

Predator Agents and Leporid Accumulations: the Case of Terrasses de la Riera dels Canyars (Gavà, Barcelona, Spain)

Nadibuska Y. Rosado-Méndez · Lluís Lloveras ·
Joan Daura · Jordi Nadal · Montserrat Sanz

Published online: 17 June 2014

© Springer Science+Business Media New York 2014

Abstract Terrasses de la Riera dels Canyars (Gavà, Barcelona, Spain) is an Upper Pleistocene fluvial deposit dated to 39.6 cal. ka BP with a few Aurignacian stone tools. Faunal remains recovered in this site contained, apart from large mammals, an important assemblage of leporid remains. This taxon (especially the European rabbit, *Oryctolagus cuniculus*) is very abundant in most Paleolithic and Epipaleolithic sites in the Iberian Peninsula. For this reason, it has been proposed that this kind of small prey must have played a key role for human prehistoric communities. Since a considerable group of non-human predators can contribute in the formation of this kind of assemblages, identification of different taphonomic signatures produced by other predators must be implemented. Based on actualistic studies carried out on modern leporid remains produced by nocturnal and diurnal raptors, terrestrial carnivores, and humans, diagnostic taphonomic indicators of different predators were identified. In this paper, the patterns observed for these predators are applied to the taphonomical analysis of archaeological leporid remains from level middle lutitic unit (MLU) of Terrasses de la Riera dels Canyars in order to understand the origin of the accumulation. The study was carried out based on the analysis of the age of death, anatomical representation, degree of breakage and digestion, types of fractures, cut marks, tooth and beak marks, and burnt marks. Our results suggest that small terrestrial carnivores (probably Iberian lynx) were the main

N. Y. Rosado-Méndez (✉) · L. Lloveras · J. Daura · J. Nadal · M. Sanz

SERP (Seminari d'Estudis i Recerques Prehistòriques), Departament de Prehistòria, Història Antiga i Arqueologia, Facultat de Geografia i Història, Universitat de Barcelona, C/Montalegre 6, 08001 Barcelona, Spain
e-mail: nyrosadomendez@gmail.com

L. Lloveras

School of Archaeology and Ancient History, University of Leicester, University Road, Leicester LE1 7RH, UK

J. Daura · M. Sanz

GRQ (Grup de Recerca del Quaternari) from SERP (Seminari d'Estudis i Recerques Prehistòriques), Departament de Prehistòria, Història Antiga i Arqueologia, Facultat de Geografia i Història, Universitat de Barcelona, C/Montalegre 6, 08001 Barcelona, Spain

responsible agent for the leporid accumulations at Terrasses de la Riera dels Canyars with a very sporadic and punctual activity of humans. Canyars moves away from other coetaneous Mediterranean Iberian sites where the anthropic systematic use of small prey beginning in the Early Upper Paleolithic has been described.

Keywords Early Upper Paleolithic · Aurignacian · Terrasses de la Riera dels Canyars · Leporid remains · *Oryctolagus cuniculus* · Small prey taphonomy

Introduction

Leporids (rabbits and hares), and especially the European rabbit (*Oryctolagus cuniculus*), are one of the most abundant taxa among faunal remains in most Upper Paleolithic and Epipaleolithic archaeological sites in the Iberian Peninsula (Aura *et al.* 2002; Hockett and Haws 2002). However, up until recently their occurrence has been undervalued in archaeological research because they were considered of little importance to human populations (Davidson 1972; Morales *et al.* 1998; Villaverde and Martínez Valle 1992). Over the last decades, studies on this type of small prey have become a major focus of interest for many researchers (Cochard 2004a, b; Cochard *et al.* 2012; Cochard and Brugal 2004; Hockett 1995, 1996, 1999; Hockett and Haws 2002; Jones 2006; Lloveras *et al.* 2008a, b, 2009a, b, 2010, 2011, 2012a, b; Martínez Valle 1996; Pérez Ripoll 1992, 2001, 2004, 2005; Schmitt and Juell 1994; Sanchis 2000, 2010; Sanchis and Fernández Peris 2008). The substantial introduction of leporids into the human diet from the Upper Paleolithic is interpreted as an indication of diet widening by many authors (Aura *et al.* 2002, 2009; Hockett and Haws 2002; Jones 2006; Stiner and Munro 2002; Pérez Ripoll 2001; Villaverde *et al.* 1996). This trend is revealed by the presence of cut marks and other anthropogenic pieces of evidence, such as characteristic bone breakage patterns (e.g., the presence of significant amounts of long bone cylinders) and combustion brands, on rabbit bones from this period (Aura *et al.* 2002; Cochard and Brugal 2004; Hockett and Haws 2002; Manne and Bicho 2009; Pérez Ripoll 1992, 2001, 2004, 2005; Villaverde *et al.* 1996). Although several studies have recently demonstrated that leporid exploitation can be found in even the oldest archaeological sites (Cochard *et al.* 2012; Rodríguez-Hidalgo *et al.* 2013a; Sanchis and Fernández Peris 2008), their consumption seems to clearly increase from Upper Paleolithic coinciding with the arrival of anatomically modern *Homo sapiens* (Aura *et al.* 2002). To explore Early Upper Paleolithic rabbit accumulations is of particular interest, in order to understand shift dynamics in human subsistence activities and to assess at what point the substantial introduction of leporids into the human diet is related to anatomically modern *Homo sapiens* strategies.

The origin of the archaeological leporid remains is a key issue underlying this debate, as small preys (and especially rabbits) are an important source of food for a large number of non-human predators (Delibes and Hiraldo 1981). Terrestrial carnivores and raptors are regular visitors to caves and rock shelters where their prey leftovers, pellets, or scats may accumulate. In addition, leporid accumulations could be intrusive as a result of natural death in their burrows (Mallye 2011). In fact, taphonomic studies on archaeological assemblages have shown that they are often the product of combinations of the activity of different anthropogenic and/or non-

anthropogenic agents (Hockett and Haws 2002; Lloveras *et al.* 2010, 2011; Pérez Ripoll 2004; Rodríguez-Hidalgo *et al.* 2013a; Sanchis and Fernández Peris 2008). Therefore, in order to understand human subsistence activities in the past, it is essential to establish how a given faunal assemblage was accumulated. With such an aim, over the last years, systematic actualistic studies on modern leporid remains originated by natural death, terrestrial carnivores, raptors and humans have been carried out in order to identify the corresponding taphonomic signatures (Lloveras *et al.* 2008a, 2008b, 2009a, 2009b, 2012a, 2012b, 2014; Rodríguez *et al.* 2013b). The data provided have proved to be a useful tool to be applied to the analysis of leporid archaeological remains (Lloveras *et al.* 2010, 2011).

In this paper, the patterns described in the actualistic studies mentioned above are applied to the assemblage of rabbit and hare remains recovered at the site Terrasses de la Riera dels Canyars (henceforth Canyars) located at Gavà (Barcelona) on the north-east of the Iberian Peninsula (Fig. 1a). This is an Early Upper Paleolithic site dated to 39.6 cal. ka BP, a period still not very well known in relation to small prey acquisition in the Iberian Peninsula because data are still very scarce. The aims of this work are twofold: first, to show how the taphonomical analysis of the remains may help in the identification of the agent responsible for the accumulation and second, to assess the anthropogenic role in the formation of such complex. The approach followed here provides an opportunity to add new data to the ongoing research on Upper Paleolithic small prey accumulations.

Archaeological Context

Canyars is a fluvial terrace (41° 17' 46" N, 01° 58' 47" E) located in an abandoned gravel pit in la Sentiú valley, one of the creeks originating at the foot of the Garraf massif and flowing into the beaches of the Mediterranean seaboard (Daura and Sanz 2009; Daura *et al.* 2013).

Canyars is located at the confluence of two creeks, Riera dels Canyars and Riera de Can Llong. The former is the main stream, and its distal part probably consisted of a floodplain crossed by channels, nowadays modified by farming activity (Daura *et al.* 2013). A total of nine lithological units have been described, consisting of a poorly sorted and coarse-grained complex of gradational and incised fluvial deposits. Paleontological and archaeological remains come from unit middle lutitic unit (MLU). The bone material deposited by carnivores on the excavated palaeochannel (LDU) was covered by a thick coarse and medium sandy mud of 30 to 50 cm transported in a event that preserved the material nearly *in situ*. After the formation of MLU, other upper units sealed the archaeological level (MLU), in posterior events (MDU, USU, and UDU) made of a matrix containing more massive elements as gravels and cobbles (Daura *et al.* 2013, Table 1).

Several charcoal samples were collected for radiocarbon dating, with a ^{14}C dating result of ~ 34.6 ^{14}C (~ 39.6 cal.) ka BP (overall mean age estimate from four radiocarbon dating by Daura *et al.* (2013)).

