5
Distribution of cut marks in the LU-IVb by anatomical element and taxon.

Element	<i>Cervus elaphus</i>	Taxa/Weight size category				
		Cervidae medium-sized	<i>Equus ferus</i>	Indeterminable	Large	Medium
Skull	–	–	–	–	1 (1 %)	–
Rib	–	5 (5.1 %)	2 (2 %)	–	5 (5.1 %)	13 (13.3 %)
Humerus	–	1 (1 %)	1 (1 %)	–	1 (1 %)	2 (2 %)
Radius	–	3 (3.1 %)	1 (1 %)	–	–	–
Tibia	–	–	–	–	–	1 (1 %)
Metapodial	–	2 (2 %)	1 (1 %)	–	–	–
Phalange	1 (1 %)	1 (1 %)	–	–	–	–
Ulna	–	1 (1 %)	–	–	–	1 (1 %)
Tarsal	–	1 (1 %)	–	–	–	–
Limb	–	–	1 (1 %)	3 (3.1 %)	9 (9.2 %)	12 (12.2 %)
Flat	–	–	–	8 (8.2 %)	2 (2 %)	3 (3.1 %)
Articular	–	1 (1 %)	–	–	–	–
Indeterminate	–	–	–	14 (14.3 %)	1 (1 %)	–
Total	1 (1 %)	15 (15.3 %)	6 (6.1 %)	25 (25.5 %)	19 (19.4 %)	32 (32.7 %)

