Journal of Paleolithic Archaeology (2024) 7:2
https://doi.org/10.1007/s41982-023-00169-5

RESEARCH

Rabbit (*Oryctolagus cuniculus*) Remains from Cueva del Gato 2 (Épila, Zaragoza): A Contribution to Human Consumption Patterns in Inland Iberia During the Late Pleistocene

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Accepted: 22 December 2023

Abstract
Since the Middle Pleistocene, rabbits have played a crucial role as a resource for subsistence in various parts of Europe. Their significance during the Upper Paleolithic period along the Iberian Mediterranean coast is well documented. However, the utilization of the rabbit as a resource in the interior lands of the Iberian Peninsula has received little attention. This paper presents an analysis of the rabbit remains from Cueva del Gato 2, a cave situated in the foothills of the Sierra de Rodanas with human Paleolithic occupation primarily dating back to approximately 22,925–22,632 to 21,714–21,330 years cal. BP. The main objectives of this study are to identify the origin of the leporid assemblage at the site, to assess the management and consumption patterns, and to determine their importance in the inland region of the Ebro Valley. The research involved taphonomic and zooarcheological analyses, and estimating age when possible. Additionally, the QGIS program was used in order to characterize the butchery pattern. The results indicate the systematic hunting, butchery, and consumption of rabbits in the Badegoulian levels of the site. This provides additional data regarding the occupation of the interior valleys during the cold periods of the Upper Paleolithic.

Keywords Leporid remains · Badegoulian occupations · Butchery patterns · Inland Iberian

Introduction

The fossil data suggests that the Iberian Peninsula is likely the original home of the European rabbit (*Oryctolagus cuniculus*). The earliest evidence for the species can be found in the Middle Pleistocene in southern Spain, around 0.6 million years ago. It later spread to other parts of Iberia and southern France (López-Martínez, 2008). Rabbits are highly reproductive mammals and thrive in favorable ecological conditions, making them a crucial species for the survival of many predators (Delibes-Mateos & Gálvez-Bravo, 2009). This is particularly true in the Iberian Peninsula, where rabbits have served as prey for numerous predators since the Middle Pleistocene (Delibes-Mateos et al., 2008; López-Martínez, 2008).

Rabbits were an important source of prey for humans, as they are a social species that live in large groups, with up to several dozen individuals per warren (Pelletier et al., 2016). It has been suggested that these animals could have been easily collected in large quantities using nets or other technological advancements, which would have greatly contributed to human subsistence (Hockett & Haws, 2002; Jones, 2006; Stiner & Munro, 2002). Numerous studies conducted in the

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Iberian Peninsula and southern France, have demonstrated the significant role that rabbits played in the diet of prehistoric humans during the Upper Paleolithic and Epipaleolithic periods. These studies have revealed the presence of large accumulations of rabbit remains in hunter-gatherer groups, with the number of remains increasing as the Upper Paleolithic advanced (Cochard & Brugal, 2004; Fa et al., 2013; Lloveras et al., 2011, 2016; Manne & Bicho, 2009; Rillardon & Brugal, 2014; Rosado-Méndez et al., 2019; among others).

In France, it has been observed that diets primarily consisting of rabbits are found in the archeological record of inland regions during the Pleistocene–Holocene transition (e.g., Cochard & Brugal, 2004; Jones, 2012). On the other hand, zooarcheological faunas from Mediterranean Spain typically show an abundance of rabbits much earlier in the Upper Paleolithic (Jones, 2012). However, most studies in Iberia focus on sites near the coast, with very few studies highlighting the significance of rabbit consumption in inland areas (e.g., Peña Estebanvela, Peña Capón, and Cueva Chaves; see Castaños, 1993; Alcaraz Castaño et al., 2013; Yravedra & Andrés, 2013; Utrilla and Laborda Lorentea, 2018). As a result, this topic remains relatively unknown in non-coastal regions (Aragoncillo-Del Río et al., 2023; Canals et al., 2010; Castaños, 1993; Yravedra & Andrés, 2013). The Cueva del Gato 2 site, located in the middle of the Ebro Valley, provides an excellent opportunity to examine the importance of small mammals in the subsistence of hunter-gatherers in these territories. It is important to emphasize that small mammal remains, especially those of rabbits, undergo complex formation processes. This is due to their status as prey for various predators and their fossorial habits (see Mallye et al., 2008; Lloveras et al., 2010, 2011; Pelletier et al., 2016, 2017, 2020). Therefore, a thorough examination of the remains from a taphonomic perspective is crucial for gaining a better understanding of their role in subsistence.

This paper presents the results of a zooarcheological and taphonomic study conducted on rabbit remains from Cueva del Gato 2 (Épila, Zaragoza). The objectives of this study are the following: (1) identifying the primary agents responsible for the leporid assemblage at the Cueva del Gato 2 site, (2) evaluating the management and consumption patterns of leporids at the site, and (3) determining the significance of leporids in the inland region of the Ebro Valley.

Cueva del Gato 2 Site

Cueva del Gato 2 is situated in the foothills of the Sierra de Rodanas in Spain's Iberian system, at an elevation of 620 m above sea level (Fig. 1). It is one of four cavities that form a karstic system, which has had a notable impact on the Jurassic dolomitic limestone found in the western region of Épila municipality in Zaragoza.

The cave offers excellent living conditions, with a main entrance measuring 3 m high and 11 m wide, facing south. This entrance, which appears to have been the original, leads to

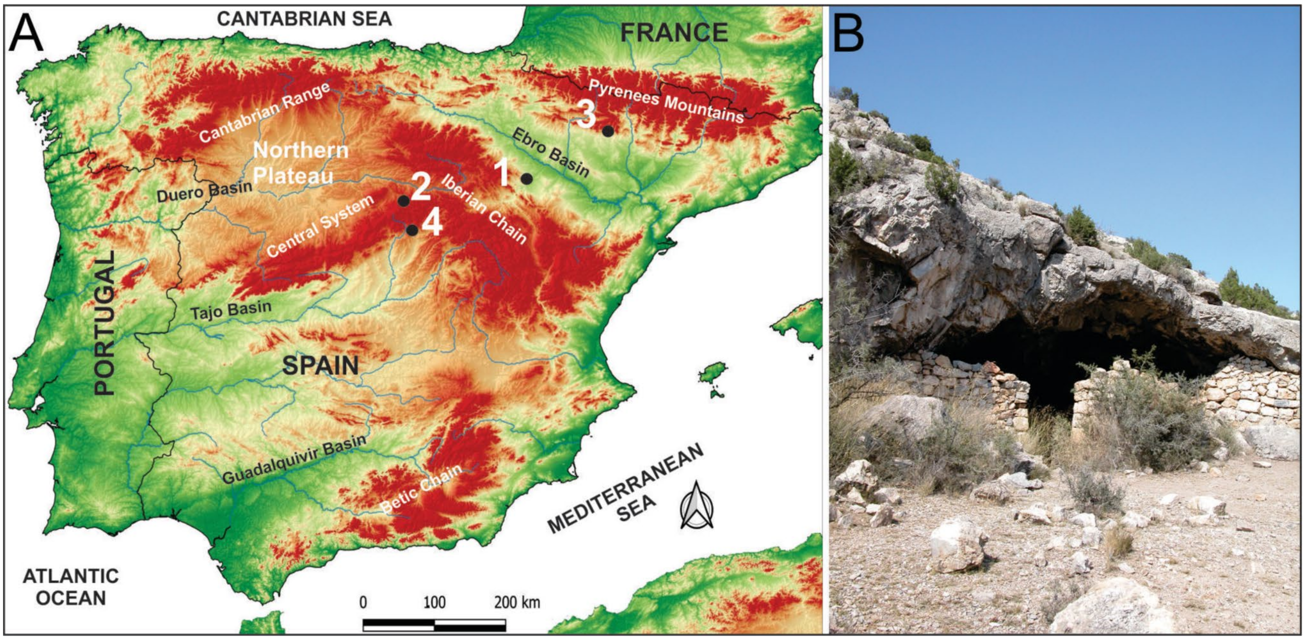

Fig. 1 **A** Geographical location of Cueva del Gato 2 (the source of the data for the base map is the Instituto Geográfico Nacional (Spain)) in the Ebro basin and other proximate sites where rabbit exploitation has been observed: (1) Cueva del Gato 2, (2) Peña de Estebanvela, (3) Cueva Chaves, and (4) Peña Capón. **B** View of the Cueva del Gato 2 site

a spacious room measuring 22 m by 15 m, which remains well-lit during daylight hours (Fig. 1B). The first recorded mention of the cave dates back to 1893. Since then, various authors have cited the cave, indicating a sustained interest in its exploration and study over time (Blasco & Rodanés, 2009: 311). Over the course of multiple fieldwork seasons, four archeological surveys have been conducted, revealing prehistoric levels from the Upper Paleolithic, Early Neolithic, and Bronze Age. Additionally, historical occupations have been identified, with the main chamber of the cave being used as a herd enclosure up until the present day (Blasco & Rodanés, 2004, 2009).