Faunal assemblage from Canyars comprise 42 taxa and >5,000 large mammal remains (including indeterminate shafts). Excluding rabbits and based on minimum number of individual (MNI) counts, the composition is dominated by herbivores

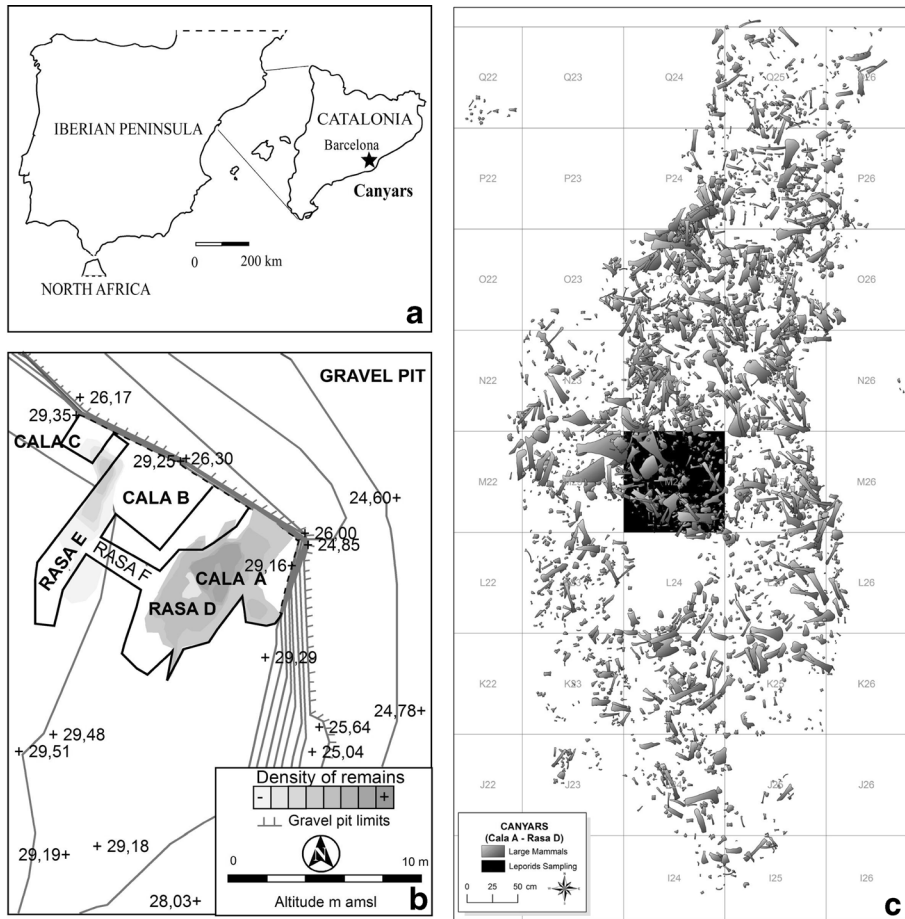


Fig. 1 The Canyars site. **a** Location of Canyars in the Iberian Peninsula. **b** Site plan showing the excavated areas. **c** Distribution of large mammals and position of leporidae sampling plotted against the excavation grid

(60 %) (including Artiodactyla, Perissodactyla, and Proboscidea), and carnivore (Carnivora) taxa are almost evenly represented (40 %). The most represented herbivores are the equids, *Equus ferus* (27) and *Equus hydruntinus* (4), followed by the large bovids, *Bos primigenius* (MNI 15); red deer, *Cervus elaphus* (MNI 7); and woolly rhino, *Coelodonta antiquitatis* (MNI 2). Wild boar, *Sus scrofa*; goat, *Capra* sp.; and elephantids, cf. *Mammuthus* sp., are present but with MNIs of 1 in all cases. Among the carnivores, lynx, *Lynx pardinus* (MNI 13), and hyena, *Crocuta crocuta* (MNI 13), are largely dominant while other taxa are merely present, such as lion, *Panthera leo* (MNI 2); leopard, *Panthera pardus* (MNI 1); wildcat, *Felis silvestris* (MNI 2); brown bear, *Ursus arctos* (MNI 1); wolf, *Canis lupus* (MNI 4); dhole, *Cuon alpinus* (MNI 1); and fox, *Vulpes vulpes* (MNI 3) (Daura et al. 2013).

The site has been used as a den mainly by hyenas, as the abundance of coprolites (NR 133), the dominance of juvenile individuals (12 of 13 MNI) of this taxon, and the anatomical representations demonstrate. Taphonomical study is still in progress, but herbivore bones show damage inflicted by hyenas, as whole cylinders, and the

anatomical representation suggests transport of selected body parts in herbivores, which contrasts with carnivore representation. The role of the carnivores is unknown (Daura *et al.* 2013).

Materials and Methods

The leporid remains analyzed here come from the site's archaeological unit MLU, Cala A (Fig. 1b). We have worked with a representative sample corresponding to the total amount of 3,458 rabbit remains from square M24 (Fig. 1c). The remains were collected manually during fieldwork and in the process of dry sieving through 5 to 1-mm superimposed meshes. Then, the material was sorted in La Guixera Laboratory (Castelldefels City Council), packed up, and studied and classified at the University of Barcelona.

The methodology used in the study follows that applied in previous works carried out with modern leporid assemblages originated by different predators (Lloveras *et al.* 2008a, b, 2009a, b, 2012a, b).

For the sake of clarity, the variables considered within each of the analytical parameters studied are presented below.

Anatomical Representation

Numbers of identified skeletal elements (N) were counted. Minimum number of elements (MNE) and MNI were calculated. Relative abundance (RA%) was also calculated for every skeleton element using the formula proposed by Dodson and Wexlar (1979). Proportions of skeletal elements were calculated using several indices (Lloveras *et al.* 2008a): postcrania in relation to crania (PCRT/CR, PCRLB/CR), loss of distal limb elements (AUT/ZE, Z/E) and the ratio of forelimb to hind limb elements (AN/PO) (see footnotes of Table 2 for abbreviations).

Breakage

Breakage patterns were described by the maximum length of all identified skeleton elements. The mean value and percentages of remains less than 1 mm were calculated. Percentages of complete elements, isolated teeth, and articulated elements were also estimated. For immature individuals, diaphyses of long bones with unfused epiphyses were considered as complete elements. Unfused proximal or distal epiphyses were classified as fragments of long bones. Long bone cylinders were also counted and registered.

Different breakage categories were used depending on bone type (Lloveras *et al.* 2008a):

- Humerus, radius, ulna, femur, tibia, metacarpus, and metatarsus were classified as complete (C), proximal epiphysis (PE), proximal epiphysis+shaft (PES), shaft (S), shaft+distal epiphysis (SDE), and distal epiphysis (DE).
- Innominate elements were recorded as complete (C), acetabulum (A), acetabulum+ischium (AIS), acetabulum+ischium+ilium (AISIL), acetabulum+ilium (AIL) ischium (IS), and ilium (IL).

- Scapula was registered as complete (C), glenoid cavity (GC), glenoid cavity+neck (GCN), neck+fossa (NF), and fossa (F).
- Elements composing the skull were registered separately. Cranium elements were classified as complete (C), incisive bone (IB), incisive bone+maxilla (IBM), maxilla (M), zygomatic arch (AZ), and neurocranium (NC), while mandible elements were categorized as complete (C), incisive part (IP), mandible body+incisive part (MBI), mandible body (MB), mandible body+branch (MBB), and condylar process (CP).
- Carpals, tarsals, patellae, calcanea, artragali, phalanges 1/2, phalanges 3 and ribs were sorted as complete (C) and fragment (F).
- Vertebrae were recorded as complete (C), vertebral body (VB), vertebral epiphysis (VE), and spinous process (SP).

Long bone cylinders (fragments of long bones with snapped ends as a result of consumption) were also recorded. Long bone fragments were also analyzed while attempting to distinguish green from dry fractures (Villa and Mahieu 1991).

Breakage of teeth was calculated separately for isolated and *in situ* elements. They were classified as complete (C) and fragment (F).

Bone Surface Damage

Damage to the bone was examined both macroscopically and microscopically. All of the skeletal remains were observed under light microscope ($\times 10$ to $\times 40$).

Digestion

Assessment of digestion damage on bone surface was based on methods proposed by Andrews (1990) and Fernández-Jalvo and Andrews (1992), and modified by Lloveras *et al.* (2008a, b). Five degrees of digestion were recorded: null (0), light (1), moderate (2), heavy (3), and extreme (4). These were valued separately for bone and dental remains.

Tooth/Beak Marks

Tooth/beak marks caused by predators were also identified and registered. Tooth/beak marks were classified as follows: tooth punctures (TPU), tooth pits (TPI), notches (NO), scoring (SCO), and crenulated/fractured edges (CRE) (Binford 1981; Haynes 1980, 1983). Data provided by other studies dealing with tooth/beak marks on small prey were also taken into account (Landt 2007; Lloveras *et al.* 2008a, b, 2009a, b, 2012a, b; Rodríguez-Hidalgo *et al.* 2013b; Sanchis 2012; Sanchis *et al.* 2011).

Cut Marks and Burnt Marks

Following the same methodology used in Lloveras *et al.* (2009b) with rabbit remains, cut marks were recorded according to the element type and the section of the bone. They were classified as longitudinal, transversal, or oblique depending on their orientation to the axis of the skeletal element on which they occurred.

Bones with burnt marks were identified by visual examination; color of burning damage was recorded (Stiner *et al.* 1995) and described as light, moderate, and strong. Areas with burnt damage were registered on each skeletal element according to portion and side.

Age Estimation

Age estimation of the individuals was based on epiphyseal fusion state of long bones, metapodials, scapulae, and innominate following Hale (1949) and Taylor (1959).