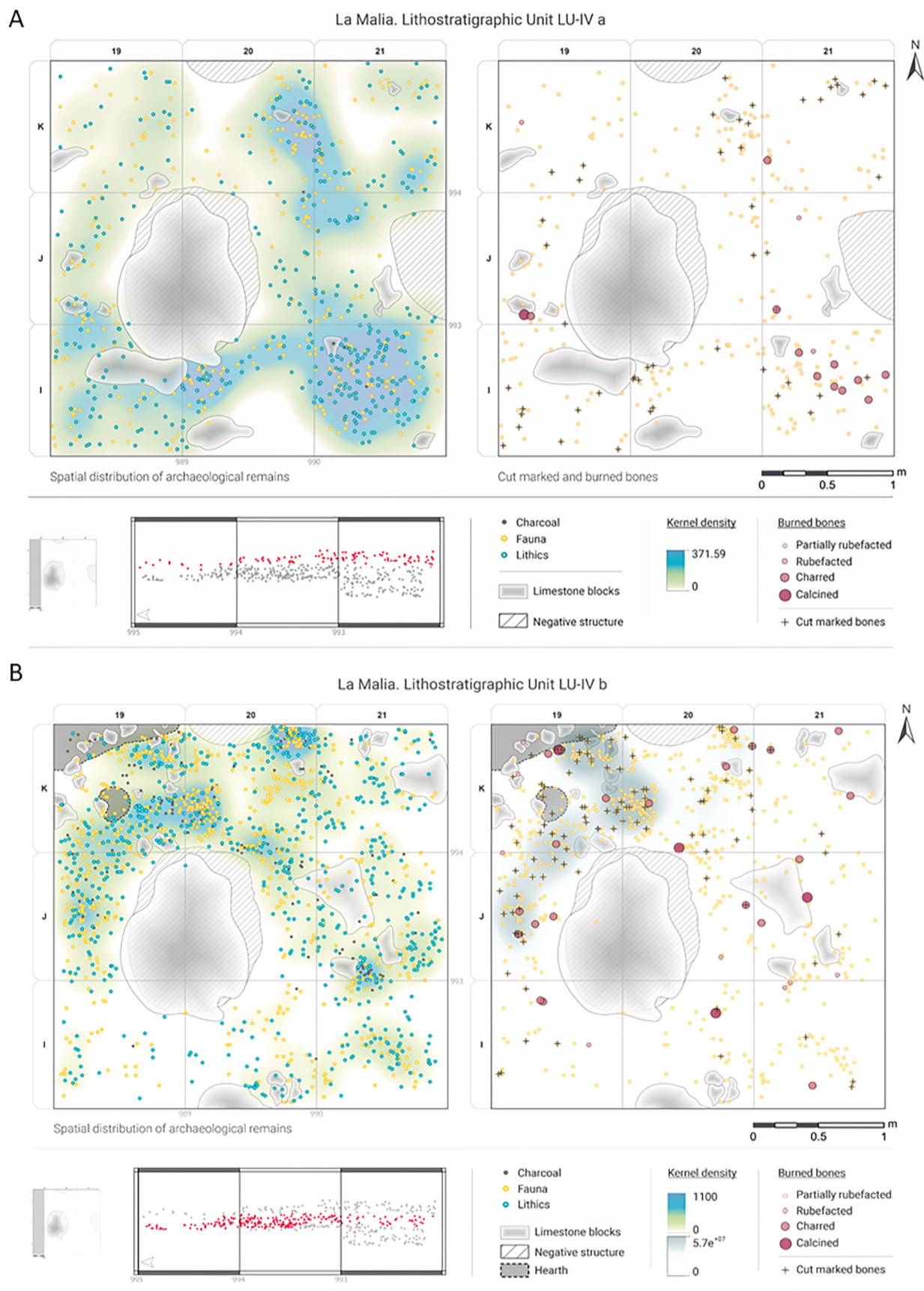


Fig. 7. Spatial distribution of archeological remains in LU-IVa (A) and LU-IVb (B). The concentrations of charcoal, faunal remains, and lithic artifacts are indicated, along with the distribution of hearths, thermally altered faunal elements, and specimens with cut marks.

Table 6

Skeletal elements of leporid remains recovered from the different LU's. NISP, number of identified specimens; %, percentage of number of identified specimens; MNE, minimum number of elements; %RA, relative abundance; MNI, minimum number of individuals.

	LU-IVa/MNI = 2				LU-IVb/MNI = 4				LU-V/MNI = 3			
	NISP	%	MNE	%RA	NISP	%	MNE	%RA	NISP	%	MNE	%RA
Skull	–	–	–	–	3	4.8	1	25.0	3	7.1	1	33.3
Mandible	3	30	1	25	6	9.7	5	62.5	2	4.8	2	33.3
Isolated tooth	–	–	–	–	3	4.8	–	–	–	–	–	–
Vertebra	3	30	3	3.8	2	3.2	2	1.3	1	2.4	1	0.8
Sacro	–	–	–	–	–	–	–	–	1	2.4	1	33.3
Rib	–	–	–	–	1	1.6	1	1.0	2	4.8	1	1.4
Scapula	1	10	1	25	4	6.5	4	50.0	2	4.8	2	33.3
Humerus	1	10	1	25	3	4.8	3	37.5	3	7.1	3	50.0
Radius	1	10	1	25	4	6.5	3	37.5	3	7.1	3	50.0
Ulna	1	10	1	25	3	4.8	2	25.0	3	7.1	3	50.0
Metacarpals	–	–	–	–	1	1.6	1	12.5	3	7.1	3	12.5
Coxae	–	–	–	–	8	12.9	6	37.5	2	4.8	2	33.3
Femur	–	–	–	–	4	6.5	2	25.0	2	4.8	2	33.3
Tibia	–	–	–	–	1	1.6	1	12.5	5	11.9	3	50.0
Talus	–	–	–	–	2	3.2	2	50.0	–	–	–	–
Calcaneum	–	–	–	–	4	6.5	4	50.0	2	4.8	2	33.3
Tarsals	–	–	–	–	1	1.6	–	–	1	2.4	1	2.2
Metatarsals	–	–	–	–	5	8.1	5	31.3	1	2.4	1	4.2
Metapodial indet	–	–	–	–	1	1.6	–	–	1	2.4	–	–
Phalanges	–	–	–	–	5	8.1	5	4.6	2	4.8	2	1.2
Limb	–	–	–	–	1	1.6	–	–	3	7.1	–	–
Total	10	100	8	–	62	100.0	47	–	42	100.0	33	–

Table 7

Breakage pattern of leporids bones of LU-IVa. N, number of specimens. Long bones, metacarpal and metatarsal bones were classified as: complete (C), proximal epiphysis (PE), proximal epiphysis shaft (PES), shaft (S), shaft distal epiphysis (SDE) and distal epiphysis (DE). Mandible as: complete (C), incisive part (IP), mandible body incisive part (MBI), mandible body (MB), mandible body branch (MBB) and condylar process (CP). Cranium as: complete (C), incisive bone (IB), incisive bone maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). Coxa as: complete (C), acetabulum (A), acetabulum ischium (AIS), acetabulum ischium illium (AISIL), acetabulum illium (AIL), ischium (IS) and illium (IL). Scapula as: complete (C), glenoid cavity (GC), glenoid cavity neck (GCN), neck fossa (NF) and fossa (F). Phalanges as: complete (C), proximal fragment, (P), distal fragment (D) and fragment (F). Patella and calcaneum as complete (C) and fragment (F).