In Survey II, a Paleolithic level was identified in a small area (~ 10 m^2) within the main chamber, which was stratigraphically well delimited (Fig. 2). This deposit adds to the growing number of sites recently found and excavated in the foothills of the Iberian System (Aragoncillo-Del Río et al., 2023; Utrilla et al., 2006, 2010, 2012). Through the study of archeological assemblages and radiocarbon dating, a Badegoulian/Archaic Magdalenian was determined. The lithic industry consists of approximately 1500 artifacts, with 138 of them being tools. The industry is mainly laminar, with a large number of large flakes, microblades, and very few cores. The initial study indicates that burins are the dominant primary type, followed by scrapers, notches, and denticulates, with only two uncertain raclettes. Further examination of the secondary types reveals the presence of "sur coche" burins, which are similar to those found in the lower levels of Badegoule or Laugerie-Haute. Additionally, the nose scrapers found are reminiscent of those discovered in level IV at Beauregard (Utrilla et al., 2018). The bone industry is significant, with 30 pieces made from antler (16), bone (3), and shell (11). Among the artifacts recovered are a fish-shaped pendant with pseudo-excise carving technique decoration and a Placard-type assegai (Rodanés et al., 2021).

The faunal remains are abundant. In an initial report, the identified taxa include deer, horse, Spanish ibex, lynx, and a small sample of bird remains. However, the European rabbit is the most prevalent species, accounting for over 97% of the total fauna (Blasco & Rodanés, 2009). The occupation levels defined as Badegoulian (level II) have dates that range from 22,925–22,632 to 21,714–21,330 years cal. BP, as shown in Table 1.

Materials and Methods

The material analyzed comprised of leporid remains that were found in a single unit, specifically unit 4C′ (1 × 1 m), from survey II (Fig. 2A). The remains were carefully recovered in their original position during the excavation, as well as through the process of sieving the sediments using sieves of widths 5 mm, 2 mm, and 0.5 mm.

Taxonomic and anatomical abundance were calculated using the following measurements: number of identified specimens (NISP), minimum number of elements (MNE), minimum number of individuals (MNI), and relative abundance (RA) (Andrews, 1990; Binford, 1978; Klein & Cruz-Uribe, 1984; among others).

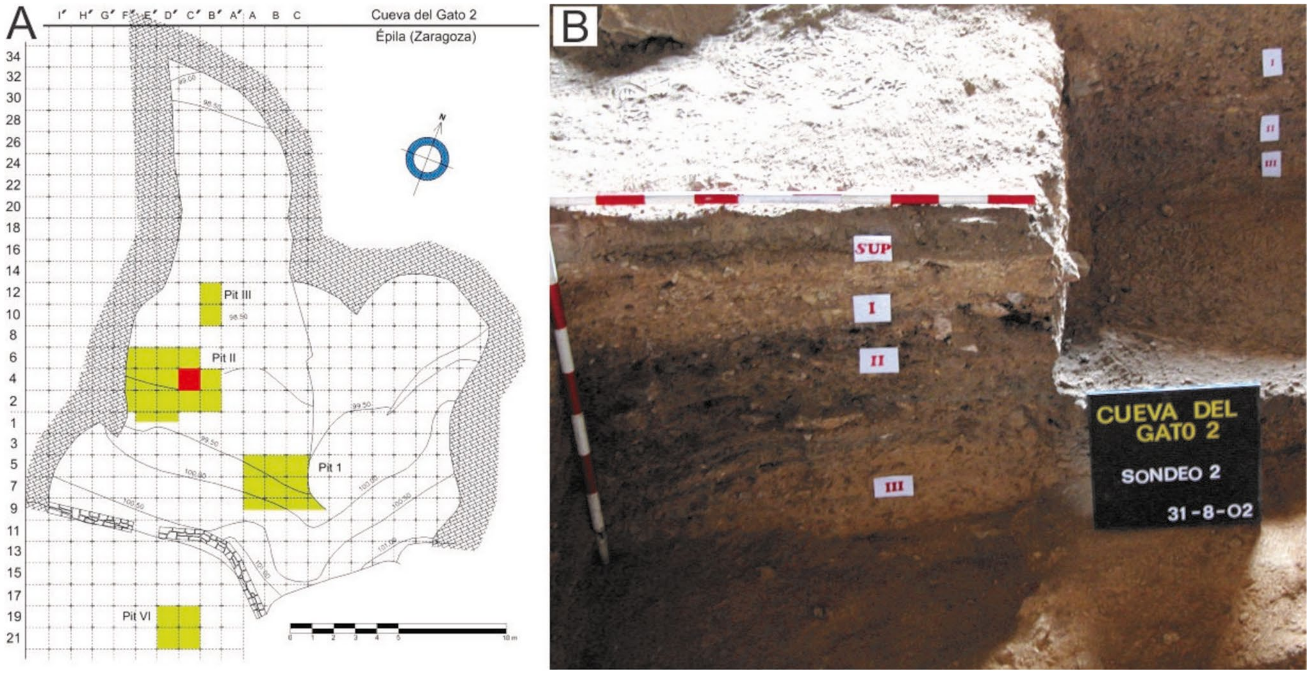

Fig. 2 Cueva del Gato 2 excavation. **A** Excavation plan of Cueva del Gato 2 site, in red Unit 4C′. **B** Stratigraphy of Cueva del Gato 2 site

Table 1 Radiocarbon dates obtained from level II of the Cueva del Gato 2 site (Rodanés et al., 2021)

Level	Material	Method	Reference	Date (BP)	Date cal* (BP) 1-sigma
II	Charcoal	AMS	GrA-30684	18,850 ± 100	22,925–22,632
II	Charcoal	AMS	GrA-22505	18,650 ± 140	22,771–22,414
II	Charcoal	AMS	GrA-22503	18,260 ± 130	22,339–22,089
II	Charcoal	AMS	GrA-30683	18,090 ± 90	22,162–21,936
II	Bone	AMS	GrA-42226	17,700 ± 70	21,714–21,330

*Radiocarbon dates were calibrated using OxCal.v4.4 (Bronk Ramsey, 2021) and the IntCal20 atmospheric curve (Reimer et al., 2020)

The integrity of each specimen was recorded using the breakage categories proposed by Lloveras et al. (2008a). Additionally, to assess the differential representation within each element, the frequency at which each portion was represented in the NISP was estimated for certain bones. To do this, the diagnostic zones proposed by Münzel (1988) were modified and utilized. The long bones and metapodials were categorized as follows: complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal epiphysis (SDE), and distal epiphysis (DE). The scapula was categorized as follows: complete (C), glenoid cavity (GC), glenoid cavity + neck (GCN), neck + fossa (NF), and neck (N). The innominate was categorized as follows: complete (C), acetabulum (A), acetabulum + ischium (AIS), acetabulum + ischium + ilium (AISIL), acetabulum + ilium (AIL), ischium (IS), and ilium (IL). The mandible was categorized as follows: complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB), branch (B), and condylar process (CP). The skull was categorized as follows: complete (C), incisive bone (IB), maxilla (IBM), zygomatic arch (AZ), and neurocranium (NC). The frequency of representation for each zone was standardized as percentages and divided into four categories (0–25%, 26–50%, 51–75%, 76–100%).

In the case of specimens corresponding to isolated molars and incisors, their abundance was evaluated by adding them to those found inside the alveoli. Therefore, the total NISP does not match the sum of the NISP of the elements presented in the anatomical table.

To assess the representation of various groups of elements (axial, cranial, and postcranial), the following indexes were utilized (Álvarez et al., 2012; Andrews, 1990; Lloveras et al., 2008b, 2016; Pelletier et al., 2020):

- $\mathrm{PCRT/CR\%} = [(\mathrm{PCRT} \times 32)/((\mathrm{PCRT} \times 32) + (\mathrm{CR} \times 184))] \times 100$, being PCRT the postcranial elements (limbs, vertebrae, and ribs; 184 bones per individual) and CR the cranial elements (mandibles, maxillae, and teeth; 32 bones and tooth per individual);
- $\mathrm{PCRAP/CR\%} = [(\mathrm{PCRAP} \times 32)/((\mathrm{PCRAP} \times 32) + (\mathrm{CR} \times 114))] \times 100$, being PCRAP is the limb elements (long bones, scapula, innominate, patella, metapodials, carpals, tarsals, and phalanges; 114 bones per individual) and CR is the cranial elements;
- $\mathrm{PCRLB/CR\%} = [(\mathrm{PCRLB} \times 32)/((\mathrm{PCRLB} \times 32) + (\mathrm{CR} \times 10))] \times 100$, being PCRLB the number of long bones (humerus, radius, ulna, femur and tibia; 10 per individual) and CR the number of cranial elements;
- $\mathrm{AUT/ZE\%} = [(\mathrm{AUT} \times 12)/((\mathrm{AUT} \times 12) + (\mathrm{ZE} \times 98))] \times 100$, being AUT is the number of autopodial elements (metapodials, carpals, tarsals, and phalanges; 98 bones per individual) and ZE the zygopodia and stylopodia (tibia, radius, ulna, humerus, femur, patella; 12 bones per individual);
- $\mathrm{AN/PO} = [(\mathrm{AN} \times 14)/((\mathrm{AN} \times 14) + (\mathrm{PO} \times 16))] \times 100$, being AN the number of anterior elements (scapula, humerus, radius, ulna, and metacarpals, 16 bones per individual), and PO the posterior elements (coxal, femur, tibia, and metatarsal, 14 bones per individual);
- $\mathrm{Z/E} = [(\mathrm{Z} \times 4)/((\mathrm{Z} \times 4) + (\mathrm{E} \times 6))] \times 100$, being Z the zygopodia (tibia, radius, and ulna; 6 bones per individual) and E the stylopodia (femur and humerus; 4 bones per individual).