Results

Anatomical Representation

A total of 3,458 rabbit remains were identified, and hare remains were not found. Based on calcanei counts, the estimated MNI is 33. Table 1 shows the anatomical composition of the identified remains. The entire skeleton is well represented. The most abundant

Table 1 *Oryctolagus cuniculus* skeletal elements identified in level MLU from Terrasses de la Riera dels Canyars

Skeletal elements				
	N	N%	MNE	RA%
Mandible	106	3.1	49	74.2
Cranium	260	7.5	22	66.6
Incisors	112	3.2	112	56.6
Upper molars	221	6.4	221	55.8
Lower molars	170	5	170	51.5
Humerus	83	2.4	38	57.6
Radius	113	3.3	52	78.8
Ulna	125	3.6	46	69.7
Femur	68	2	38	57.6
Tibia	124	3.6	49	74.2
Patellae	2	0.1	2	3
Scapula	54	1.6	39	59
Innominate	127	3.7	53	80
Metacarpus	132	3.8	112	33.9
Metatarsus	300	8.7	231	87.5
Phalanges 1/2	338	9.8	323	28.8
Phalanges 3	95	2.7	95	15.9
Calcaneum	63	1.8	62	93.9
Astragalus	11	0.3	11	16.7
Carpal/tarsal	12	0.3	12	1.5
Vertebrae	433	12.5	320	21.1
Ribs	509	14.7	273	34.5
Total	458			

N number of skeletal elements, *N%* percentage of skeletal elements, *MNE* minimum number of elements, *RA%* relative abundance

Table 2 Proportions of different parts of the skeleton

Indices	Percent (%)
PCRT/CR	59.3
PCRAP/CR	56.9
PCRLB/CR	124.3
AUT/ZE	38.7
Z/E	128.9
AN/PO	60.2

PCRT/CR total numbers of postcranial (limb elements, vertebrae, and ribs) compared with total numbers of cranial elements (mandibles, maxillae, and teeth), *PCRAP/CR* limb elements (long bones, scapulae, innominate, patellae, metapodials, carpals, tarsals, and phalanges) compared with cranial elements (mandibles, maxillae, and teeth), *PCRLB/CR* long bones (humeri, radii, ulnae, femorae, and tibiae) compared with cranial elements (mandibles and maxillae), *AUT/ZE* autopodium elements (metapodials, carpals, tarsals, and phalanges) compared to zygopodium and stylopodium (tibiae, radii, ulnae, humeri, femorae, and patellae), *Z/E* zygopodium elements (tibiae, radii, and ulnae) compared to stylopodium (humeri and femorae), *AN/PO* humeri, radii, ulnae, and metacarpals compared with femorae, tibiae, and metatarsals

elements (N%) were vertebrae, ribs, phalanges 1/2, and metatarsal while patellae, scapulae, calcanei, astragali, and carpal/tarsals were the scarcest. Relative abundance of skeletal remains (RA%) is also shown in Table 1 and Fig. 2. The mean value (50.8 %) indicates an important loss of skeletal elements. The most represented elements are calcanei, metatarsus, long bones, mandibles, and cranium elements. Mandibles, scapulae, innominate, and teeth also show high percentages (Fig. 2). Skeletal elements like carpals/tarsals, patellae and phalanges 3 are poorly represented.

Relative proportions of skeletal elements are shown in Table 2. Results show the following:

- Indices that compare postcranial to cranial elements (PCRT/CR, PCRAP/CR) points to a deficiency in the numbers of postcranial remains (59.3 and 56.9).
- When cranial elements are compared to long bones (PCRLB/CR), the sample shows a deficit of cranial elements (124.3), indicating a good representation of long bones.
- Comparing upper limb elements (AUT/ZE), there is an important loss of distal elements (38.7). The value of the Z/E index shows a greater representation of elements corresponding to zygopodium (128.9).
- The AN/PO index reveals that posterior limb elements survived better than anterior limbs (60.2). The difference observed falls primarily on the various values obtained for metapodial elements.

Breakage

The size of the analyzed remains varies, with values of maximum length between 3 and 105.1 mm. The average maximum length was 17.7 and more than 83.3 % of the rabbit remains had length values over 10 mm. No articulated elements were found.

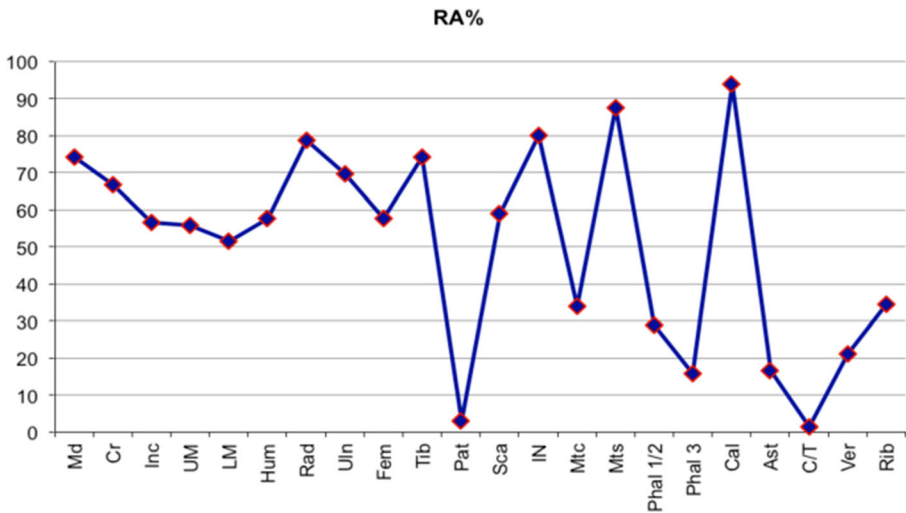


Fig. 2 Relative abundance of the different parts of the skeleton in Canyars leporid samples. *Md* mandible, *Cr* cranium, *Inc* incisors, *UM* upper molars, *LM* lower molars, *Hum* humerus, *Rad* radius, *Uln* ulna, *Fem* femur, *Tib* tibia, *Pat* patella, *Sca* scapula, *IN* innominate, *Mtc* metacarpals, *Mts* metatarsals, *Phal 1/2* phalanges 1/2, *Phal 3* phalanges 3, *Cal* calcaneum, *Ast* astragalus, *C/T* carpal/tarsal, *Ver* vertebrae, *Rib* ribs

The average percentage of complete elements was 39.6 % (Table 3; Fig. 3). If we consider only the long bones, the percentage of complete bones is reduced to 6 %. As expected, values obtained vary depending on the size of the skeletal elements. The smallest ones, like patellae, astragali, teeth, phalanges, and carpals/tarsals, appear less fragmented.

Breakage categories (Table 3) show that

- Cranial elements never appeared complete, and they were mainly identified by parts of the NC, AZ, M, and IB.
- Mandibles were mostly represented by body fragments (MB) and body fragments including the incisive part (MBI).
- For the innominate, it was common to find fragments containing the acetabulum (AIS, AIL, and AISIL).
- Scapulae never appeared complete. Most fragments contained the GCN.
- Eighty-seven percent of isolated teeth and all the *in situ* teeth were complete.
- Vertebrae were complete in 44.1 % of the cases. The fragments were represented mainly by the VB and by the SP.
- Ribs were always fragmented.
- All breakage categories were represented for limb bones. The humerus, femur, and tibia were complete in almost 10 % of cases. Femur remains are best represented by fragments of PES, whereas humeri and tibiae remains were well represented by S and SDE fragments. For the radius, fragments from the distal part (SDE) are more abundant. The ulna was especially represented by shaft fragments.
- Metacarpals were 68.2 % complete while metatarsals were 42.3 % complete.
- Astragali and patellae were all complete. Carpals/tarsals were always complete (91.7 %) and so were also calcanei (82.5 %), phalanges 1/2 (90.8 %), and phalanges 3 (91.6 %).

Table 3 Numbers and percentages of parts of the skeleton included in each breakage category

	C		PE		PE+S		S		S+DE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
Long bones and metapodials												
Humerus	9	10.8	8	9.6	5	6	32	38.6	28	33.7	1	1.2
Radius	3	2.7	0	0	31	27.4	30	26.5	49	43.4	0	0
Ulna	0	0	13	10.4	33	26.4	43	34.4	32	25.6	4	3.2
Femur	7	10.3	6	8.8	26	38.2	12	17.6	12	17.6	5	7.4
Tibia	12	9.7	8	6.5	23	18.5	42	33.9	34	27.4	5	4
Metacarpus	90	68.2	0	0	17	12.9	2	1.5	19	14.4	4	3
Metatarsus	127	42.3	0	0	104	34.7	7	2.3	62	20.7	0	0
Mandible	N	%	Cranium	N	%	Innominate	N	%	Scapula	N	%	
C	0	0	C	0	0	C	0	0	C	0	0	
IP	19	17.9	IB	33	12.7	A	3	2.4	GC	2	3.7	
MBI	26	24.5	IBM	1	0.4	AIS	18	14.2	GCN	30	55.6	
MB	27	25.5	M	41	15.8	AISIL	26	20.5	NF	12	22.2	
MBB	16	15.1	AZ	45	17.3	AIL	24	18.9	F	1	1.9	
CP	18	16.9	NC	140	53.8	IS	47	37	N	9	16.7	
Vertebrae	N	%	Phalanges 1/2	N	%	Phalanges 3	N	%				
C	191	44.1	C	307	90.8	C	87	91.6				
VB	129	29.8	F	31	9.2	F	8	8.4				
VE	10	2.3										
SP	103	23.8										
Patellae	N	%	Carpal/Tarsal	N	%	Calcaneum	N	%	Astragalus	N	%	Ribs
C	2	100	C	11	91.7	C	52	82.5	C	11	100	C
												7
												1.4

Table 3 (continued)

Teeth	0		F		1		8.3		F		11		17.5		F		0		0		F		502		98.6	
	In situ		Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
C	20	100	24	100	100	100	89	100	85	92.4	169	85.8	68	83.9												
F	0	0	0	0	0	0	0	0	7	7.6	28	14.2	13	16												