Long bones and Metapodials	C		PE		PES		S		SDE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
Humerus									1	100		
Radius									1	100		
Ulna					1	100						
Mandible	N		Scapula		N		Vertebra		N		%	
C			C				C					
IP			GC				VB		3		100	
MBI	1	50	GCN		1	100	VE					
MB			NF				SP					
MBB			F									
PC	1	50										

quercinus and *Apodemus*. Additionally, the predominance of *Quercus* in the charcoal remains suggests the presence of both open and isolated wooded spaces. In regard to the avifauna, *P. graculus* (the yellow-billed chough) is the only taxon in the assemblage that was identified up to a species level. This species currently inhabits high mountain ranges (Madge, 2020), although its distribution during the Late Pleistocene was ampler (Carrera et al., 2022). The spite its appearance nowadays in cold areas, its distribution seems to be more related to changes in the landscape than to temperature changes. In this case, it is likely associated with the expansion of open dry and rocky areas (Holm and Svenning, 2014). The evidence indicates that, although the region experienced generally harsh climatic conditions during much of late MIS-3, periods of diverse and more favorable habitats coincided with occasional human presence. This suggests that environmental and climatic challenges were not insurmountable obstacles to the survival of human groups during these intervals.

For horses, medium-sized cervids, and large-sized bovids, while there are some post-cranial elements, cranial elements are the most represented, according to %MAU. In comparison, the post-cranial

skeleton is less represented, especially the axial skeleton, and in the case of horses and large-sized bovids, the appendicular skeleton's absence is also noteworthy. The correlation between %MAU and bone mineral density suggests that factors beyond density may explain the absence of certain elements, though these results lack statistical significance and should be considered indicative rather than conclusive. The assemblage exhibits high and green breakage, and the main modification agents seem to be human groups. Their activity is evidenced by cut marks, percussion marks, and signs of thermoalteration. This evidence is mainly observed on cervids, indicating exhaustive processing of this taxon. However, the evidence documented for other taxa, as well, such as horse or chamois, suggests that exploitation was not focused exclusively on cervids but rather on diverse resources provided by the environment, while it is true that the MNI of the assemblages is low so far, this must be taken into account.

So far, the relatively low density of archeological remains also aligns with the interpretation of ephemeral and low-intensity occupations such in Cova de les Cendres (Villaverde et al., 2021). The values of anthropic activity are close to those of early Upper Paleolithic assemblages

Table 8

Breakage pattern of leporids bones of LU-IVb. N, number of speciemes. See abbreviation of fracture categories in caption of Table 7.

Long bones and Metapodials		C		PE		PES		S		SDE		DE	
		N	%	N	%	N	%	N	%	N	%	N	%
Humerus								2	66.6			1	33.3
Radius						1	25	3	75				
Ulna						1	33.3	1	33.3	1	33.3		
Femur				1	25	1	25	2	50				
Tibia								1	100				
Metacarpal		1	100										
Metatarsal		4	80							1	20		
Mandible	N	%	Cranium	N	%	Coxa	N	%	Scapula	N	%		
C			C			C			C				
IP			IB			A	1	12.5	GC	3	75		
MBI	3	50	IBM	1	50	AIS	2	25	GCN	1	25		
MB	1	16.7	M			AISIL	2	25	NF				
MBB	1	16.7	ZA			AIL	3	37.5	F				
PC	1	16.7	NC	1	50	IS							
						IL							
Vertebra	N	%	Phalange 1/2	N	%	Phalange 3	N	%		N	%		
C			C	4	100	C							
VB	2	100	P			P							
VE			D			D				1	100		
SP													
Calcaneum	N	%	Talus	N	%	Ribs	N	%		N	%		
C	5	100.0	C			C							
F			F	2	100.0	F	1	100.0					

Table 9

Skeletal elements of birds remains recovered from the LU-IVb. NISP, number of identified specimens; %, percentage of number of identified specimens; MNE, minimum number of elements; %RA, relative abundance; MNI, minimum number of individuals.

	LU-IVb/MNI = 4				LU-V/MNI = 3			
	NISP	%	MNE	%RA	NISP	%	MNE	%RA
Skull	1	10	1	25				
Mandible	1	10	1	25				
Humerus	2	20	2	25				
Ulna					2	33.3	2	33.3
Carpometacarpus	3	30	3	37.5				
Tibiotarsus					1	16.7	1	16.7
Tarsometatarsus					2	33.3	2	33.3
Limb	3	30	3	–	1	16.7	1	–
Total	10	100	10	–	6	100	6	–

interpreted as short-term camp occupations, as in Cova Eirós (Lombera-Hermida et al., 2021) or Cova de les Malladetes (Sanchis et al., 2023). This interpretation aligns with the lack of spatial distribution in domestic areas (Fig. 9), as well as with the data presented by Sala et al. (2024), that must be related to the brief human occupations. This includes the fragmentation of the *Chaînes opératoires* and the expedient nature of the lithic assemblage, characterized by limited exploitation activity and the introduction of already-configured tools, likely produced outside the rock shelter, in addition to the identification of a proximal fragment of an assegai point made on bone. Future findings could be useful for expanding the available data and the inferences made here, including the biases on the skeletal part representation. The scarce carnivore activity documented in this level, evident in the digestion of some remains, allows us to rule out these agents as accumulators, at least in terms of ungulate carcasses.

