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Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats

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Abstract

Distinguishing leporid bones accumulated by diurnal raptors, owls, mammals and humans is essential to understand not only past human subsistence activities but also past ecology. This is particularly relevant in Iberian Palaeolithic sites where leporid remains usually constitute the most abundant taxon. As far as terrestrial mammal carnivores are concerned, the Iberian lynx (*Lynx pardinus*) would be the main leporid predator in the Iberian Peninsula. Up until now its contribution as a rabbit bone accumulator in archaeological sites has never been properly assessed. In order to investigate the taphonomic signature of this predator the analysis of 33 samples of modern Iberian lynx scats was carried out. Results show that leporid remains consumed by this carnivore appear very fragmented and exhibit a strong degree of corrosion digestion. Cranial elements are most abundant followed by long bones. Whereas there seem to be clear differences in relation to breakage and digestion alteration caused by owls, some of the patterns obtained are closest to those established with diurnal raptors.

Keywords: Taphonomy; Leporid remains; Iberian lynx; Terrestrial carnivores; Digestion; Breakage

1. Introduction

Leporids (rabbits and hares) occupy a significant position in the trophic relationships in the Iberian Peninsula since the cooler stages of the Pleistocene (Delibes and Hiraldo, 1982), when this region became an important refuge for many animal species (Altuna, 1992; Callou, 2003; García and Arsuaga, 2003). In most Palaeolithic and Epipalaeolithic Iberian sites leporids and in particular the European rabbit (*Oryctolagus cuniculus*) are the dominant taxon among faunal archaeological remains. Recently, several studies have demonstrated the importance that small game exploitation (i.e., leporids) would have had to the daily diet of prehistoric people, their relevance being used to explain mobility patterns and increase of populations (Hockett and Bicho, 2000; Hockett and Haws, 2002; Stiner et al., 1999, 2000; Villaverde et al., 1996).

At the same time, leporids are an important source of food for a large number of non-human predators (terrestrial carnivores, diurnal and nocturnal birds of prey). In the Iberian Peninsula, wolf (*Canis lupus signatus*), fox (*Vulpes vulpes*) and Iberian lynx (*Lynx pardinus*) are the main mammal carnivore species that feed on leporids, although their consuming habits differ greatly. While for wolves and foxes leporids are occasional, seasonal or complementary preys (Calzada and Palomares, 1996; Castroviejo et al., 1975; Salvador and Abad, 1987), for the Iberian lynx rabbits constitute 80−100% of their diet (Aldama and Delibes, 1997; Calzada and Palomares, 1996; Delibes, 1980; Delibes and Hiraldo, 1982). Thus, the

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high specialization of this mammal on rabbits accounts partly for the reduction in their present day populations (Aldama et al., 1991; Delibes et al., 1998).

These terrestrial predators are regular visitors to caves and rock-shelters where their prey leftovers and scats, containing digested bone fragments, may accumulate. Taphonomic studies on this kind of material have proved to be a valuable source of information to distinguish between competing predators (Haynes, 1983; Rensberger and Krentz, 1988). Their results have been used to try to identify the predators responsible for the accumulation of faunal remains in archaeological contexts (Cruz-Uribe, 1991; Palmqvist et al., 1996; Richardson, 1980; Ruiter and Berger, 2000). In the case of leporid remains, while some works attempt to distinguish those modified by humans (Pérez Ripoll, 1993, 2004) from those modified by other predators like coyote (Schmitt and Juell, 1994), fox (Cochard, 2004; Sanchis Serra, 2000), Golden Eagle (Hockett, 1995, 1996; Schmitt, 1995), Spanish Imperial Eagle (Lloveras et al., in press), Eagle Owl (Cochard, 2004; Guillem Calatayud and Martínez Valle, 1991; Sanchis Serra, 2000; Yravedra, 2004) and other birds of prey (Cruz-Uribe and Klein, 1998; Hockett, 1989, 1991, 1995), little research has been carried out to characterize rabbit remains after being consumed by the Iberian lynx. A topic that should be tackled to assess the contribution this carnivore might have had in the accumulation of archaeological leporid assemblages in the Western Mediterranean region. Thus, our aim is to fill the present lack of information regarding this issue, by analyzing the taphonomy of leporids remains extracted from recently collected Iberian lynx scats.