Long bones, metacarpals, 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 was classified as complete (C), incisive part (IP), mandible body+incisive part (MBI), mandible body (MB), mandible body+branch (MBB), and condylar process (CP). Cranium was classified as complete (C), incisive bone (IB), incisive bone+maxilla (IBM), maxilla (M), zygomatic arch (AZ), and neurocranium (NC). Innominate was classified as complete (C), acetabulum (A), acetabulum+ischium (AIS), acetabulum+ischium+ilium (AISIL), acetabulum+ilium (AIL), ischium (IS), and ilium (IL). Scapulae were classified as complete (C), glenoid cavity (GC), glenoid cavity+neck (GCN), neck+fossa (NF), fossa (F), and neck (N). Vertebrae were classified as complete (C), vertebral body (VB), vertebral epiphysis (VE), and spinous process (SP). Carpals/tarsals, patellae, calcanea, astragali, ribs, and teeth were classified as complete (C) and fragment (F)

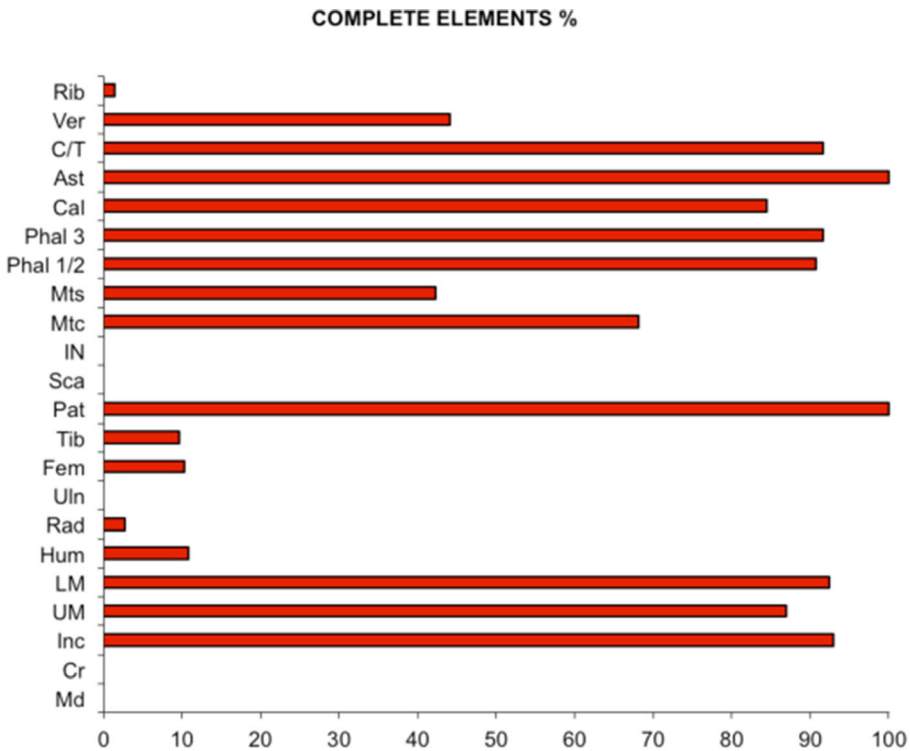


Fig. 3 Percentage of complete *Oryctolagus cuniculus* remains in MLU from Terrasses de la Riera dels Canyars. *Rib* ribs, *Ver* vertebrae, *C/T* carpal/tarsal, *Ast* astragalus, *Cal* calcaneum, *Phal 3* phalanges 3, *Phal 1/2* phalanges 1/2, *Mts* metatarsals, *Mtc* metacarpals, *IN* innominate, *Sca* scapula, *Pat* patella, *Tib* tibia, *Fem* femur, *Uln* ulna, *Rad* radius, *Hum* humerus, *LM* lower molars, *UM* upper molars, *Inc* incisors, *Cr* cranium, *Md* mandible

The study of long bone fragments revealed a significant number of shaft fragments, but the number of cylinders is scarce; only a total of ten cases were registered. Long bones (18.1 %) show green fractures (FF), 22.3 % show dry fractures (DF), while 59.6 % presented modern fractures (MF) due to the excavation and transport of the materials.

Digestion

Only 46 cases (1.3 %) from the sample presented digestion corrosion damage (Table 4); among them there were no dental remains. Of the 46 cases, most show a light degree of digestion (82.6 %). Moderate and heavy degrees of digestion were equally represented by 8.7 % (Fig. 4).

Tooth/Beak Marks

Tooth/beak marks were observed on 87 skeletal elements (2.9 % of the sample). The presence of gnawing damage, the number of punctures and pits which were often multiple (in the same bone), and the location of marks (many bones with bilateral punctures) suggested that most of the marks appeared to be caused by the carnivores' teeth.

Taking into account the total of bone remains with tooth/beak marks, 60.9 % of TPU were registered, followed by a 27.5 % of TPI, 8.0 % of SCO, 2.3 % of CRE, and 1.1 % of NO associated with tooth marks. The skeletal element with the largest number of marks was the innominate with a total of 26 cases (29.9 % of the cases), followed by the tibia, 19.5 % (Table 5). In the innominate remains, tooth marks are mostly located in the internal face, beneath the acetabulum. Tooth punctures and tooth pits can be observed in long bone's epiphysis. Calcanei remains also show tooth pit marks. Scoring marks were visible in epiphysis and diaphysis. CRE are best seen in innominate remains, in the ilium area. A unique notch mark was seen in a fragmented rib (Fig. 5).

Cut and Burnt Marks

A total of six bones display cut marks. They were observed on long bones (two), metapodials (two) (Fig. 6), innominates (one), and ribs (one). Most of the cut marks were oblique to the principal axis of the bone. The two long bone diaphysis shows various parallel marks in transversal orientation and of moderate intensity. In the case of the innominate remain, transversal and oblique marks, of moderate intensity, were recorded in the ischium area. The only remain with possible burning damage was a distal epiphysis of an ulna.

Table 4 Numbers and percentages of *Oryctolagus cuniculus* bones included in each digestion category

Digestion in bone remains	Null		Light		Moderate		Heavy		Extreme	
	N	%	N	%	N	%	N	%	N	%
Mandible	106	100	0	0	0	0	0	0	0	0
Cranium	259	99.6	1	0.4	0	0	0	0	0	0
Humerus	76	91.6	6	7.2	1	1.2	0	0	0	0
Radius	107	94.7	5	4.4	0	0	1	0.9	0	0
Ulna	121	96.8	2	1.6	2	1.6	0	0	0	0
Femur	63	92.6	5	7.4	0	0	0	0	0	0
Tibia	121	97.6	2	1.6	0	0	1	0.8	0	0
Patellae	2	100	0	0	0	0	0	0	0	0
Scapula	54	100	0	0	0	0	0	0	0	0
Innominate	120	94.5	7	5.5	0	0	0	0	0	0
Metacarpus	130	98.5	1	0.8	1	0.8	0	0	0	0
Metatarsus	299	99.7	1	0.3	0	0	0	0	0	0
Phalanges 1/2	338	100	0	0	0	0	0	0	0	0
Phalanges 3	95	100	0	0	0	0	0	0	0	0
Calcaneum	58	92.1	3	4.8	0	0	2	3.2	0	0
Astragalus	10	90.9	1	9.1	0	0	0	0	0	0
Carpal/Tarsal	12	100	0	0	0	0	0	0	0	0
Vertebrae	431	99.5	2	0.5	0	0	0	0	0	0
Rib	507	99.6	2	0.4	0	0	0	0	0	0



Fig. 4 Digestion corrosion. **a** Distal epiphysis of a radius affected by moderate (2) degree; **b, c** Calcaneum affected by a heavy (3) degree of digestion

Age Estimation

Taking into account the fusion stage of long bones and metapodial epiphyses, scapulae, calcanei, and innominate, the percentage of adult individuals was 79 %.

Discussion

A matter of great importance in taphonomic studies is to determine whether faunal assemblages, in this case leporid accumulations, are the result of intrusive activity (natural cause), non-human predators, or anthropogenic activity. This type of information is critical in the analysis of Upper Paleolithic archaeological sites since there is an apparent systematic consumption of small prey by human groups from this period onward. Given that a large number of rabbit remains recovered in Canyars appear in a single context, with other faunal remains probably accumulated by carnivores and with lithic tools that demonstrate the anthropic presence, it is essential to identify the nature of the leporid. With such an aim, our results are compared to the taphonomic signatures of some raptors, terrestrial carnivores, and humans as recorded in previous studies.

Table 5 Number of tooth/beak marks counted in skeletal elements from *Oryctolagus cuniculus* remains recovered at Canyars

Skeletal element	TPU	TPI	SCO	CRE	NO	Total
Md	1	0	0	0	0	1
Sca	2	3	1	1	0	7
Cal	1	2	0	0	0	3
Tib	8	7	2	0	0	17
Phal	5	0	0	0	0	5
Fem	11	3	1	0	0	15
IN	16	8	1	1	0	26
Rib	2	0	1	0	1	4
Hum	5	1	1	0	0	7
Ver	2	0	0	0	0	2
Total	53	24	7	2	1	87

TPU tooth punctures, TPI tooth pits, SCO scoring, CRE crenulated edges, NO notches, Md mandibles, Sca scapulae, Cal calcanea, Tib tibiae, Phal phalanges, Fem femorae, IN innominate, Rib ribs, Hum humeri, Ver vertebrae

Accumulations of intrusive origin are characterized for presenting an age range similar to that of a living community (with all ages represented in different proportions depending on the type and cause of death of the population); fragmentation of the remains are located in most fragile areas (related to structural density values); and traces of predators do not appear (Callou 2003; Cochard 2004a). None of these features are met in the study sample of Canyars where the individuals were mostly adults (79 %), and when compared to Pavao and Stahl's (1999) independent measures of rabbit bone density, it was found that there was no statistically significant correlation between the frequency of rabbit skeletal portions and their density ($r_s=0.07$, $p=0.78$). This indicates that preservation of rabbit remains at Canyars have been generally unaffected by structural density-mediated attrition. Therefore, the available evidence appears to rule out the intrusive character of the Canyars leporid assemblages. Works carried out with modern leporid remains accumulated by nocturnal and diurnal raptors and terrestrial carnivores show that the percentage of adult individuals consumed can vary depending on the abundance of prey (Table 6, Lloveras *et al.* 2012b). Furthermore, in anthropic accumulations, the sample is characterized by values of 85 % or more of adult individuals (Brugal 2006; Cochard 2004a; Hockett 1991; Hockett and Bicho 2000; Lloveras *et al.* 2011); however, this type of accumulations could also show important variability, with percentages of 60 % (Martínez Valle 1996; Sanchis and Fernández Peris 2008). Therefore, the percentage of adult individuals registered in Canyars (79 %) could correspond to an anthropic accumulation as well as an accumulation produced by other types of predators.