Leporids, despite being the most represented taxon, show no signs of human modification, so their role as accumulation agents is discarded so far; thus, their presence could be attributed to carnivore activity or could represent natural deaths into the levels analyzed here. The assemblage of birds recovered to date in LU-V is small (NISP = 6), and so far, there is no definitive information regarding its origin, before the absence of anthropic and carnivore modifications.

The occupation of the Malia rock shelter during the early Upper Paleolithic could represent a singular event or, in any case, constitute evidence of human presence in a hostile paleoclimatic context during MIS-3. This presence could reflect short-term occupations, likely constrained by severe environmental conditions (Finlayson, 2004; Schmidt et al., 2012; Bradtmöller et al., 2012). The Malia rock shelter challenges the prevailing view that early Upper Paleolithic human groups were unable to adapt to the climatic conditions of the Iberian plateau (Straus, 2015; Alcaraz-Castaño et al., 2017, 2021). However, given that the site is the only documented site in inland Iberia dated to the early Upper Paleolithic, the findings presented here lack close geographical parallels. The Iberian Peninsula, however, has other regions with early Upper Paleolithic sites featuring faunal records which have given rise to taphonomic studies, subsistence interpretations, and occupation patterns, primarily on the Cantabrian range (Arrizabalaga and Altuna, 2000; Arrizabalaga et al., 2003; Tejero et al., 2005; Yravedra and Gómez-Castanedo, 2011; Yravedra et al., 2016; De la Rasilla et al., 2020; Lombera-Hermida et al., 2021; Marín-Arroyo and Sanz-Royo, 2021; Sanz-Royo et al., 2024), but also on the Mediterranean range (Soler and Soler, 2016; Real and Villaverde, 2022; Sanchis et al., 2023) and the Portuguese coast (Valente, 2004). Most of them, such as El Castillo, La Viña or Labeko Koba in the Cantabrian range or Cova de les Cendres and