To determine the age structure of the bone assemblage, we followed the methodology outlined by O'Connor (2000:94–95), which takes into account the state of skeletal fusion. For our analysis, we divided the sample into two groups based on the timing of fusion: an early fusion group and a late fusion group. To establish the fusion schedule, we referred to the documented fusion patterns of the European *Oryctolagus cuniculus* (see Jones, 2006: Table 1). Additionally, we categorized the bone assemblage into three age groups:

- Juveniles (< 3 months): characterized by the presence of unfused distal epiphysis in their humerus and tibia bones.
- Subadults (3 to 9 months): characterized by the difference in the proportion of unfused elements between the late fusing group (adult to old) and the proportion of unfused elements of the early fusing group (infants), assuming that the specimens of both fusion groups derive from the same population (O'Connor, 2000).
- Adults (> 9 months): characterized by the complete fusion of the proximal epiphysis of the humerus and tibia bones.

The age profile of Cueva del Gato 2 was plotted on a ternary graph and compared with the data obtained for different assemblages of natural and cultural origin reported by Pelletier et al. (2019). Zones proposed by Discamps and Costamagno (2015) and modified by Pelletier et al. (2019) were considered. However, since bone fusion does not allow differentiation between adult and senile individuals, the zone names proposed by Discamps and Costamagno (2015) were modified to consider the age categories mentioned earlier.

We conducted an evaluation to determine if the density of the elements played a role in differential preservation. To achieve this, we analyzed the correlation between bone density and the relative abundance of each element using Spearman's correlation coefficient. The bone density values proposed by Pavao and Stahl (1999) were utilized for this analysis.

All specimens were observed using both the naked eye and an optical stereo microscope (Olympus SZ60) at magnifications ranging from × 6 to × 45. The survey of taphonomic variables included examining chemical alterations, such as the presence of manganese, carbonate concretions, and cave soil corrosion, as well as identifying trampling, weathering, root, and rodent marks (Behrensmeyer, 1978; Fernández-Jalvo & Andrews, 2016; Lyman, 1994). Additionally, tooth marks were observed and counted, with marks classified as punctures, pits, scores, furrows, and crenulated edges (Binford, 1981; Haynes, 1980). Although these mark types were originally defined for carnivorous mammals, the possibility that the modifications were caused by human agents was also considered due to the origin of the assemblage. Various authors have studied these types of marks, although the criteria for differentiating them from marks made by other animals are generally ambiguous (Fernández-Jalvo & Andrews, 2011; Landt, 2007; Saladié et al., 2013; among others). When present, digestive corrosion was recorded and categorized as light, moderate, heavy, or extreme (Fernández-Jalvo & Andrews, 1992; Lloveras et al., 2008a, 2008b). Damage caused by fire was also recorded through visual examination and described as light (yellow-light brown), moderate (brown), or strong (black) following Shipman et al. (1984), Stiner et al. (1995), and Krap et al. (2019). Burnt areas were recorded for each skeletal element, specifying the portion (e.g., distal, proximal) and side.

The type of fracture was classified as green, dry, modern, anthropic, or indeterminate (Johnson, 1985). Fractures were considered to be of anthropic origin when they exhibited associated features such as impacts or flaking negatives.

Cut or scrape marks were analyzed according to the criteria proposed by Binford (1981; see also Nilssen, 2000). The following aspects were recorded for each specimen: location, number, frequency, grouping or isolation, orientation with respect to the bone axis, and intensity defined as strong, medium, or light based on mark depth (Lloveras & Nadal, 2020). To aid in interpreting the activity represented by each mark and identifying human butchery patterns, the marks were documented using the QGIS software (version 3.22.16). Templates of the different elements of the rabbit skeleton were created, providing detailed views of the posterior, anterior, lateral, and medial faces of long bones.

Results

A total of 2319 specimens of *Oryctolagus cuniculus* were identified. The minimum number of individuals estimated from the tibia was 121. In terms of skeletal parts, the tibia had the highest representation, followed by the femur and mandible. The forelimb, skull, and pelvis had medium representation. The vertebrae, ribs, and distal parts of the limbs had low representation (Table 2; Fig. 3).

The analysis of breakage revealed that the long bones are primarily represented by the diaphysis, except for the ulna, which is better represented by the proximal portion. The

Table 2 Anatomic representation of *Oryctolagus cuniculus*

Skeletal element	NISP	NISP%	MNE	MNI	RA%
Mandible	229	9.65	219	115	90.49
Maxilla	226	9.53	110	61	45.45
Incisor	71	2.99	71	12	9.77
Upper molar	16	0.67	16	2	1.1
Lower molar	151	6.36	151	16	12.47
Humerus	160	6.74	149	75	61.57
Radius	134	5.65	123	62	50.82
Ulna	116	4.89	89	49	36.77
Femur	256	10.79	228	114	94.21
Tibia	272	11.47	241	121	99.58
Patella	-	-	-	-	-
Scapula	144	6.07	128	67	52.89
Innominate	180	7.59	152	76	62.8
Metacarpal	15	0.63	15	2	1.23
Metatarsal	112	4.72	109	14	11.26
Phalanx 1/2	8	0.34	8	1	0.19
Phalanx 3	-	-	-	-	-
Calcaneum	19	0.8	19	9	7.85
Astragalus	6	0.25	6	6	2.47
Carpal/tarsal	-	-	-	-	-
Cervical vertebra	11	0.46	11	3	1.81
Atlas vertebra	4	0.17	4	4	3.3
Axis vertebra	3	0.13	3	3	2.47
Thoracic vertebra	21	0.88	20	2	1.37
Lumbar vertebra	83	3.5	73	11	8.61
Sacrum	2	0.08	2	2	1.65
Rib	61	2.57	61	3	2.1
Long bone	72	3.03	-	-	-
Total	2372	100	-		

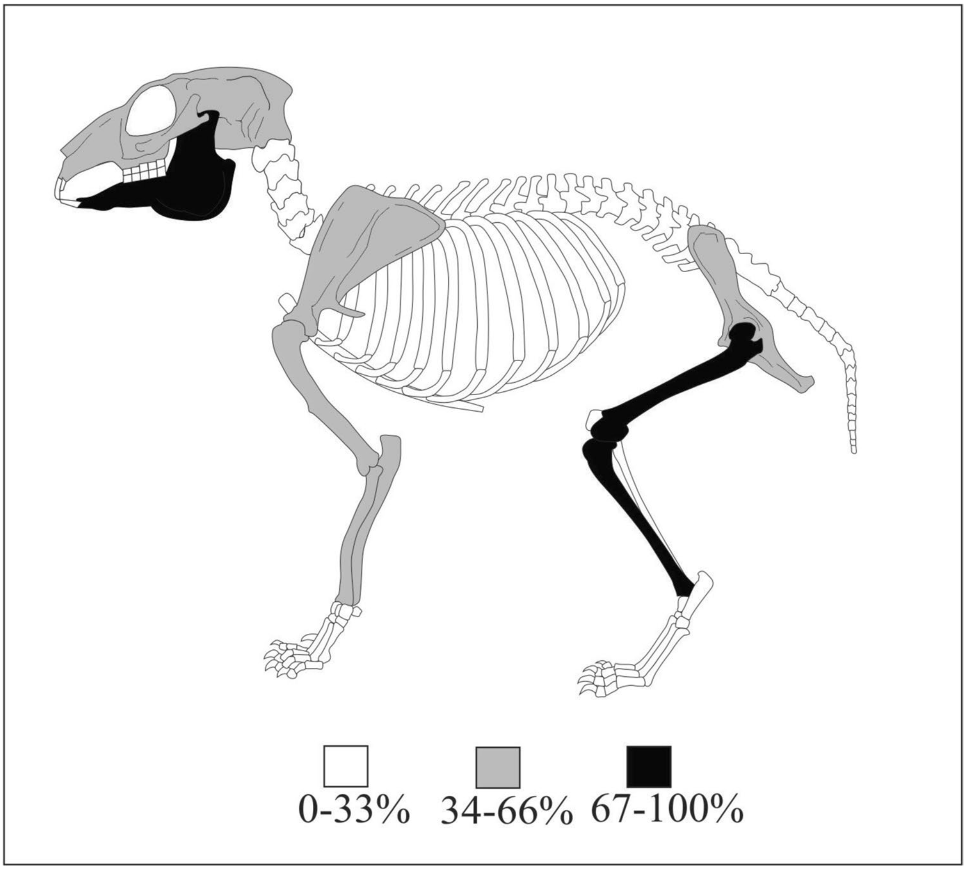

Fig. 3 Graphical anatomic representation of *Oryctolagus cuniculus* RA%

metapodial bones are mostly complete. In terms of the mandible and cranium, the body with the incisive part is the most well-preserved, along with the neurocranium and maxillae. In the case of the innominate, complete elements and the acetabulum with the ilium or ischium are predominant. The glenoid cavity with the neck is the most well-preserved portion of the scapula. Among the vertebrae, the body is the most abundant part. The phalanges, calcaneus, and astragalus are complete in all cases. However, the majority of rib specimens are fragmented. Lastly, teeth were complete in almost all cases, both in their original position and outside the alveoli (Table 3).

The results of the indices evaluating the representation of different groups of elements can be seen in Table 4. PCTR/CR indicates a higher representation of the cranial portion compared to the postcranial. PCRAP/CR shows a higher representation of the cranial portion compared to the limbs. PCRLB/CR indicates a significantly higher representation of the long bones compared to the cranial skeleton. AUT/ZE indicates a much lower representation of the autopodium compared to the zygopodium/stylopodium. AN/PO indicates a lower representation of the forelimb compared to the hind limb. Z/E shows a similar representation of the zygopodium and stylopodium.