The indicators of anatomical representation show that all skeletal elements are well represented. No selective transport of the rabbit carcasses was detected. The relative abundance profile show that the best-represented skeletal elements are calcanei, metatarsals, innominate, long bones (especially radii, ulnae, and tibiae), skull remains (particularly mandibles), and scapulae (Fig. 2). This is a profile that approximates to the one expected in anthropic accumulations, where despite the important variability that may exist, the best-represented skeletal elements use to be long bones, mandibles, scapulae, and innominate (Brugal 2006; Cochard 2004a; Hockett 1991; Hockett and Haws 2002). By comparison with our data for non-human predators (Table 6) the closest anatomical representation pattern appears to be that of terrestrial carnivores,



Fig. 5 Tooth/beak marks. **a** Innominate presenting tooth punctures (TPU) on the internal face and beneath the acetabulum; **b** Calcaneum with tooth pit (TPI) marks; **c** Innominate showing crenulated edges (CRE) in the ilium area; **d** Femur shaft with TPI and scoring (SCO); **e** Fragment of a rib with traces of SCO and notches (NO)

particularly non-ingested remains accumulated by lynx (Fig. 7), since samples coming from scats suffer considerable destruction, and consequently, bone percentage values are lower than those here obtained (Lloveras *et al.* 2008a, 2012a).

In Canyars, cranial elements are more abundant than postcranial elements (PCRT/CR=59.3); long bones are also abundant (PCRLB/CR=124.4); distal elements are scarcer than proximal elements (AUT/ZE=38.7); and elements from the forelimbs are less represented than elements from the hind limbs (AN/PO=60.2). When comparing these proportions with the values obtained for terrestrial carnivores and diurnal and nocturnal raptors (Table 6), again our results resemble the values obtained for terrestrial carnivores. However, it is observed that our results could also fit a pattern of human activity such as that registered in anthropic accumulations of leporid remains at Anecrial and Caldeirão caves in Portugal (Brugal 2006; Lloveras *et al.* 2011).

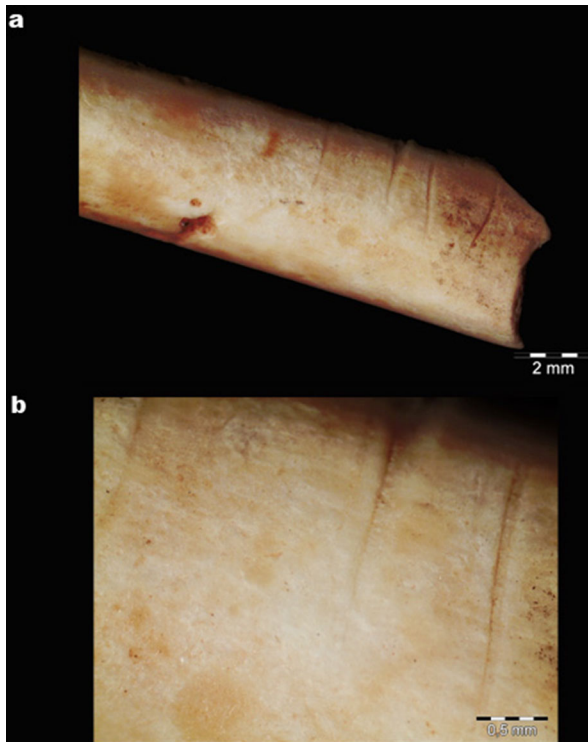


Fig. 6 Humerus shaft with cut marks

As for the long bone breakage, only 16.7 % of the analyzed remains present a maximum length inferior to 10 mm. Most accumulations created by different types of predators give values higher than 50 % (Table 6). This result is similar to that obtained with sets of non-ingested remains accumulated by terrestrial carnivores such as foxes (28 %) (Lloveras *et al.* 2012a) and especially the lynx (17.4 %) (Rodríguez-Hidalgo *et al.* 2013b). The percentages of complete remains (39.6 %) and complete long bones (6 %) are lower than those registered in modern eagle owl accumulations and higher than those obtained for diurnal raptors (Table 6). These values could fit within a set of remains accumulated by terrestrial carnivores that may present variable frequencies of complete bones depending on the origin of the remains (scats, ingested or mixed). Still, two factors that may have contributed to underestimate the percentage of complete bones in our sample should be taken into account. First, some skeletal elements of small size (carpal/tarsal, third phalanges, patella) are poorly represented, which suggest a loss of these elements during the process of recovery on the field; second, the high presence of elements showing modern fractures (46.1 %).

Ethnographically, it has been documented that people may create small animal limb shafts by snapping or biting off the proximal and distal ends of long bones (Jones 1983). Similarly, it has also been well documented that prehistoric hunters extracted bone marrow from the medullary cavity of rabbit long bones, creating large numbers of rabbit bone cylinders in archaeological sites (Brugal 2006; Cochard 2004a; Hockett 1991; Hockett and Bicho 2000; Hockett and Haws 2002; Pérez Ripoll 1992, 2002, 2004; Sanchis and Fernández Peris 2008). Cochard (2004a) note that the evidence of

Table 6 Anatomical representation, breakage, digestion and teeth/beak marks data for leporid remains accumulated by different types of predators (nocturnal raptors, diurnal raptors, terrestrial carnivores) compared with the results obtained in the present study

Comparisons	Eagle owl		Spanish imperial eagle		Iberian lynx		Fox		Present study	
	<i>Bubo bubo</i>		<i>Aquila adalberti</i>		<i>Lynx pardinus</i>		<i>Vulpes vulpes</i>		Canyars	
Reference	Lloveras <i>et al.</i> (2009a)		Lloveras <i>et al.</i> (2008b)		Lloveras <i>et al.</i> (2008a)		Rodríguez-Hidalgo <i>et al.</i> (2013b)		Lloveras <i>et al.</i> (2012a)	
Origin	Nest	Nest	Pellet		Scat	Non-ingested	Scat	Non-ingested	Mixed	MLU (M24)
<i>N</i>	1,808	1,932	824		1,522	9,564	265	639	781	3,458
RA > values	pat-cal-in-fem	cal-in-tib-mis	phal 3-um-tib		md-teeth-cr	tib-cal-mts-ast	Long bones-sca-cr	mts-cal-ast-tib	mts-cal-ast-tib	cal-mts-in-long bones-md
RA < values	mtc-c/t	rad-c/t-mtc	rib-fem-rad-ver		c/t-ver-rib	sca-ver-hum-rib-fem	mtc-c/t-in	cr-sca-rib-in-ver	rib-in	c/t-pat-phal 3-ast
PCRT/CR	+Postcranial	=	+Cranial		+Cranial	+Postcranial	=	+Postcranial	+Postcranial	+Cranial
P/D	+Proximal	+Proximal	+Distal		+Proximal	+Distal	+Proximal	+Distal	+Distal	+Proximal
AN/PO	+Hind limb	+Hind limb	+Hind limb		+Forelimb	+Hind limb	+Hind limb	+Hind limb	+Hind limb	+Hind limb
Complete elements %										
Mean value long bones	14.6	10.8	0		2.5	37.6	0	5.4	3.6	6
Mean value total	53.9	45.9	27		43	73.2	12	89.4	77	39.6
Length (mm)										
Minimum	2.3	2.5	1.8		1.1	3	3	4	2.6	3
Maximum	86.3	90	36.1		30.1	69	26.8	86.2	86.2	105.1
% <10 mm	49	40	73		80	19.7	61	28	33.9	16.7
% Digested remains	68.8	65.6	98		97.2	-	99.5	-	15	1.3

Table 6 (continued)

Comparisons	Eagle owl	Spanish imperial eagle	Iberian lynx	Fox	Present study
	<i>Bubo bubo</i>	<i>Aquila adalberti</i>	<i>Lynx pardinus</i>	<i>Vulpes vulpes</i>	Canyars
% Digested long bones	88.9	100	100	100	36.2
Degree					
Null	31.2	2	2.8	0	0
Light	40.2	18.2	12	6	1
Moderate	19.8	46.8	22	26	26.7
Heavy	8	27.4	43.8	43	43.5
Extreme	0.7	5.6	19.3	25	28.7
Teeth/beak marks	2	0.5	0.26	3	8.3
Age % of adults	50	—	21.4	87	—