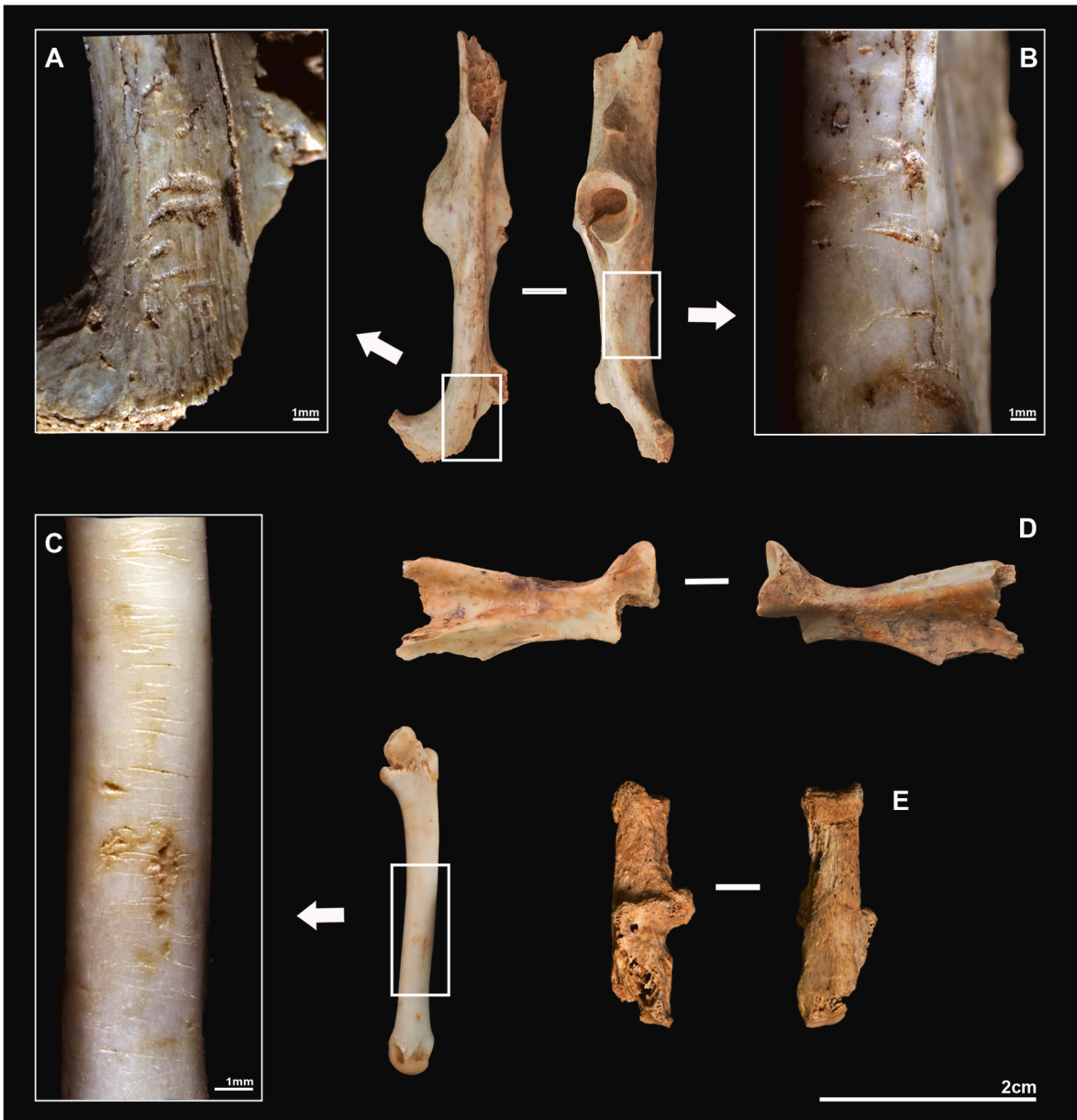


Fig. 8. Taphonomic modifications observed in leporids from Malia. A, B) Scores produced by carnivores on an innominate fragment from LU-IVb (J19-2-UE4); C) Scratching observed on a metapodial from LU-IVb (I20-20-UE4); D) Crenulated edges produced by carnivores on a scapula from LU-IVb (J21-45-UE4); E) Corrosion produced by digestion in a calcaneus from LU-V (I20-15-UE4).

Table 10
Distribution of cut marks in the LU-V by anatomical element and taxon.

Elements	<i>Cervus elaphus</i>	Taxa/Weight size category							Total
		Cervidae medium-sized	<i>Equus ferus</i>	<i>Rupicapra</i> cf. <i>pyrenaica</i>	Large	Medium	Small	Indet.	
Mandible	–	1 (4.5 %)	–	–	–	–	–	–	1 (4.5 %)
Rib	–	–	–	–	1 (4.5 %)	–	1 (4.5 %)	–	2 (9.1 %)
Coxal	–	–	1 (4.5 %)	–	–	–	–	–	1 (4.5 %)
Metapodial	–	2 (9.1 %)	–	–	–	–	–	–	2 (9.1 %)
Phalange	1 (4.5 %)	–	–	2 (9.1 %)	–	–	–	–	3 (13.6 %)
Limb	–	1 (4.5 %)	–	–	1 (4.5 %)	5 (22.7 %)	–	–	7 (31.8 %)
Flat	–	–	–	–	1 (4.5 %)	2 (9.1 %)	–	–	3 (13.6 %)
Indet.	–	–	–	–	–	–	–	3 (13.6 %)	3 (13.6 %)
Total	1 (4.5 %)	4 (18.2 %)	1 (4.5 %)	2 (9.1 %)	3 (13.6 %)	7 (31.8 %)	1 (4.5 %)	3 (13.6 %)	22 (100 %)

Cova de l'Arbreda on the Mediterranean range, were interpreted as long-term camps (Arrizabalaga and Altuna, 2000; Yravedra and Gómez-Castanedo, 2011; Mafillo-Fernández et al., 2014; Soler and Soler,

2016; de la Rasilla et al., 2020; Marín-Arroyo and Sanz-Royo, 2021; Real and Villaverde, 2022), since they have a series of features typical of these types of assemblages: complete *chaîne opératoire*, abundant hearths

Table 11
Breakage pattern of leporids bones of LUV. N, number of specimens. See abbreviation of fracture categories in caption of Table 7.

Long bones and Metapodials	C		PE		PES		S		SDE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
Humerus	1	50							1	50		
Radius	1	50							1	50		
Ulna	1	33.3			2	66.7						
Femur	1	50			1	50						
Tibia			1	20			4	80				
Metacarpal	2	66.7							1	33.3		
Metatarsal									1	100		
Mandible	N	%	Cranium	N	%	Coxa	N	%	Scapula	N	%	
C	1	50	C			C			C			
IP	1	50	IB			A			GC	1	50	
MBI			IBM			AIS			GCN	1	50	
MB			M			AISIL	1	50	NF			
MBB			ZA	1	50	AIL	1	50	F			
PC			NC	1	50	IS						
						IL						
Phalange 1/2	N	%				Phalange 3	N	%				
C	1	100				C	1	100				
P						P						
D						D						
Carpal/Tarsal	N	%	Calcaneum	N	%	Ribs	N	%				
C			C			C						
F	1	100	F	1	100	F	2	100				

that structure domestic spaces, intense processing of medium and large-sized ungulates, art and symbolic elements, and even, in the case of Cueva Morín, the existence of a hut-like structure (Maíllo-Fernández et al., 2014).