The fusion state was assessed for a total of 766 specimens, which accounted for 33% of the analyzed sample. Out of these, 130 (17%) were identified as subadult individuals, while 636 (83%) were classified as adults. When considering only the diagnostic elements for age estimation (humerus and tibia; $n = 432$), the fusion state could be determined in 40 cases (9%). The results of the portions that could be assigned to either the early or late fusing groups are presented in Table 5. Specifically, 7.14% were found to be younger than 3 months, 21.44% were between 3 and 9 months, and 71.42% were older than 9 months (Table 5; Fig. 4).

Correlation analyses between relative abundance and bone density revealed a positive but non-significant result ($\mathrm{Rs} = 0.26769$; $p = 0.050348$). However, it is worth noting that this value is very close to the threshold of significance, suggesting that, in general, elements with lower bone density are less represented.

In regards to taphonomic agents, a significant occurrence of specimens containing manganese was observed. Trampling, chemical agents, rodent, and root marks were found in minimal proportions, approximately 1% or less. Additionally, gastric corrosion was detected in eight instances, classified as moderate to heavy. Tooth marks were identified in 13% of the specimens, primarily consisting of scores, pits, and furrows (Table 6; Fig. 5).

A significant portion of the specimens are fractured, with a majority of them being green fractures. This is followed by anthropic cylinders, and to a lesser extent, dry,

Table 3 Breakage categories recorded in the sample. Detailed references for these categories can be found in the Materials and Methods section

L. bones/metap	C		PE		PES		S		SDE		DE	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Humerus	2	1.25	1	0.62	-	-	146	91.25	3	1.87	8	5
Radius	22	16.41	-	-	50	37.3	41	30.59	21	15.67	-	-
Ulna	15	12.93	2	1.72	69	59.48	24	20.68	6	5.17	-	-
Femur	-	-	8	3.12	24	9.37	215	83.98	4	1.56	5	1.95
Tibia	-	-	6	2.2	5	1.83	243	89.33	9	3.3	9	3.3
Metacarpus	15	100	-	-	-	-	-	-	-	-	-	-
Metatarsus	99	88.39	-	-	8	7.14	1	0.89	4	3.57	-	-
Mandible	*N*	%	Cranium	*N*	%	Inn	*N*	%	Scap	*N*	%	
C	52	22.7	C	-	-	C	40	22.22	C	44	30.55	
IP	3	1.3	IB	43	19.02	A	3	1.66	GC	-	-	
MBI	141	61.57	IBM	-	-	AIS	30	16.66	GCN	70	48.61	
MB	16	6.98	M	82	36.28	AISIL	42	23.33	NF	13	9.02	
MBB	10	4.36	AZ	4	1.76	AIL	44	24.44	F	17	11.8	
B	-	-	NC	97	42.92	IS	7	3.88				
CP	7	3.05				IL	14	7.77				
Vertebrae	*N*	%	Phal. 1/2	*N*	%	Phal. 3	*N*	%	Ribs	*N*	%	
C	30	24.19	C	8	100	C	-	-	C	3	4.91	
VB	84	67.74	P	-	-	P	-	-	F	58	95.08	
VF	-	-	D	-	-	D	-	-				
SP	10	8.06	F	-	-	F	-	-				
Patella	*N*	%	Carp/tars	*N*	%	Calc	*N*	%	Astr	*N*	%	
C	-	-	C	-	-	C	19	100	C	6	100	
F	-	-	F	-	-	F	-	-	F	-	-	
Tooth	In situ	Isolated										
	Incisors	Upp. molars	Lo. molars	Incisors	Upp. molars	Lo. molars						
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	9	100	3	100	41	100	24	38.7	13	100	102	92.72
F	-	-	-	-	-	-	38	61.29	-	-	8	7.27

Table 4 Results of the indices that evaluate the representation of different groups of elements

Index	Result
PCTR/CR	30.65%
PCRAP/CR	38.55%
PCRLB/CR	82.40%
AUT/ZE	2.26%
AN/PO	37.66%
Z/E	44.47%

Table 5 *Oryctolagus cuniculus* long bone fusion sequence

	Element portion	Unfused	Fused
Early-fusing	Distal humerus	0	13
	Distal tibia	2	13
Total		2 (7.15%)	26 (92.85%)
Late-fusing	Proximal humerus	1	2
	Proximal tibia	3	8
Total		4 (28.57%)	10 (71.42%)

indeterminate, anthropic, and modern fractures (Table 6). An interesting observation is that scapulae, in 25 cases (17.36%), have a fractured acromion. Instances of thermal alteration in the specimens were very rare. Cut marks were found on eight percent of the remains, which are further described below (Table 6; Fig. 5). Additionally, four tibia diaphysis with technological modifications were documented. In general, these elements exhibit the removal of the epiphyses and the reduction of cortical tissue through longitudinal scraping (Table 6).

A total of 196 bones (8.5% of the total) exhibit cut marks. The scapula had the highest occurrence rate, with 60% of the specimens showing cut marks. Other bones with notable frequencies of cut marks include the long bones, mandible, maxilla, innominate, metatarsal, and lumbar vertebrae. To

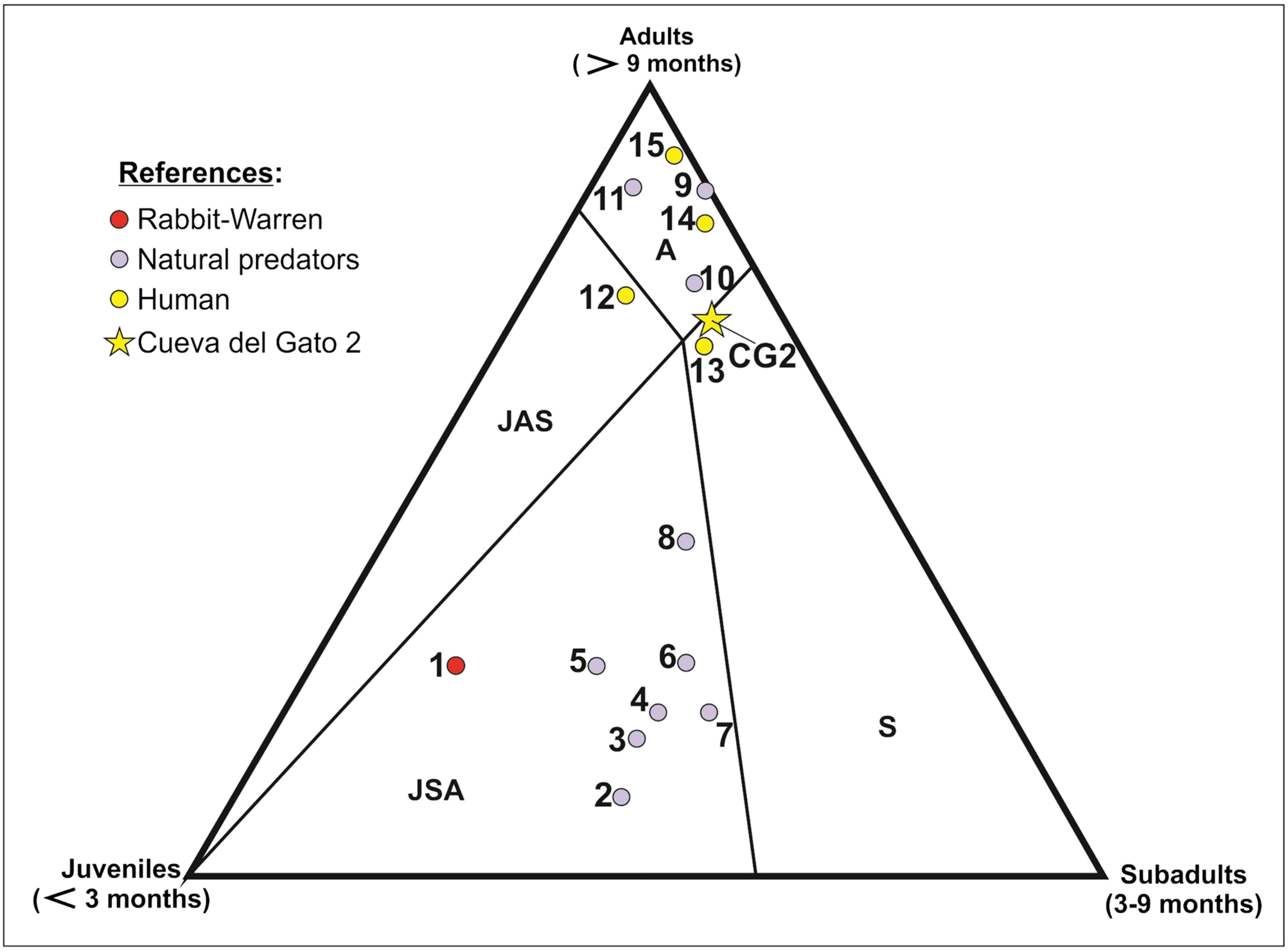

Fig. 4 Age profile of the Cueva del Gato 2 (CG2) and other assemblages containing rabbit remains. References: (1) Rabbit-warren, Les Six Chemins (Pelletier et al., 2016); (2) Eagle-owl, Penya la Zafra (Sanchis Serra, 2000); (3) Eagle-owl, Aigües de Busot II (Sanchis Serra, 2000); (4) Eagle-owl, Aigües de Busot I (Sanchis Serra, 2000); (5) Fox accumulation (outside the den) (Sanchis Serra, 2000); (6) Fox accumulation, El Conjunto de Coveta 3 (Sanchis Serra & Pascual Benito, 2011); (7) Fox den (inside the den) (Sanchis Serra, 2000); (8) Egyptian vulture, Benaxuai Caves (Sanchis Serra et al., 2014); (9) European badger, Bettant I (Mallye et al., 2008); (10) European badger, Bettant VIII (Mallye et al., 2008); (11) Dhole; Vaufrey (Cochard, 2007); (12) Human; Anecrial (Brugal, 2006); (13) Human; Les Canalettes (Cochard et al., 2012); (14) Human; Pie Lombard Mousterian complex (Pelletier et al., 2019); (15) Human; La Faurelie II (Cochard, 2004). Figure modified from Pelletier et al. (2019)

a lesser extent, cut marks were also observed on the tibia, ulna, mandible, humerus, and femur (Table 7).