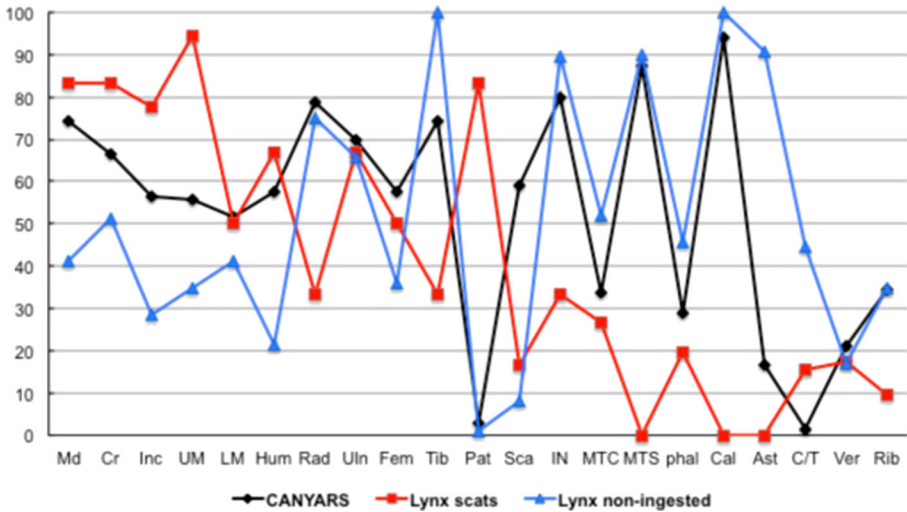


Fig. 7 Relative abundance of the different parts of the skeleton in Canyars leporid samples compared to remains recovered in lynx scats (Lloveras *et al.* 2008a) and non-ingested remains (Rodríguez-Hidalgo *et al.* 2013b) (for abbreviations, see caption to Fig. 2)

human predation of leporids results in more than 5 % of long bone cylinders (especially femorae, tibiae, and humeri) and multiple fragments of epiphysis. However, it has also been noted that most predators (raptors and carnivores) may also create samples with some amount of bone cylinders (Hockett 1991; Hockett and Bicho 2000; Pérez Ripoll 2005). Those created by carnivores and raptors may mimic cylinders created by humans, but these bones are usually scarce and vastly outnumbered by complete to nearly complete rabbit limb bones deposited in the same site by these predators (Hockett 1995; Pérez Ripoll 1993). This is the case of the Canyars sample where the number of long bone cylinders is low (ten cases, 3.6 % of long bone fragments) and so are the epiphysis fragments. Although this does not rule out a human intervention without evidence of marrow procurement, the scarce number of cylinders is clearly closer to a non-anthropic accumulation.

The remains that present damage caused by digestion are very scarce, only 1.3 % of the sample. This result does not match the values recorded in accumulations created by raptors, nor these derived from terrestrial carnivores scats (Table 6). It is closer to the values found in anthropogenic assemblages or terrestrial carnivore accumulations of non-ingested remains. An additional factor worth examining is the degree of digestion displayed on the surface of the remains. In the Canyars sample, most of the digested remains were altered in a light degree being the extreme category absent. This category of damage is always well represented in modern rabbit remain accumulations (of ingested remains) created by carnivores (Lloveras *et al.* 2008a, 2012a). However, it should be taken into account that extreme digestion degree tends to be underestimated in archaeological samples in comparison with modern referential material because due to their fragility, strongly digested remains do not preserve well. For this reason, the activity of carnivore terrestrial mammals cannot be discarded from this data.

The percentage of remains with tooth/beak marks in the Canyars sample is 2.5 %. This value clearly indicates a non-human intervention on the sample. The occurrence of

perforations on opposite sides of a single bone is indicative of the activity of carnivores; this may correspond to either fox or lynx activity (Lloveras *et al.* 2008a, 2012a; Rodríguez-Hidalgo *et al.* 2013b). On the other hand, the marks analyzed in our sample are quite different from those observed in experimental studies on the human consumption of rabbits. The human marks are characterized by broad but not deep punctures related with cracks and the association of teeth marks and bending fractures (Sanchis 2012; Sanchis *et al.* 2011).

The presence of cut marks, although in a low percentage (0.2 %), clearly relates to human activity. These kinds of marks are usually abundant in accumulations of anthropic origin; however, they are subject to an important degree of variability (Brugal 2006; Cochard 2004a; Hockett and Bicho 2000). The number of cut marks is too low to confidently infer a specific butchery activity; however, taking into account their location and orientation, they may be related to the skinning and disarticulation of rabbit carcasses. The nearly absence of remains showing burnt damage rules out the accumulated rabbit remains were in direct contact with a heat source as a result of a cooking process.

In summary, rabbit remains from level MLU of Canyars, analyzed in this work, display attributes that can be created by different types of predators. The anatomical representation, the degree of breakage, and the presence of tooth marks point to a terrestrial carnivore as the main agent responsible for accumulation. The scarce number of elements affected by digestion and the high frequency of complete remains indicates that it could be an accumulation mainly formed by non-ingested remains with a small contribution of scat remains. The taphonomical pattern obtained is close to that described for Iberian lynx from actualistic studies (Rodríguez-Hidalgo *et al.* 2013b). The preliminary taphonomic analysis carried out by Daura *et al.* (2013) on the large faunal remains recovered at Canyars suggested that carnivores were the responsible agents for the bone, specifically, large carnivores such as hyenas and lynx. Our results agree with this hypothesis; however, hyenas should be discarded as the predators of the leporid accumulation. Numerous taphonomical studies have been conducted in hyenas' dens (Cruz-Uribe 1991; Kuhn *et al.* 2010; Lansing *et al.* 2009; Pickering 2002; Pokines and Kerbis Peterhans 2007; Schick *et al.* 2007). These works show that these carnivores, and especially the larger species *Crocota crocuta*, are specialized hunters of large ungulates. Small prey remains, such as leporids, are never accumulated in so large amounts as in Canyars site. Furthermore, when large carnivores prey on small mammals (such as rabbits) most of the prey carcasses are consumed, and non-ingested remains are scarce and much more fragmented than in Canyars sample. Zooarchaeological studies also show that the sites of hyena bone deposits were also often used in the Middle and Upper Pleistocene as dens or food storage of common smaller carnivores or raptors, which resulted in the accumulation of bones from smaller animals such as leporids (Diedrich and Zák 2006; Steele and Klein 2013). This may be the case of Canyars site; the taphonomic analysis of leporid remains shows that a small carnivore, probably the Iberian lynx, mostly accumulated rabbits. The significant number of remains of this taxon recovered among the carnivore sample present on the site (MNI 13, Daura *et al.* 2013) is consistent with this inference. This emphasizes the role that this carnivore may have played in Canyars small prey accumulation; the site was also probably used as a den by this carnivore.

On the other hand, the anatomical profile and the scarce presence of cut marks points to a minor anthropogenic contribution, but significant enough to slightly alter the

characteristic pattern defined for carnivores. Palimpsests in which various agents intervened independently are common in prehistoric sites. The results are bone and artifact accumulations composed of multiple singular events that could make the archaeological interpretations difficult (Binford 1981). From this perspective, animals that compose the assemblages could reflect more than one method of acquisition. At Canyars, site formation scenario showed that a flash flood acted as an agent of concentration in a single locus of remains originally deposited over a wider area of a paleochannel and the immediately adjacent floodplain (Daura *et al.* 2013). Our results suggest that the leporid assemblage was mostly accumulated in the framework of Iberian lynx denning in the riverside area. This material eventually came together with a large number of other faunal remains (most of them primarily accumulated by hyenas), and a few artifacts, burnt bones, and charcoal from a human camp site (Daura *et al.* 2013).

In the Iberian Mediterranean regions, the regular anthropic acquisition and consumption of small prey, particularly rabbits, has been described since the Aurignacian levels at the beginning of the Early Upper Paleolithic. The emphasis on rabbits documented from this period has been related to the arrival of the anatomically modern *Homo sapiens*, as a consequence of changes in settlement structure and in the consolidation of a short-radius migration model that was well adapted to the characteristics of the Mediterranean environment. This territorial system was based on the seasonal exploitation of deer and ibex by alternating between coastal and mountainous inland areas and was characterized by the use of rabbits and other small prey as complementary resources (Aura *et al.* 2002; Martínez Valle 2001; Villaverde *et al.* 1996). However, this is an issue that needs to be further explored. On one hand, in light of the evidence from Cova Bolomor, where leporids and other small prey were exploited by Neanderthals (Blasco and Fernández Peris 2012; Sanchis and Fernández Peris 2008). On the other hand, data about Aurignacian rabbit accumulations is still scarce, basically limited to three archaeological sites: Arbreda Cave, Cova Beneito, and Cova de les Malladetes. In all these sites, rabbit remains dominate the fauna from the Aurignacian levels analyzed (80–90 % NISP) and evidence for their use by humans has been described through the presence of butchery marks, burnt bones, and anthropic fractures (Davidson 1989; Estévez 1987; Maroto *et al.* 1996; Martínez Valle 1996). The problem is that up until now, deep taphonomic studies of rabbit accumulations from these sites have not been conducted, which does not allow us to make comparisons with results obtained in the present study. Anyway, concerning to the anthropic activity, it is clear that Canyars moves away from these coetaneous Mediterranean sites where the anthropic systematic use of small prey beginning in the Early Upper Paleolithic has been evidenced. In any case, Canyars should not be understood as an archaeological station itself but as a carnivore's occupation with a certain human activity in Canyars riverside.

Conclusions

The taphonomic analysis of rabbit remains from Canyars excludes the possibility of it being of an anthropogenic origin. This is consistent with the archaeological record of the site: There is little human activity (few lithic tools) to support the existence of a

human settlement. The analysis also rules out the possibility that the leporid accumulation was intrusive.

Instead, the characteristics of the assemblage data are consistent with an accumulation generated by terrestrial carnivores, especially exhibiting a pattern of non-ingested remains. Moreover, anatomical representation and breakage patterns rule out the hyenas, a species well represented in the site, as the main agents responsible for the accumulation. Therefore, we conclude that the main accumulator of rabbit remains was probably the lynx, another species well represented at the site.