However, as previously mentioned, the Malia rock shelter exhibits certain characteristics that may indicate shorter occupations. There are two early Upper Paleolithic sites that are described as short-term hunting camps that share many of these characteristics: level 2 of Cova Eirós in the Cantabrian range (Lombera-Hermida et al., 2021) and level AU of Cova de les Malladetes in the Mediterranean range (Sanchis et al., 2023). These are levels in which human occupations had little impact, with a low density of lithic artifacts, primarily made outside the sites, in addition to a predominance of cranial skeletons and no complete carcasses. These were interpreted as the result of opportunistic and seasonal visits by human groups during hunting trips, indicative of non-specialized consumption, albeit with a certain predominance of deer and Pyrenean chamois in Cova Eirós (Lombera-Hermida et al., 2021), while there is an almost exclusive specialization of *Capra pyrenaica* in Cova de les Malladetes (Sanchis et al., 2023). In general, a pattern of occupation similar to that identified in Malia LU-V is described in these assemblages, which could be the result of opportunistic occupations of the rock shelter, within the logistic mobility framework described by Binford (1978). At the subsistence level in Malia, as in Cova Eirós, no specialized exploitation of any taxon is documented, but there appears to be an exploitation of the various resources provided by the landscape, although the low MNI of our assemblage does not allow us to make inferences about the seasonality of the occupations. The primary distinction between Malia and the aforementioned assemblages pertains to the observed patterns of carnivore activity and the alternation between human and carnivore occupations in Cova Eirós and Cova de les Malladetes. In contrast, Malia exhibits distinct characteristics that differentiate it from these other sites.

5.2. Subsistence strategies during the LU-IV formation

Paleoecological data available for LU-IV shows a climatic deterioration and a landscape change during its formation (Sala et al., 2024). Greater aridity and worsening climatic conditions are indeed observed

as compared to LU-V. Data derived from isotopic, paleobotanical, and micromammal paleontological studies indicate a gradual cooling of the climate and a progressive drying of the environment, with a decrease in rodent species typical of humid environments present in LU-V, and their replacement by species from drier environments, such as *Alexandromys oeconomicus*. The opening of landscapes is mainly documented through the reduction of thermomediterranean forests and the increase in the presence of *Pinus* tp. *sylvestris-nigra* and grasses, indicating a shift towards a more open environment (Sala et al., 2024).

The climatic deterioration during this period does not appear to have been an obstacle for the AMH occupation of the Tamajón karst, as evidenced by activity documented in LU-IV of Malia (Sala et al., 2024; present paper), as well as in the nearby site of Los Enebrales rockshelter (Álvarez-Alonso et al., 2024). Nor do the subsistence patterns of the groups that occupied this shelter appear to have been significantly affected, as the subunits LU-IVa and LU-IVb of Malia show, in general, no big changes in the characteristics of the assemblages found in LU-V. The taxonomic list is, in fact, similar, with the only exception being the absence of *R. cf. pyrenaica* and the presence of *C. capreolus*, though horses and deer gained weight in relation to leporids, which could be related to climatic deterioration.

The representation of skeletal elements in this case provides partial information due to the scarcity of remains identifiable at the anatomical element level. In general, the axial skeleton, including vertebrae, ribs, and pelvis, is underrepresented across all body size categories of ungulates. Long bones and cranial elements are predominant, particularly in medium-sized ungulates, whereas in large-sized ungulates (horses and large sized bovids), the identified elements are so scarce that they do not allow for meaningful inferences (Fig. 4). The correlation between % MAU and bone mineral density suggests that its absence is not related to mineral density. At the taphonomic level, the data are very similar to what was found in LU-V, as human groups once again emerge as the main modifying agent of our assemblage, with their activity focused on medium and large-sized ungulates, while carnivore activity remains marginal. Once again, in the case of leporids and birds, the only modifications documented were likely produced by carnivores and no signs of anthropic modifications is documented in any case.