Butchery marks on the skull are rare and mostly found in specific areas, such as the zygomatic and nasal processes. These marks correspond to skinning activities (Fig. 6). On the mandible, there are oblique marks on both the lateral and medial sides of the molar section (Fig. 6).

Only one specimen from the lumbar vertebrae presents cut marks, which are obliquely located on the dorsal side of the transverse processes. These marks are associated with filleting activities. In the scapula, cut marks can be found on all sides of the element, with different orientations, particularly on the posterior, lateral, and medial side of the neck, as well as in the glenoid cavity and acromion. Additionally, there are smaller percentages of longitudinally oriented scrape marks on the blade sector. These marks primarily correspond to the disarticulation of the forelimb and the filleting of the meat attached to this element (Fig. 7). The humerus exhibits cut marks on all sides of the diaphysis, with oblique and transverse orientations. Some specimens also display scrape marks on the diaphysis, oriented longitudinally. The activities associated with these marks are mainly filleting and scraping (Fig. 7). On the radius, the cut marks are mainly located on the anterior and lateral aspect of the diaphysis and distal epiphysis, with a predominantly transverse orientation. One specimen shows a longitudinal scrape mark on the medial diaphysis. These processing marks suggest filleting and disarticulation activities (Fig. 7). The ulna displays transverse and oblique cut marks on the diaphysis on all sides. One specimen exhibits a scrape mark on the medial diaphysis of the lateral face (Fig. 7).

Table 6 Taphonomic variables recorded in the sample

	Taphonomic effect	Number	Percent
	Manganese	868	37.4
	Trampling	3	0.13
	Carbonate concretion	4	0.17
	Cave soil corrosion	32	1.38
	Root mark	1	0.04
	Rodent mark	6	0.26
Tooth mark	Puncture	23	0.99
	Pit	108	4.65
	Score	117	5.04
	Furrow	76	3.27
	Crenulated edge	39	1.68
	Total	292	12.6
Digestive corrosion	Moderate	6	0.26
	Heavy	2	0.09
	Fracture	1959	84.5
Fracture type	Green	1215	45.44
	Dry	418	15.63
	Modern	59	2.21
	Anthropic	156	5.83
	Anthropic (cylinder)	632	23.64
	Indeterminate	194	7.26
	Thermal alteration	8	0.34
	Cut mark	196	8.45
	Technological modification	4	0.17

Only a few innominates display cut marks, primarily on the lateral and ventral sides of the ilium, ischium, and acetabulum. These marks suggest activities involving filleting and disarticulation (Fig. 8). On the femur, the marks are mainly found on the anterior and posterior sides of the diaphysis, indicating filleting activities. Additionally, marks were observed on the neck and lesser trochanter, potentially linked to disarticulation activities. On the tibia, the marks are concentrated on all sides of the diaphysis, with a longitudinal orientation to the bone's main axis. These marks are likely a result of filleting (Fig. 8). Lastly, the metatarsals exhibit transverse cut marks on the diaphysis of the lateral, ventral, and dorsal faces, which are associated with skinning activities.

Discussion

Rabbits were a significant prey for human groups along the Iberian Mediterranean coast. The Pleistocene–Holocene transition period saw an increase in hunting pressure on this species, as evidenced by Jones (2006), Fa et al. (2013), Carbajo Arana and Fernández Rodríguez (2020), and Real (2020). However, the use of rabbits as a resource in the interior lands of the Iberian Peninsula has received little attention. Recent findings have shed light on this topic. The Upper Paleolithic levels of Cueva del Gato 2, associated with the Badegoulian culture, reveal human occupations in the interior of the Iberian Peninsula during the harsh climatic conditions of the Last Glacial Maximum (LGM: 26–19 kyr cal BP; Clark et al., 2009). Archaeobotanical findings associated with these occupations support the existence of an open and cold environment (Badal et al., 2012). Recent discussions have highlighted that sites close to Cueva del Gato 2, such as Charco Verde II in Guadalajara show that late Pleistocene hunter-gatherers were capable of adapting to diverse landscapes and environments, including highlands and extremely cold regions (Aragoncillo-del-Río et al., 2023).

In contrast to Charco Verde II, the occupations of Cueva del Gato 2 indicate that during the LGM, rabbits were the primary resource exploited at the site, with a significantly higher number of individuals compared to other mammals such as deer, horses, Spanish ibex, and lynx. Other sites, such as Peña de Estebanvela (Yravedra & Andrés, 2013; Yravedra et al., 2019), Cueva Chaves (Castaños, 1993; Utrilla and Laborda Lorentea, 2018), and Peña Capón (Alcaraz Castaño et al., 2013; Yravedra et al., 2016; Alcaraz-Castaño et al., 2021), located in caves and rock shelters near large Iberian valleys away from the coast, also provide evidence of rabbit exploitation during Solutrean and Magdalenian times (Fig. 1).

In addition to being a recurring item in the human diet, leporids also serve as prey for carnivorous mammals and raptors (Brugal, 2006; Lloveras et al., 2008a, 2008b; Rodríguez-Hidalgo et al., 2013; Rufà Bonache, 2017; among others). Additionally, due to their burrowing habits and gregarious behavior, their remains may be found in assemblages as a result of natural deaths (Pelletier et al., 2016, 2017, 2020). Therefore, a common issue addressed in European Paleolithic sites with rabbit specimens is determining the agents or processes that led to their accumulation (e.g., Hockett, 1999; Lloveras et al., 2010). The rabbit remains discovered in Cueva del Gato 2 exhibit taphonomic patterns that support their human origin. There are numerous indications of skinning, disarticulation, and filleting, as well as a clear pattern of intentional fracture of the long bones to extract the marrow.

The significant number of rabbits (MNI 121) discovered in a single sampling unit (1 m^2) at Cueva del Gato 2 highlights the importance of these leporids in sustaining the human groups that inhabited the site towards the end of the LGM. Even this number would increase if it were possible to consider the fusion state of the tibia, which was not achievable since most of the portions corresponded to diaphyseal sectors. The mortality profile of Cueva del Gato 2 was based on a very small sample in relation to the number of individuals represented in the site. This aspect would be intimately

Fig. 5 Examples of the modifications recorded in the sample. **A** Manganese on the radius; **B** puncture on distal epiphysis of the femur; **C** extreme digestion on the femur; **D** scraping marks on the scapula; **E** cut marks on the scapula; **F** examples of rabbit shaft cylinders (femora); **G** examples of rabbit shaft cylinders (tibiae)

Table 7 Number and frequency of specimens with cut marks (CM)

Element	NISP	NISP with CM	%NISP with CM	CM frequency	CM mean
Skull	226	5	2.21	14	2.8
Mandible	229	16	6.99	44	2.75
Lumbar vertebra	83	1	1.20	19	19
Scapula	144	87	60.42	624	7.17
Humerus	160	11	6.88	44	4
Radius	134	8	5.97	55	6.87
Ulna	116	12	10.34	38	3.16
Innominate	180	4	2.22	8	2
Femur	256	16	6.25	96	6
Tibia	272	33	12.13	124	3.75
Metatarsal	112	3	2.68	6	2
Total	2319	196	8.45	1072	5.46

related to the butchery that humans performed on the prey, which reduced the identifiability of the specimens. In this sense, the systematic gnawing of the epiphyses of the long bones for the consumption of the marrow destroyed these portions and limited the possibility of estimating the degree of fusion of most of them. Nevertheless, the representation of the mortality profile in the tripolar graph (Fig. 4) places it in a borderline zone between subadults (S) and adults (A), which is evidence that there was a selective human hunting strategy that prioritized rabbits that would have completed their body development, beyond bone maturation. This strategy is typical of assemblages created by humans and large predators like badgers and dholes (Cochard, 2007; Mallye et al., 2008; Pelletier et al., 2019). Selective hunting of adult individuals