Despite the low impact of humans on the leporid accumulation, the results do not contradict the general pattern established for the human consumption of small prey between the Middle Paleolithic and Upper Paleolithic in the Iberian Peninsula. This model is applicable to sites where human impact is important but not at places where human activity seems marginal as in Canyars.

Acknowledgments We would like to thank the anonymous reviewers for their valuable comments and suggestions. Ll. Lloveras was funded by a postdoctoral grant (BP-A 00334 2011) and M. Sanz by a predoctoral grant (FI) from the Secretaria d'Universitats i Recerca Del Departament d'Economia i Coneixement de la Generalitat de Catalunya. J. Daura was funded by a postdoctoral grant (Juan de la Cierva Subprogram JCI-2011-09543). Financial support from research projects HAR2011-26193 from the Ministerio de Ciencia e Innovación (MICINN) and SGR2014-108 from the Generalitat de Catalunya are gratefully acknowledged. Fieldworks were sponsored by GTI (Gavanenca de Terrenys i Inmobles, Ajuntament de Gavà) and research project *Humans, carnívors i medi natural durant el Plistocè al massís del Garraf-Ordal I curs baix del riu Llobregat*.

References

- Andrews, P. (1990). *Owls, caves and fossils*. London: Natural History Museum.
- Aura, J. E., Villaverde, V., Pérez Ripoll, M., Martínez Valle, R., & Calatayud, P. G. (2002). Big game and small prey: Paleolithic and Epipaleolithic economy from Valencia (Spain). *Journal of Archaeological Method and Theory*, 9, 215–267.
- Aura, J. E., Jordá, J., Morales, J. V., Pérez, M., Villalba, M. P., & Alcover, J. H. (2009). Economic transition in finis terra: the western Mediterranean of Iberia, 15–7 ka BP. *Before Farming*, 2009(2), 255–265.
- Binford, L. R. (1981). *Bones: ancient men and modern myths* (p. 235). New York: Academic Press.
- Blasco, R., & Fernández Peris, J. (2012). A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International*, 252, 16–31.
- Brugal, J. P. (2006). Petit gibier et fonction de sites au Paléolithique supérieur. Les ensembles fauniques de la grotte d'Anecrial (Porto de Mos, Estremadura, Portugal). *Paléo*, 18, 45–68.
- Callou, D. (2003). De la garenne au clapier: étude archéozoologique du Lapin en Europe occidentale. Mémoires du Muséum National d'Histoire Naturelle, Tome 189, Paris.
- Cochard, D. (2004a). Les léporidés dans la subsistance Paléolithiques du Sud de la France. Ph. D. Thesis. Université Bordeaux I, France.
- Cochard, D. (2004b). Etude taphonomique des léporidés d'une tanière de renard actuelle: apport d'un référentiel à la reconnaissance des accumulations anthropiques. *Revue de Paléobiologie, Gen.*, 23(2), 659–673.
- Cochard, D., & Brugal, J. P. (2004). Importance des fonctions de sites dans les accumulations paléolithiques de léporidés. In J. P. Brugal & J. Desse (Eds.), *Petits animaux et sociétés humaines. Du complément alimentaire aux ressources utilitaires. XXIV Actes des XXIV Rencontres Internationales d'Archéologie et d'Histoire d'Antibes* (pp. 283–296). Sophia Antipolis: Editions APDCA.
- Cochard, D., Brugal, J. P., Morin, E., & Meignen, L. (2012). Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. *Quaternary International*, 264, 32–51.
- Cruz-Urbe, K. (1991). Distinguishing hyaena from hominid bone accumulations. *Journal of Field Archaeology*, 18, 467–486.

- Daura, J., & Sanz, M. (2009). *Jaciments Plistocens i ocupacions humanes en el Paleolític de Gavà. Homenatge a Alicia Estrada. Col·lecció La Nostra Gent*, 5 (pp. 1–44). Gavà: Ed Associació d'Amics del Museu de Gavà i Ajuntament de Gavà.
- Daura, J., Sanz, M., García, N., Allué, E., Vaquero, M., Fierro, E., Carrión, J. S., López-García, J. M., Blain, H. A., Sánchez-Marco, A., Valls, C., Albert, R. M., Fornós, J. J., Julià, R., Fullola, J. M., & Zilhão, J. (2013). Terraces de la Riera dels Canyars (Barcelona, Spain): the landscape of Heinrich Event 4 north of the “Ebro Frontier” and implications for modern human dispersal into Iberia. *Quaternary Science Review*, 60, 26–48.
- Davidson, I. (1972). The fauna from la Cueva del Volcán del Faro (Cullera, Valencia): a preliminary report. *Archivo de Prehistoria Levantina*, 13, 7–21.
- Davidson, I. (1989). La economía del final del Paleolítico en la España oriental. Servicio de Investigación Prehistórica de la Diputación de Valencia, Serie Trabajos Varios 85, Valencia.
- Delibes, M., & Hiraldo, F. (1981). The rabbit as prey in the Iberian Mediterranean ecosystem. In K. Myers & C. D. MacInnes (Eds.), *Proceedings of the World Lagomorph Conference* (pp. 614–622). Guelph: University of Guelph.
- Diedrich, C. G., & Zak, K. (2006). Prey deposits and den sites of the Upper Pleistocene hyena *Crocota crocuta spelaea* (Goldfuss, 1823) in horizontal and vertical caves of the Bohemian Karst (Czech Republic). *Bulletin of Geosciences*, 81, 237–276.
- Dodson, P., & Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, 5, 275–284.
- Estévez, J. (1987). La fauna de L'Arbreda (s. alfa) en el conjunt de faunes del Pleistocè superior. *Cypselia*, VI, 73–87.
- Fernández Jalvo, Y., & Andrews, P. (1992). Tafonomía de microvertebrados de Dolina. Revisión de un estudio previo. In J. M. Bermúdez, J. L. Arsuaga, E. Carbonell (Eds.), *Evolución humana en Europa y los yacimientos de la Sierra de Atapuerca* (pp. 167–201). Junta de Castilla y León.
- Hale, J. B. (1949). Aging cottontail rabbit by bone growth. *J. Wildl. Manage.*, 13, 216–225.
- Haynes, G. (1980). Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. *Paleobiology*, 6, 341–351.
- Haynes, G. (1983). A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology*, 9, 164–172.
- Hockett, B. S. (1991). Toward distinguishing human and raptor patterning on leporid bones. *American Antiquity*, 56, 667–679.
- Hockett, B. S. (1995). Comparison of leporid bones in raptor pellets, raptor nest, and archaeological sites in the great basin. *North American Archaeologist*, 16, 223–238.
- Hockett, B. S. (1996). Corroded, thinned and polished bones created by Golden Eagles (*Aquila chrysaetos*): taphonomic implications for archaeological interpretations. *Journal of Archaeological Science*, 23, 587–591.
- Hockett, B. S. (1999). Taphonomy of a carnivore accumulated rabbit bone assemblage from Picareiro Cave, Central Portugal. *Journal of Iberian Archaeology*, 1, 251–257.
- Hockett, B. S., & Bicho, N. (2000). The rabbit of Picareiro Cave: small mammal hunting during the Later Upper Paleolithic in the Portuguese Estremadura. *Journal of Archaeological Science*, 27, 715–723.
- Hockett, B. S., & Haws, J. A. (2002). Taphonomic and methodological perspectives of leporid hunting during the Upper Paleolithic of the Western Mediterranean Basin. *Journal of Archaeological Method and Theory*, 9(3), 269–302.
- Jones, K. (1983). Foraging archaeology: the Ache of Eastern Paraguay. In G. M. Lemoine, A. S. MacEachern (Eds.), *Carnivores, human scavengers, and predators: a question of bone technology* (pp. 171–191). Archaeological Association of The University of Calgary.
- Jones, L. E. (2006). Prey choice, mass collecting, and the wild European rabbit (*Oryctolagus cuniculus*). *Journal of Anthropological Archaeology*, 25, 275–289.
- Kuhn, B. F., Berger, L. R., & Skinner, J. D. (2010). Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. *International Journal of Osteoarchaeology*, 20, 15–35.
- Landt, M. J. (2007). Tooth marks and human consumption: ethnoarchaeological mastication research among foragers of the Central Africa Republic. *Journal of Archaeological Science*, 34, 1629–1640.
- Lansing, S., Cooper, S., Boydston, E., & Holekamp, E. (2009). Taphonomic and zooarchaeological implications of spotted hyena (*Crocota crocuta*) bone accumulations in Kenya: a modern behavioral ecological approach. *Paleobiology*, 35(2), 289–309.
- Lloveras, L., Moreno-García, M., & Nadal, J. (2008a). Taphonomic analysis of leporid remains obtained from modern Iberian Lynx (*Lynx pardinus*) scats. *Journal of Archaeological Science*, 35, 1–13.