Similarly, the attributes related to the lithic assemblage, the

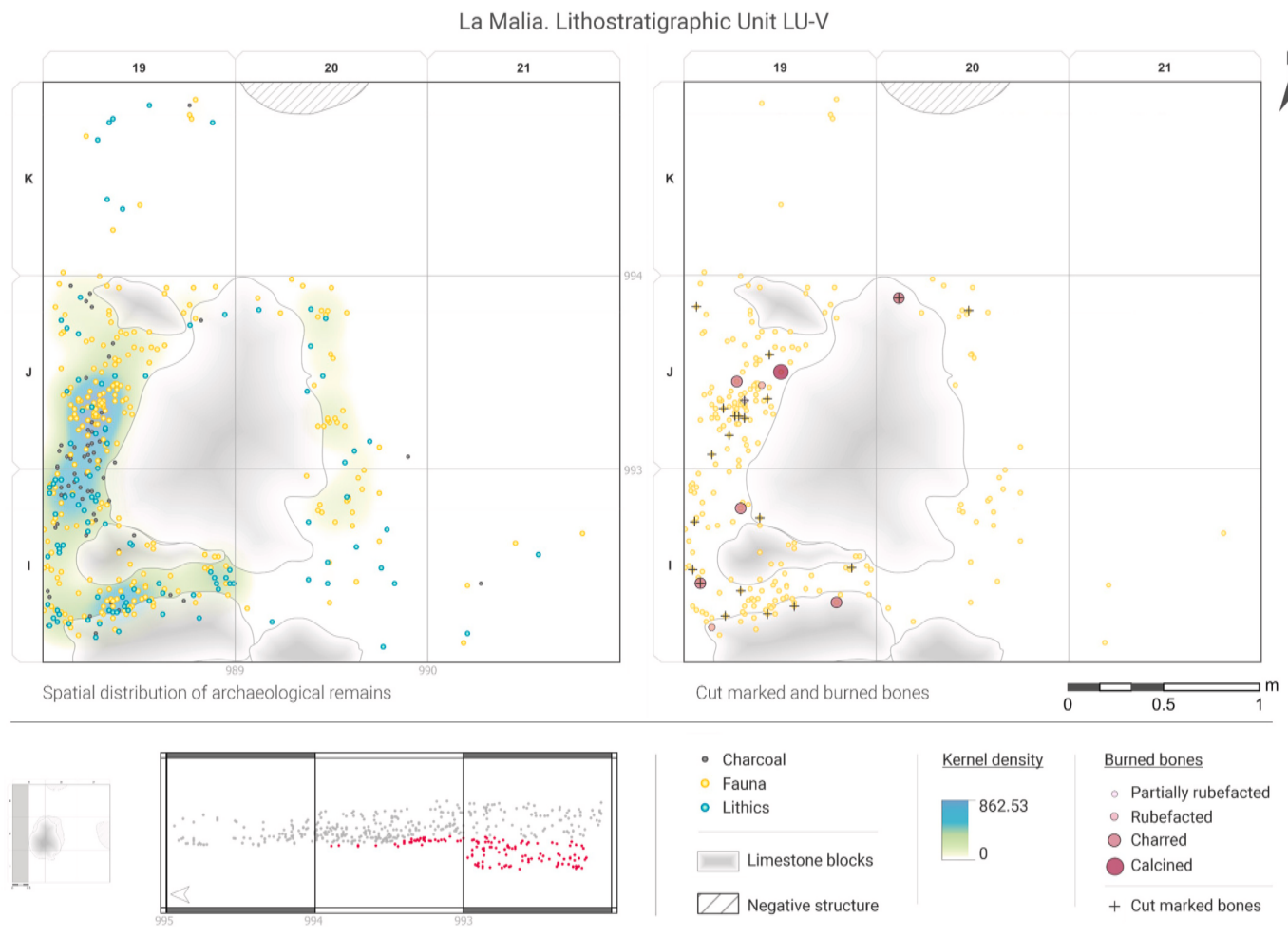


Fig. 9. Spatial distribution of archeological remains in LU-V. The concentrations of charcoal, faunal remains, and lithic artifacts are indicated, along with the distribution of hearths, thermally altered faunal elements, and specimens with cut marks.

identification of a proximal fragment of an assegai point made on deer antler or the low stratigraphic potential of the lithostratigraphic unit as described by Sala et al. (2024), also align. The main difference documented so far in relation to LU-V is the identification of two hearths in LU-IVb. The only one that has been completely excavated so far is a small hearth in which anthropized bones (both thermoaltered and cut marked specimens) are concentrated (Fig. 1E; Fig. 7B). The second hearth, partially excavated, is at the edge of the excavation surface. Sanchis et al. (2023) already described the presence of small hearths in the Cova de les Malladetes short-term camp. They seem to be mainly associated with food activities (presence of bones with taphonomic signs of consumption) which are interpreted as the result of brief, sporadic occupations by small groups, similar to what is proposed in Malia. All these data lead us to infer that Malia might reflect a short-term occupation likely related to hunting activities, consistent with what has been described for LU-V.

Unlike what occurred during the early Upper Paleolithic, there are geographically and chronologically close references to Malia during the middle and late Upper Paleolithic. One such example is the aforementioned Los Enebrales rock-shelter. This site was also interpreted as a short-term occupation, which contains some evidence of ungulate processing but low intensity of human activity (Álvarez-Alonso et al., 2024). Although the data, particularly the taphonomic data, are preliminary and should be interpreted with caution, the data presented would align with the results discussed here regarding Malia. This could suggest patterns of resource exploitation in the Tamajón karst area that,