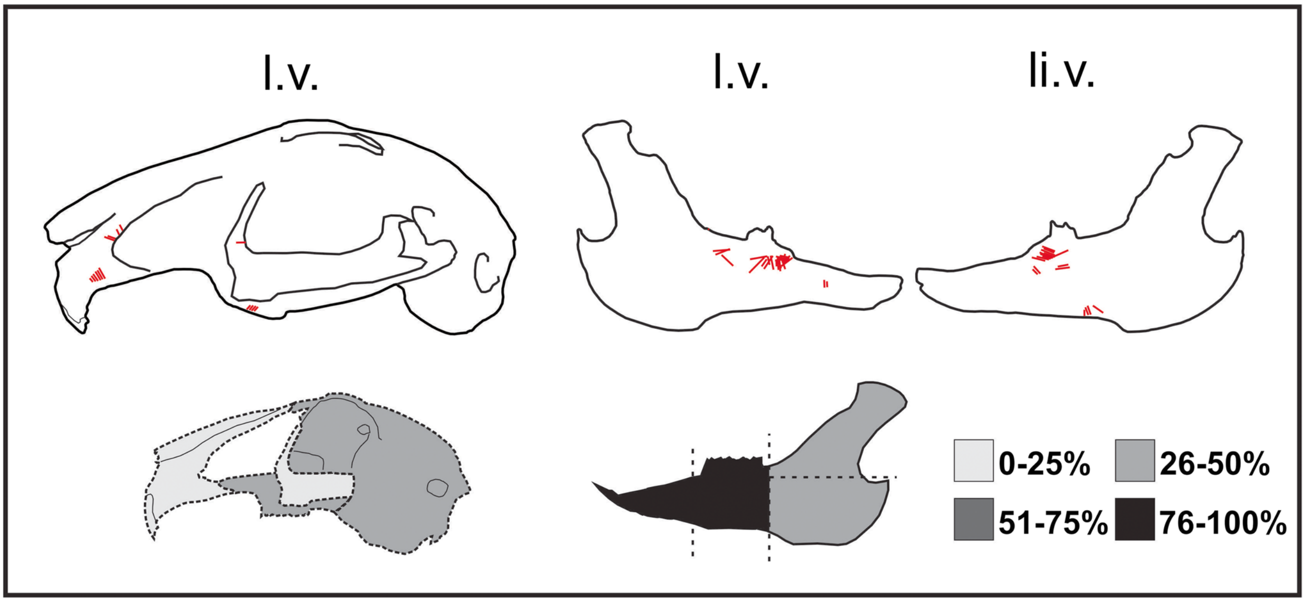

Fig. 6 GIS templates showing the location cut marks on skulls and mandibles, and representation of the frequency for each portion. References: l.v., lateral view; li.v., lingual view

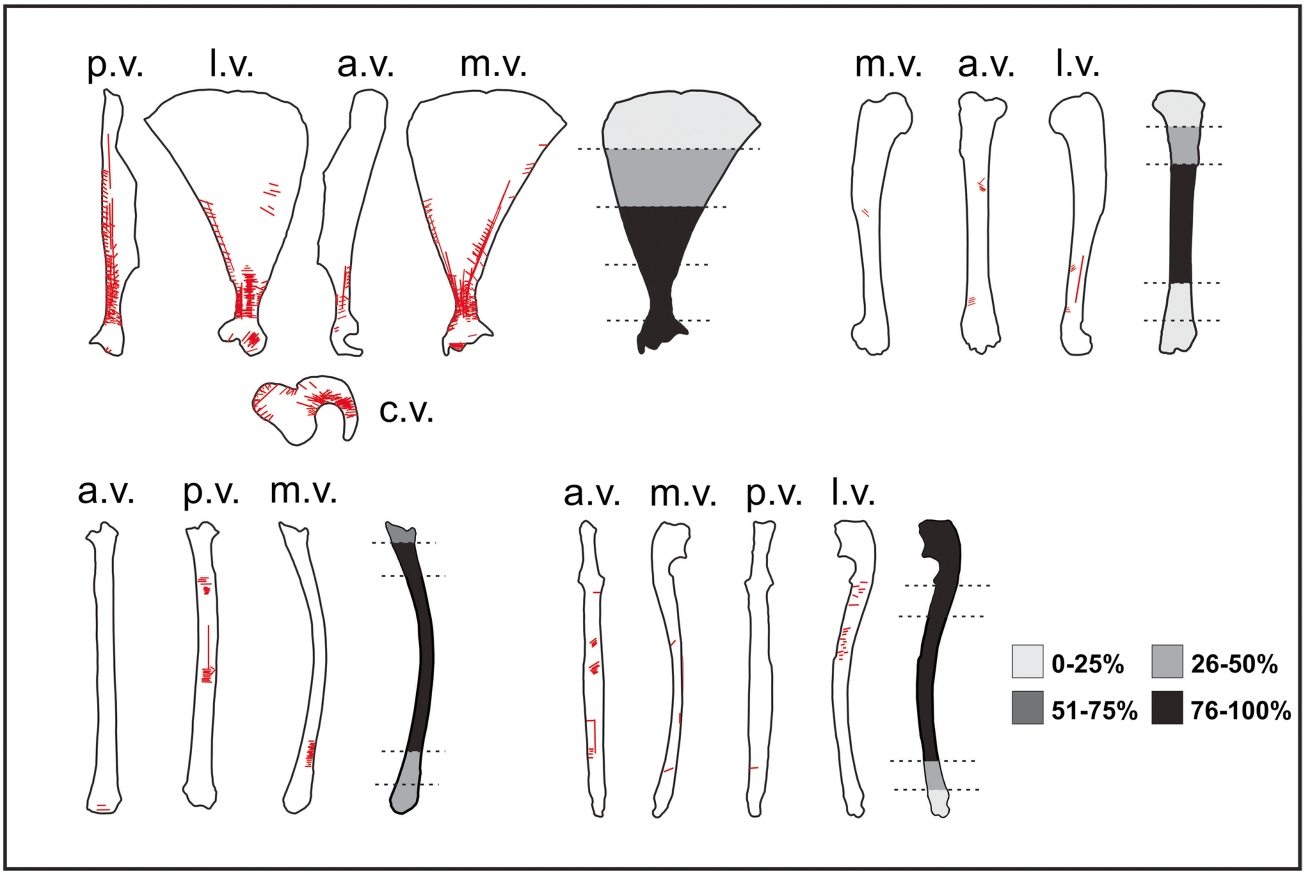

Fig. 7 GIS templates showing the location cut marks on the scapula, radius, and ulnae, and representation of the frequency for each portion. References: p.v., proximal view; l.v., lateral view; a.v., anterior view; m.v., medial view; c.v., cranial view

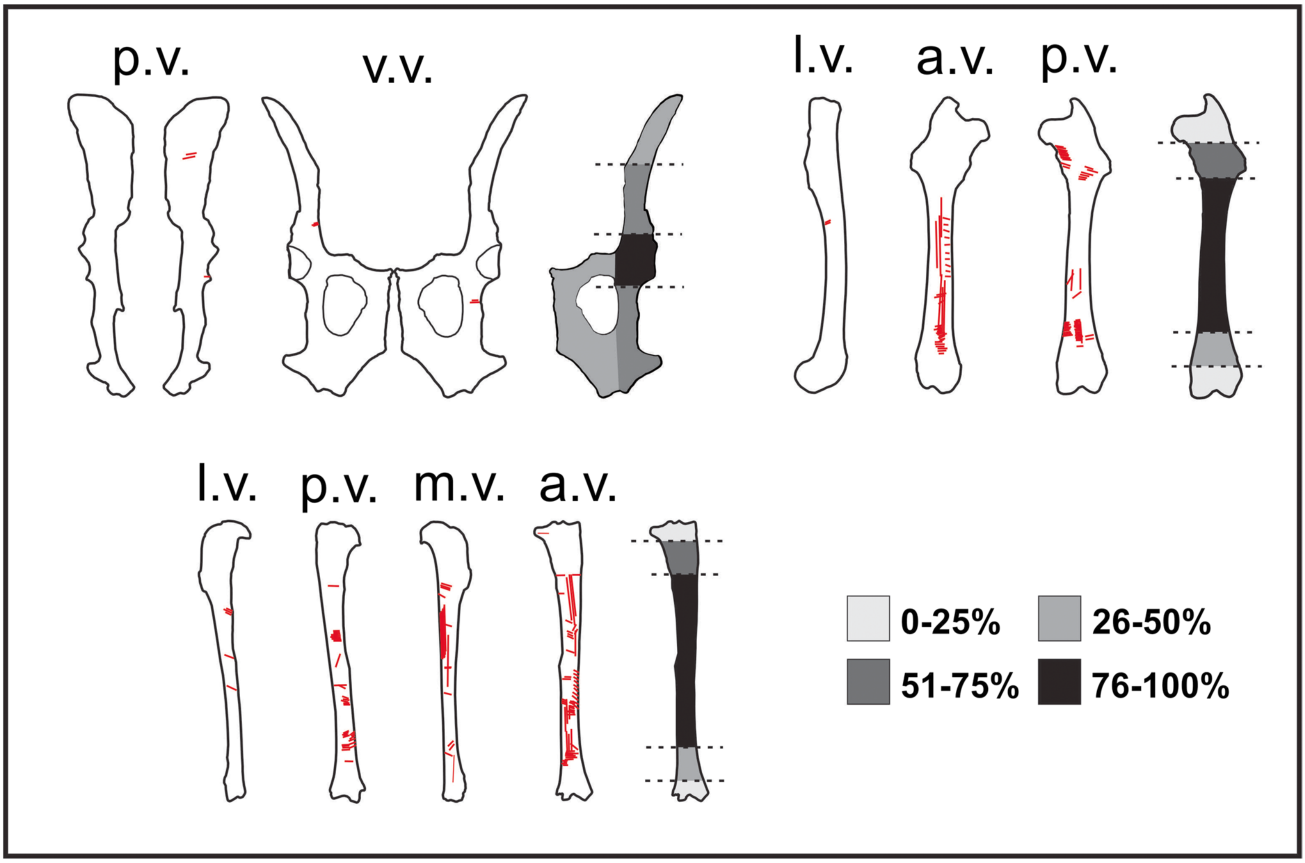

Fig. 8 GIS templates showing the location of cut marks on the innominate, femur, and tibia, and representation of the frequency for each portion. References: p.v., posterior view; p.v., ventral view; l.v., lateral view; a.v., anterior view; m.v., medial view

has been consistently observed in most Iberian and southern French sites (Fig. 4). This type of hunting differs from the targeting of other small predators such as foxes and eagle-owls (Sanchis Serra, 2000; Sanchis Serra & Pascual Benito, 2011), which focus on immature individuals with smaller body sizes tan subadults and adults (Pelletier et al., 2016, 2019).