- Lloveras, L., Moreno-García, M., & Nadal, J. (2008b). Taphonomic study of leporid remains accumulated by Spanish Imperial Eagle (*Aquila adalberti*). *Geobios*, 41, 91–100.
- Lloveras, L., Moreno-García, M., & Nadal, J. (2009a). The Eagle Owl (*Bubo bubo*) as a leporid remains accumulator. Taphonomic analysis of modern rabbit remains recovered from nest of this predators. *International Journal of Osteoarchaeology*, 19, 573–592.
- Lloveras, L., Moreno-García, M., & Nadal, J. (2009b). Butchery, cooking and human consumption marks on rabbit (*Oryctolagus cuniculus*) bones: an experimental study. *Journal of Taphonomy*, 7(2–3), 179–201.
- Lloveras, L., Moreno-García, M., Nadal, J., Maroto, J., Soler, J., & Soler, N. (2010). The application of actualistic studies to assess the taphonomic origin of Musterian rabbit accumulations from Arbrede Cave (North-East Iberia). *Archaeofauna*, 19, 99–119.
- Lloveras, L., Moreno-García, M., Nadal, J., & Zilhão, J. (2011). Who brought in the rabbits? Taphonomical analysis of Mousterian and Solutrean leporid accumulations from Gruta do Caldeirão (Tomar, Portugal). *Journal of Archaeological Science*, 38, 2434–2449.
- Lloveras, L., Moreno-García, M., & Nadal, J. (2012a). Feeding the foxes: an experimental study to assess their taphonomic signature on leporid remains. *International Journal of Osteoarchaeology*, 22(5), 577–590.
- Lloveras, L., Moreno-García, M., & Nadal, J. (2012b). Assessing the variability in taphonomic studies of modern leporid remains from Eagle Owl (*Bubo bubo*) nest assemblages: the importance of age of prey. *Journal of Archaeological Science*, 39, 3754–3764.
- Lloveras, L., Nadal, J., Moreno-García, M., Thomas, R., Anglada, J., Baucells, J., Martorell, C., & Vilasis, D. (2014). The role of the Egyptian Vulture (*Neophron percnopterus*) as a bone accumulator in cliff rock shelters: an analysis of modern bone nest assemblages from North-eastern Iberia. *Journal of Archaeological Science*, 44, 76–90.
- Mallye, J.B. (2011). Taphonomie et archeozoologie d'un animal fouisseur: method de caracterisation des accumulations de restes de Blaireau. In V. Laroulandie, J. B. Mallye, C. Denys (Eds.): Taphonomie des Petits Vertébrés: référentiels et transferts aux fossils. Actes de la Table Ronde du RTP Taphonomie, Talence 20–21, Octobre 2009, Oxford, *British Archaeological Reports*, International Series, 2269, 43–55.
- Manne, T., & Bicho, N. F. (2009). Vale Boi: rendering new understanding of resources intensification and diversification in southwest Iberia. *Before Farming*, 2(1), 1–21.
- Maroto, J., Soler, N., & Fullola, J. M. (1996). Cultural change between Middle and Upper Paleolithic in Catalonia. In E. Carbonell & M. Vaquero (Eds.), *The last Neandertals, the first anatomically modern human: a tale about human diversity, cultural change and human evolution, the crisis at 40 ka BP* (pp. 219–250). Tarragona: Universitat Rovira i Virgili.
- Martínez Valle, R. (1996). Fauna del Pleistoceno superior en el País Valenciano: aspectos económicos, huella de manipulación y valoración paleoambiental. Ph. D. Thesis. Universitat de València, València.
- Martínez Valle, R. (2001). Cazadores de pequeñas presas. In: Villaverde, V. (Ed.) *De Neandertales a Cromañones. El inicio del poblamiento humano en tierras valencianas* (pp. 129–130). Universitat de València.
- Morales, A., Roselló, E., & Hernández, F. (1998). Late Upper Palaeolithic subsistence strategies in southern Iberia: Tardiglacial faunas from Cueva de Nerja (Málaga, Spain). *European Journal of Archaeology*, 1, 9–50.
- Pavao, B., & Stahl, P. W. (1999). Structural density assays of Leporid skeletal elements with implications for taphonomic, actualistic and archaeological research. *Journal of Archaeological Science*, 26, 53–66.
- Pérez Ripoll, M. (1992). *Marcas de carnicería, fracturas intencionadas y mordeduras de carnívoros en huesos prehistóricos del Mediterráneo español*. Instituto de Cultura Juan Gil Albert. Diputación Provincial de Alicante.
- Pérez Ripoll, M. (1993). Las marcas tafonomicas en huesos de lagoformos. *Estudios Sobre Cuaternario*, 1993, 227–231.
- Pérez Ripoll, M. (2001). Les marques antròpiques en ossos de conill. In V. Villaverde (Ed.), *De Neandertals a Cromanyons. L'inici del poblament humà a terres valencianes*. Fundació General de la Universitat de València.
- Pérez Ripoll, M. (2002). The importance of taphonomic studies of rabbit bones from archaeological sites. In M. De Renzi (Ed.), *Current topics on taphonomy and fossilization* (pp. 499–508). Valencia.
- Pérez Ripoll, M. (2004). La consommation humaine des lapins pendant le Paléolithique dans la région de València (Espagne) et l'étude des niveaux gravétiens de la Cova de les Cendres (Alicante). In J. P. Brugal & J. Desse (Eds.), *Actes des XXIV Rencontres Internationales d'Archéologie et d'Histoire d'Antibes* (pp. 191–206). Sophia Antipolis: Editions APDCA.
- Pérez Ripoll, M. (2005). Caracterización de las fracturas antrópicas y sus tipologías en huesos de conejo procedentes de los niveles gravetienses de la Cova de les Cendres (Alicante). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 57, 239–254.
- Pickering, T. R. (2002). Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology*, 12, 127–141.

- Pokines, J. T., & Kerbis Peterhans, J. C. (2007). Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. *Journal of Archaeological Science*, *34*, 1914–1931.
- Rodríguez-Hidalgo, A., Saladié, P., & Canals, A. (2013a). Following the white rabbit: a case of a small game procurement site in the Upper Paleolithic (Sala de las Chimeneas, Maltravieso Cave, Spain). *International Journal of Osteoarchaeology*, *23*, 34–54.
- Rodríguez-Hidalgo, A., Lloveras, L., Moreno-García, M., Saladié, P., Canals, A., & Nadal, J. (2013b). Feeding behavior and taphonomic characterization of non-ingested rabbit remains produced by the Iberian Lynx (*Lynx pardinus*). *Journal of Archaeological Science*, *40*, 3031–3045.
- Sanchis, A. (2000). Los restos de *Oryctolagus cuniculus* en la tafocenosis de *Bubo bubo* y *Vulpes vulpes*, y su aplicación a la caracterización del registro faunístico arqueológico. *Saguntum*, *32*, 31–50.
- Sanchis, A. (2010). Los lagomorfos del Paleolítico Medio de la región central y sudoriental del Mediterráneo Ibérico. Caracterización tafonómica y taxonómica. Ph. D. Thesis. Universitat de València, Valencia.
- Sanchis, A. (2012). *Los lagomorfos del Paleolítico Medio en la vertiente mediterránea ibérica. Humanos y otros predadores como agentes de aporte y alteración de los restos óseos en yacimientos arqueológicos*. Valencia: Trabajos Varios del Servicio de Investigación prehistórica del Museo de Prehistoria de Valencia. n° 115.
- Sanchis, A., & Fernández Peris, J. (2008). Procesado y consumo antrópico de conejo en la Cova del Bolomor (Tavernes de la Vallidigna, Valencia). El nivel XVIIc (ca 350 ka). *Complutum*, *19*(1), 25–46.
- Sanchis, A., Morales, J.V., Pérez Ripoll, M. (2011). Creación de un referente experimental para el estudio de las alteraciones causadas por dientes humanos sobre huesos de conejo. In A. Morgado, J. Baena, D. García (Eds.), *La Investigación experimental aplicada a la Arqueología* (pp. 343–349). Universidad de Granada-Universidad Autónoma de Madrid.
- Schick, K., Toth, N., Gehling, T., Pickering, T.R. (2007). Taphonomic analysis of an excavated striped hyena den from the eastern Desert of Jordan. In T. R. Pickering, K. D. Schick, N. P. Toth (Eds.), *Breathing life into fossils : taphonomic studies in honor of C.K. (Bob) Brain* (pp. 75–106). Stone Age Institute Press.
- Schmitt, D. N., & Juell, K. E. (1994). Toward the identification of coyote scatological faunal accumulations in archaeological context. *Journal of Archaeological Science*, *21*, 249–262.
- Steele, T. E., & Klein, R. G. (2013). The Middle and Later Stone Age faunal remains from Diepkloof Rock Shelter, Western Cape, South Africa. *Journal of Archaeological Science*, *40*, 3453–3462.
- Stiner, M. C., & Munro, N. D. (2002). Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. *Journal of Archaeological Method and Theory*, *9*, 181–214.
- Stiner, M. C., Kunh, S. L., Weiner, S., & Bar-Yosef, O. (1995). Differential burning, recrystallization and fragmentation of archaeological bone. *Journal of Archaeological Science*, *22*, 223–237.
- Taylor, R. H. (1959). Age determination in wild rabbits. *Nature*, *184*, 1158–1159.
- Villa, P., & Mahieu, E. (1991). Breakage patterns of human long bones. *Journal of Human Evolution*, *21*, 27–48.
- Villaverde, V., & Martínez Valle, R. (1992). Economía y aprovechamiento del medio en el Paleolítico de la región central del Mediterráneo español. In A. Moure Romanillo (Ed.), *Elefantes, ciervos y ovicaprinos: economía y aprovechamiento del medio en la Prehistoria de España y Portugal* (pp. 75–95). Santander: Universidad de Cantabria.
- Villaverde, V., Martínez Valle, R., Guillem, P., & Fumanal, M. (1996). Mobility and the role of small game in the Middle Paleolithic of the central region of the Spanish Mediterranean: a comparison of Cova Negra with other Paleolithic deposits. In E. Carbonell & M. Vaquero (Eds.), *The last Neandertals, the first anatomically modern human: a tale about human diversity, cultural change and human evolution, the crisis at 40 ka BP* (pp. 267–288). Tarragona: Universitat Rovira i Virgili.