in some way, reflect recurrent strategies among early Upper Paleolithic AMH. With more solid subsistence data (Yravedra et al., 2016), there is also the geographically nearby site of Peña Capón dated to Proto-Solutrean and Solutrean chronologies (Alcaraz-Castaño et al., 2013, 2019, 2021). The faunal assemblage shows similarities to Malia in terms of taxonomy (predominance of medium to large ungulates, mountain taxa, etc.) and taphonomy (anthropic processing of carcasses, secondary access by carnivores, etc.). Certain elements, such as the identification of hunting projectiles or marginal activity of carnivores, led Yravedra and colleagues (2016) to propose short-term occupations focused on hunting activities, while the presence of a high number of domestic tools, such as burins and end-scrapers, could suggest a more residential use at other times, possibly reflecting different uses of the same space at different times. A holistic view of the data provided by the archeological sites from the Tamajón karst allows us to affirm that, despite the adverse climatic conditions that could have existed from the beginning of the early Upper Paleolithic until the arrival of the Solutrean, this region would have provided sufficient resources for these human populations, who would have visited it recurrently. But, above all, it demonstrates the ability to adapt to different climatic conditions throughout this temporal span.

When analyzing some of the main Gravettian assemblages from the Iberian Peninsula, a progressive increase in the presence of bone artifacts, ornamental elements, and artistic manifestations such as portable art, and even human remains can be observed. However, it is true that their presence and abundance tend to correlate with this type of

occupation, with these elements being more common in domestic or long-term camps, such as in La Viña, Cova de les Cendres or Cova del Reclau Viver (e.g., Soler and Soler, 2016; Villaverde et al., 2021; de la Rasilla et al., 2020), and more anecdotal in short-term camps, as in Los Enebrales, Llonín, El Parpalló or L'Arbreda Cave (e.g., Davidson, 1989; Soler and Soler, 2016; Villaverde et al., 2021; de la Rasilla et al., 2020; Álvarez-Alonso et al., 2024). The absence of such elements at Malia (with the exception of the proximal fragment of an assegai point made of deer antler) might be attributed to the brevity of the occupations and the possible use of the shelter as a hunting camp. There is a possibility that evidence of more intensive occupations may be identified in nearby sites or even in other levels in Malia. Such findings could, as observed in coastal contexts, contribute to a more comprehensive understanding of the behavioral patterns of these groups in relation to different types of occupations.

The zooarchaeological and taphonomic evidences presented in this study document short but recurrent occupations over at least 10,000 years at the Malia rock shelter (36,200–26,260 cal BP). This pattern demonstrates that the climatic deterioration during the Early Upper Paleolithic does not appear to have significantly altered the settlement patterns or subsistence strategies of AMH. These findings highlight the remarkable adaptive capacities of these populations in the face of environmental challenges.

6. Conclusions

Unraveling the subsistence patterns in a region and period as little known as Central Iberia during the early and middle Upper Paleolithic is crucial, as it highlights the potential of this area, apparently scarce in resources, for the first AMH. The Malia rock shelter offers a valuable opportunity to document the faunal resources exploited by these groups, as well as their patterns of site occupation and environmental exploitation. Taphonomic data suggests primary and almost exclusive anthropic processing of medium and large-sized ungulates, from skinning to marrow extraction. Data derived from the density of recovered elements in the lithostratigraphic units, the degree of anthropization, and the lack of spatial distribution, among other factors, suggest that Malia might have been occupied during brief but recurrent episodes over time. Evidence of the consumption of localized taxa, such as the chamois, has been identified in the LU-V, dated to the early Upper Paleolithic, indicative of the exploitation of nearby resources. Carnivore activity evidence is scarce and does not seem to focus on the same carcasses.

In this complex ecological landscape, the Malia rock shelter provides a record of a notable versatility in the ability to obtain resources in open, semi-open, and mountainous areas. Such behavior is comparable to that observed in contemporary sites, both on the Iberian Peninsula's coast ranges and in other sites on the plateau. In sum, Malia allows us to characterize human behavior in the early Upper Paleolithic from a zooarchaeological point of view and provides insight into the resilience of the first *Homo sapiens* to successfully colonize challenging and resource-scarce territories. All of this evidence suggests that occupations in the interior of the Iberian Peninsula were recurrent not only starting in the Proto-Solutrean period, as previously proposed, but also in the Aurignacian, corresponding to the arrival of the first AMH to Iberia. This study invites us to reconsider current models of environmental exploitation, as well as the population dynamics of *Homo sapiens* in the early Upper Paleolithic.

CRediT authorship contribution statement

Edgar Téllez: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Antonio Rodríguez-Hidalgo:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Manuel Rodríguez-Almagro:** Writing – review & editing, Methodology, Investigation, Data curation.

Carmen Núñez-Lahuerta: Writing – review & editing, Writing – original draft, Investigation, Data curation. **Andion Arteaga-Brieba:** Writing – review & editing, Formal analysis, Data curation. **Adrián Pablos:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation. **Nohemi Sala:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

Authors confirm there are no financial or personal conflicts of interest to declare. Financial support has been indicated in acknowledgements.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.qsa.2025.100297>.

Data availability

Data available is included in the Supplementary Material

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