According to Jones (2006), the age profile of rabbits taken isolated should primarily consist of adult individuals. However, the presence of young individuals suggests that some of them were captured in or near the rabbit warrens. While the current sample size for age estimation is limited and there is a lack of direct evidence regarding the hunting method at the site, ethnographic and historical data suggest that Paleolithic hunters likely employed traps, nets, or snares to capture their prey (Hockett & Haws, 2002; Jones, 2006; Stiner & Munro, 2002). It is possible that cooperative hunts were used in conjunction with rabbit mass trapping, as well as individual hunting of a few prey per event. Another option is a mass capture with the selective discarding of individuals based on age, as suggested by Cochard and Brugal (2004).

The skeletal profile of the analyzed sample shows a distinct representation of the rabbit, with some anatomical units being well represented while others are scarce or absent. This variation in representation could be attributed to differential preservation or human activities such as processing and discarding. The taphonomic analysis results indicate that, overall, the bones are in very good condition and there is no significant evidence of bone destruction caused by natural processes. The most common diagenetic modification observed in the bones is the deposition of manganese, which does not impact the skeletal representation and is characteristic of the cave's specific sedimentary environment and matrix. Therefore, the differential skeletal representation is likely more closely associated with human butchery and consumption. In general, there is a higher prevalence of the mandible and hind limb, while the forelimb, skull, and girdles have a moderate representation. The relative frequency of vertebrae (particularly cervicals and thoracic), ribs, and autopodium is quite low, and patellae and third phalanges are completely absent.

The scarcity of elements from the podium region, as well as caudal vertebrae and patellae, is a common occurrence in rabbit accumulations that are of human origin. The reason for the absence of these elements is believed to be their attachment to the leather during transportation, as these bones tend to remain with the skins. This has been supported by studies conducted by Callou (2003), Cochard (2004), and Cochard and

Brugal (2004). As suggested by Pelletier et al. (2019) for the Pié Lombard site, the infrequent presence of these elements suggests that the tanning process may have taken place in a different area of the site or outside of the cave. Additionally, the presence of cut marks on prominent areas of the skull, the lateral face of the mandible, and the metatarsals further confirms the skinning activities were carried out on the rabbits (Fig. 6).

On the other hand, the infrequent occurrence of ribs and vertebrae may be attributed to increase butchering of the less dense axial skeleton. Some authors have also observed the grinding of these parts for the production of bone meal (Bean, 1974; Cochard & Brugal, 2004; Haws et al., 2006; Hockett, 1991; Real, 2020, Rufà Bonache, 2017). Another possibility is that these anatomical units were specifically chosen for drying and followed different trajectories during storage (Cochard, 2004; Cochard & Brugal, 2004; Rosado-Méndez, et al., 2016; Sanchis et al., 2017). Ethnographic studies have described the practice of meat drying with smoke (Bean, 1974; Spier, 1978). According to Cochard and Brugal (2004), this strategy would result in an assemblage with a low occurrence of axial elements, numerous processing marks, and a reduced number of burned bones. The bone assemblage at Cueva del Gato 2 exhibits consistent and patterned skinning marks on the raw rabbits. The diaphyses of the long bones (humeri, tibiae, and femurs) and the shoulder girdle display filleting and scraping marks, indicating that the muscle bundles were obtained in their raw state. This supports the hypothesis of meat drying for delayed consumption.

The occurrence of specimens with thermal alteration is quite rare. It is likely that the rabbits were cooked indirectly through contact with fire, using methods like boiling or smoking. A comparable scenario was noted at the Les Canalettes site in southern France (Middle Paleolithic), leading to the suggestion that carcasses were boiled instead of roasted (Cochard, 2004). In experimental cases where rabbits were roasted, burnt areas were predominantly found on the skeletal extremities, which were less protected by flesh (Lloveras et al., 2009).

The percentage of cut marks recorded in Cueva del Gato 2 is similar to that found in most leporid assemblages of anthropogenic origin, as noted by Real (2020). The dismemberment pattern indicates that the scapula was separated from the humerus. Over 60% of the specimens display signs of butchery, such as filleting and scraping on the neck, as well as disarticulation on the cranial view of the glenoid cavity (Fig. 9). In some cases, these actions also resulted in the removal of the acromion. The extensive butchery of the shoulder girdle contrasts with the minimal modifications observed on the innominate bones. The pelvic girdles likely underwent different processes and methods of butchery. It is speculated that the scapulae, along with the long bones, were defleshed in their raw state, while the coxal bones were defleshed after boiling, a technique that left minimal marks on them. Only a few femur specimens showed marks on the neck and lesser trochanter, which may be associated with disarticulation activities.

The limited occurrence of epiphyses of long bones hinders the understanding of rabbit dismemberment patterns at the site. However, cut marks and related fractures were identified, particularly on the forelimb, indicating the presence of this process. The butchery pattern of the radius-ulna differs from that of the other long bones, possibly due to its low bone marrow content, which allowed the survival of the proximal portion of this element. Although no cut marks were found on the epiphyses, bone damage was observed in 20% of the olecranon, which could be attributed to the disarticulation of the radius-ulna from the humerus (Fig. 10). Laroulandie et al. (2008) suggest that hyperextension is an alternative technique to cutting and fracturing, facilitating bone disarticulation. Through studies involving birds and medium and small-sized ungulates, these authors observed that due to the elbow's morphological characteristics, disarticulation by hyperextension results in the fracture of the olecranon fossa of the humerus and the proximal radioulnar joints.

The consumption of bone marrow is indicated by the frequent occurrence of cylinders. Many femora, tibiae, and humeri show signs of epiphysis breakage, which suggests that biting or bending actions were used to extract the raw marrow. This pattern has been observed in various sites where this prey was consumed (e.g., Martínez-Polanco et al., 2016; Pérez Ripoll, 2005). According to Hockett (1991), the tibia of leporids contains the highest amounts of marrow, which may explain its prevalence in the assemblage. Similar to other Iberian and southern French sites, the marrow from long bones was consistently utilized, likely to compensate for the low fat content of the meat from these mammals. While there is no direct evidence of intentional skull breaking for brain consumption, the absence of complete elements could be linked to the use of this resource, as suggested in other sites with evidence of rabbit butchery (Cochard & Brugal, 2004). Lastly, the presence of cut marks on the lingual portion of the mandibles indicates processing and consumption of the tongue (Fig. 6).

Another aspect to consider is the presence of tooth marks and scarce specimens with signs of digestion. Both carnivorous mammals and humans could have made these types of modifications. In terms of digestion, this variable can be similar for both agents (Crandall & Stahl, 1995). Like other authors, we can hypothesize that humans may have consumed some bone fragments while eating rabbits (Gordón, 2017; Real, 2020; Sanchis et al., 2016; among others). However, it is also possible that some of the specimens in the assemblage entered through the feces of small carnivorous mammals, such as foxes, as has been observed at other sites (e.g., Rosado-Méndez et al., 2015). Regarding tooth marks, similar or higher frequencies have been documented in experimental and ethnoarcheological studies

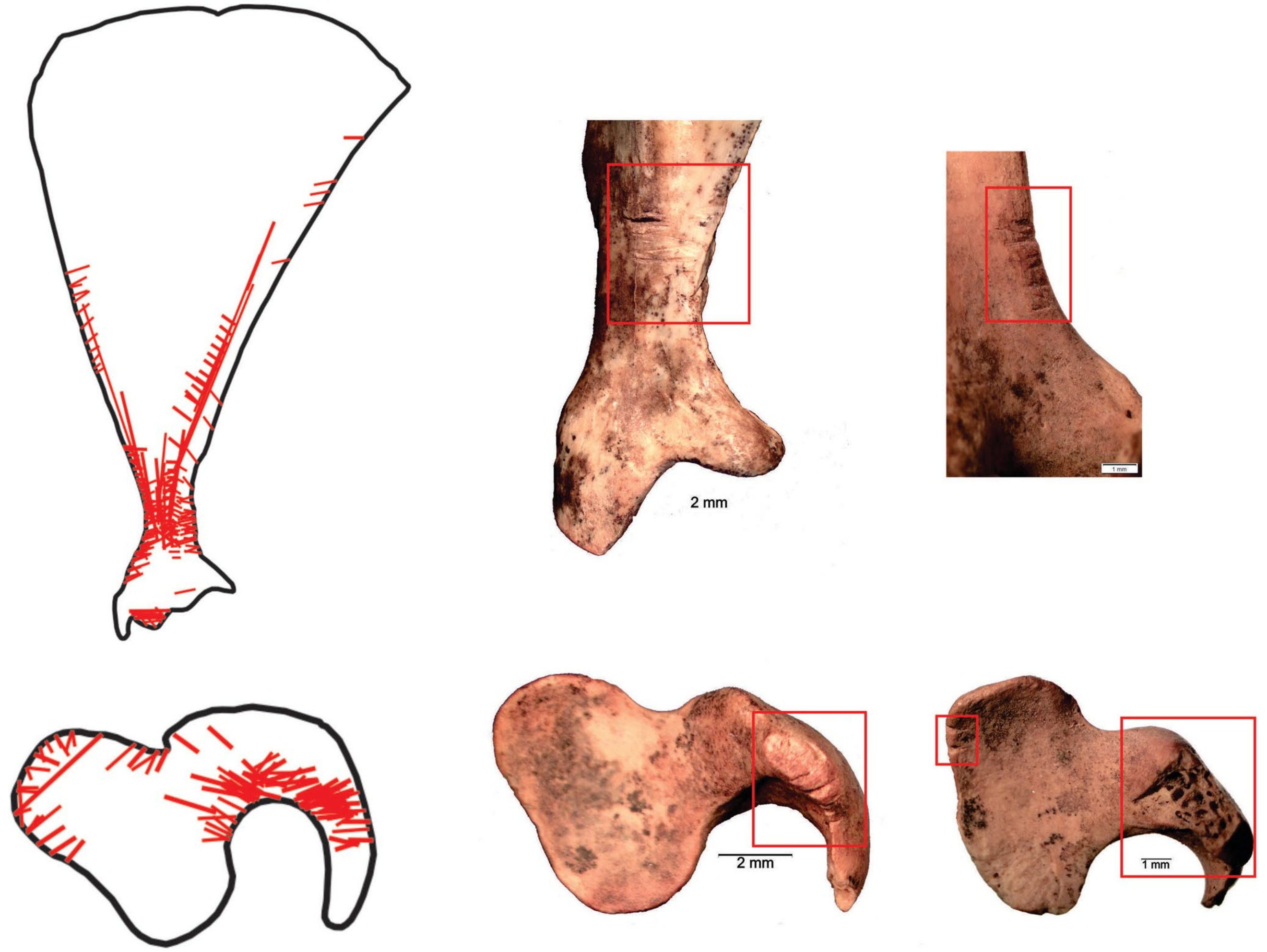

Fig. 9 Examples of scapulae exhibiting cut marks on the neck and acromion

involving human modifications (e.g., Landt, 2007; Lloveras et al., 2009). The location of these marks aligns with human behavior, such as chewing on the ends of long bones. In summary, the high frequency of anthropogenic cut marks and fractures leads us to believe that tooth marks were likely also created by humans when consuming rabbit portions although a minor impact from a non-human secondary predator cannot be totally ruled out.

Conclusions

The exploitation of small fauna, particularly rabbits, was significant during the upper Paleolithic in the Mediterranean and Atlantic coast of the Iberian Peninsula (Cacho et al. 1995; Villaverde et al. 1996; Aura et al. 2002, 2009; Morales 2013). The ecological conditions in these regions were favorable for the growth of rabbit populations during the cold phases of the Late Pleistocene (Callou, 2003; Pelletier, 2018). However, in the interior of Iberia, sites like Cueva del Gato 2 demonstrate that the consumption of rabbits was also crucial and involved systematic butchery practices. Although most of these contexts are found in caves and rock shelters at high elevations, they are all located near valleys. The archeological evidence indicates that the inhabitants utilized both the mountain and valley environments. In Cueva del Gato 2, rabbits were the primary resource, along with larger ungulates like deer and horses, forming the basis of subsistence. The systematic hunting, butchery, and consumption of rabbits observed in the Badegoulian levels of the site suggest that the interior valleys were effectively occupied during the cold periods of the upper Paleolithic. The model of population dynamics (Straus, 1991; Straus et al., 2000) that assumes occasional use of the interior of Iberia during intense cold periods, as previously proposed based on human occupations in the Madrid Basin and southeastern foothills of the Central System mountain range (Alcaraz-Castaño, 2015) needs to be reconsidered. As previously mentioned,

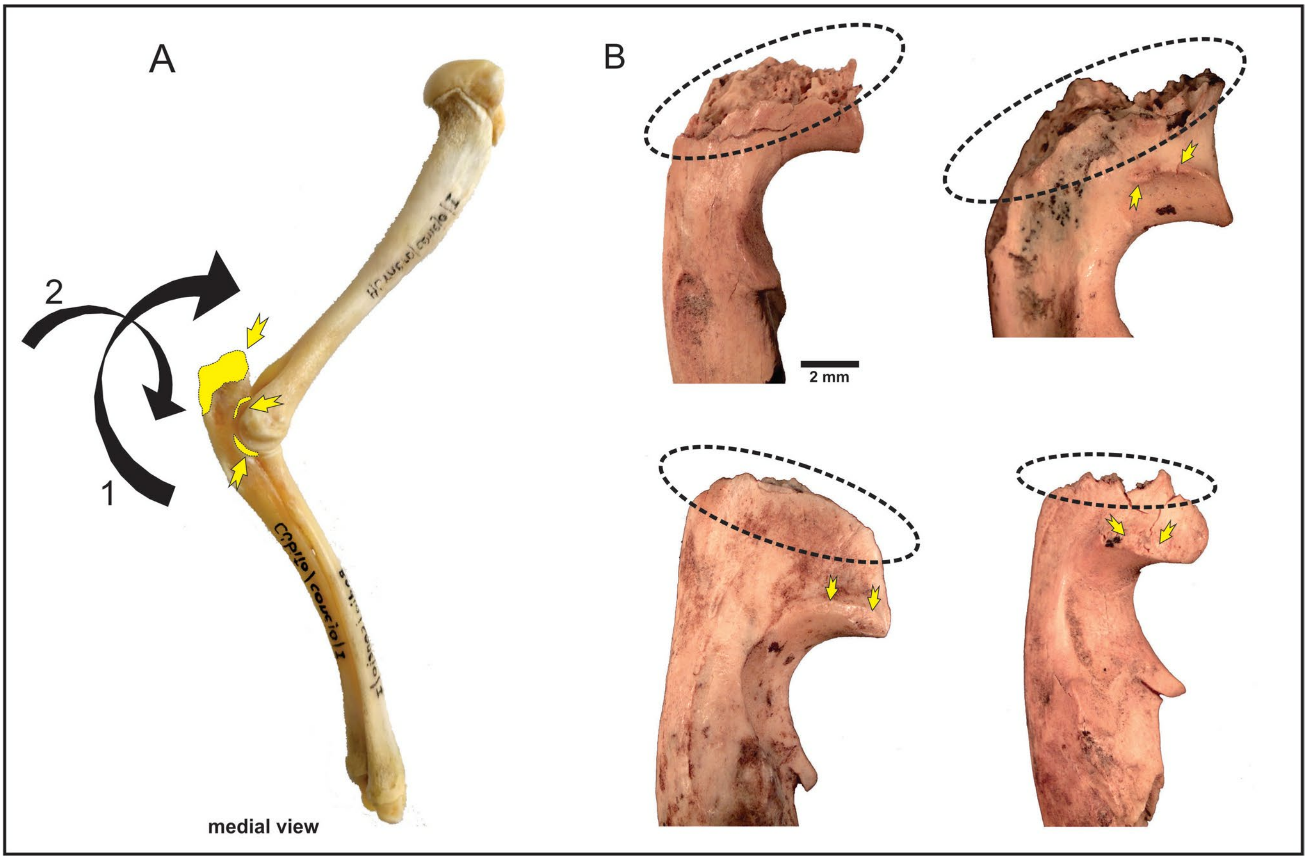

Fig. 10 **A** The process of disarticulation by hyperextension and bone sectors that would be damaged (modified from Laroulandie et al., 2008); (1) movement in the anteroposterior direction; (2) lateral rotation associated with ulnar morphology. **B** A rabbit ulna recovered in Cueva del Gato 2 showing damage to the olecranon and the articular facet

it has been recently noted that late Pleistocene hunter-gatherers were capable of adapting highlands and extremely cold regions (Aragoncillo-del-Río et al., 2023). Accordingly, in this study, we propose that large inland valleys, such as the Ebro Basin south of the Pyrenees or the upper Tajo Basin in the central plateau, would have served as environmental refuges capable of sustaining permanent habitats for animal and human populations during the most severe moments of the Last Glacial Maximum.

Acknowledgements We are grateful to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), INCUAPA-CONICET, Universidad Nacional del Centro de la Provincia de Buenos Aires, Spanish Government, Gobierno de Aragón, and Generalitat de Catalunya. We would like to express our sincere gratitude to the three reviewers for their valuable comments, which have significantly contributed to the improvement of this work.

Author contributions C.K. conducted the analysis of the faunal remains, prepared figures 1, 5-9, and wrote the main manuscript text. M.C.A. prepared figures 3-4 and wrote the main manuscript text. J.N.L. prepared figure 2 and wrote the main manuscript text. J.M.R. conducted the fieldwork and the sample condinioning. L.L. prepared figure 2 and wrote the main manuscript text. All authors reviewed the manuscript.

Funding This work has been funded by research project PID2020 113960 GB-100 of MINECO (Spanish Government) and SGR2021-00337 (Generalitat de Catalunya). *Consejo Nacional de Investigaciones Científicas y Técnicas* (CONICET) granted an external scholarship to one of the authors (CK) through which part of the analysis of the faunal analysis was carried out.

Declarations

Competing Interests The authors declare no competing interests.

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