2. Material and methods

The rabbit remains analyzed come from two series of Iberian lynx scats (series 1 and series 2). Both were collected from wild individuals in the Natural Park of Doñana, Seville (Spain), in an area where rabbits are abundant (Calzada, 2000; Calzada and Palomares, 1996).

Series 1 comprises nine scats collected in February 1992. Each scat was placed into water for 24 h to be rehydrated. Then the scat was carefully sieved and disaggregated in a 1.5 mm mesh.

Series 2 includes 24 scats collected between February and April 1995. These scats were also sieved but they were given to us already disaggregated (Calzada, 2000).

Each scat was numbered individually and all the faunal remains (bones, teeth, fur and nails) were extracted manually using tweezers. The osteological material was sorted through under a microscope (×10 to ×40) and stored separately.

2.1. Anatomical representation

Numbers of identified skeletal elements (N) were counted and relative abundance was also calculated (Andrews, 1990; Dodson and Wexlar, 1979) using the formula:

$$R_i = \mathrm{MNE}_i/\mathrm{MNI} \times E_i$$

(R_i = the relative abundance of element i, MNE_i = the minimum number of skeleton element i, MNI = the minimum number of individuals based on the highest number of any single element in the assemblage, and E_i = the number of element i in the prey skeleton).

In addition, proportions of skeletal elements were evaluated using three indices for postcrania in relation to crania (Andrews, 1990):

(a) PCRT/CR – total numbers of postcranial compared with total numbers of cranial elements (mandibles, maxillae and teeth);
(b) PCRAP/CR – limb elements (long bones, scapulae, innominate, patellae, metapodials, carpals, tarsals and phalanges) compared with cranial elements (mandibles, maxillae and teeth);
(c) PCRLB/CR – humerus, radius, ulna, femur and tibia compared with mandibles and maxillae.

Loss of distal limb elements was shown by two indices (Lloveras et al., in press):

(a) AUT/ZE – autopodium elements (metapodials, carpals, tarsals and phalanges) compared with zigopodium and stylopodium (tibia, radius, ulna, humerus, femur and patellae);
(b) Z/E – zigopodium elements (tibia, radius and ulna) compared with stylopodium (femur and humerus).

A further index compared forelimb to hindlimb elements:

AN/PO – humerus, radius, ulna and metacarpus compared with femur, tibia and metatarsus.

2.2. Breakage

The breakage pattern was described by the maximum length of all the identified skeletal elements. Percentages of complete elements, isolated teeth and articulated elements were also calculated. Different breakage categories were used depending on the bone type following an established methodology (Lloveras et al., in press).

2.3. Digestion

Damage to bone surface was observed under light microscope (×10 to ×40). Based on the methodology used for micromammals by Andrews (1990) and Fernández-Jalvo and Andrews (1992), different categories of digestion damage were applied to leporid bones and teeth (Lloveras et al., in press). Five degrees of digestion were distinguished: null (0), light (1), moderate (2), heavy (3) and extreme (4). These were valued separately for bones and dental remains. Finally, damage to the bone surfaces caused by the predator teeth were also noted and counted.

3. Results

Series 1 and series 2 are similar enough to be treated as one homogeneous data set. The differences in both samples are probably due to the bias produced for the small sample size in series 1, which may not be representative enough. For this reason, the results are treated as a single sample to avoid confusion and to obtain one unique pattern for this predator.

3.1. Anatomical representation

After disaggregating all scats (33), a total of 4213 rabbit remains were recovered. Of these, 1522 (36.1%) bones and teeth fragments were identified to skeletal element. Based on lower incisor counts a minimum number of individuals (MNI) of 14 was estimated.

Table 1 shows the anatomical composition of the identified remains for each series and for the assemblage. The entire skeleton was represented – phalanges, teeth and vertebrae were the most frequent elements (*N*). Relative abundance of skeletal elements (RA%) is shown in Table 1 and Fig. 1. The mean value (49.2%) indicates an important loss of the prey bones. Cranial elements were the best represented and showed the highest percentages. Long bones were also well represented, especially humerus, ulna and femur. Third phalanges, innominate and scapula fragments were also important. Carpal, tarsal, metatarsals, vertebrae and rib fragments were scarce in both series.

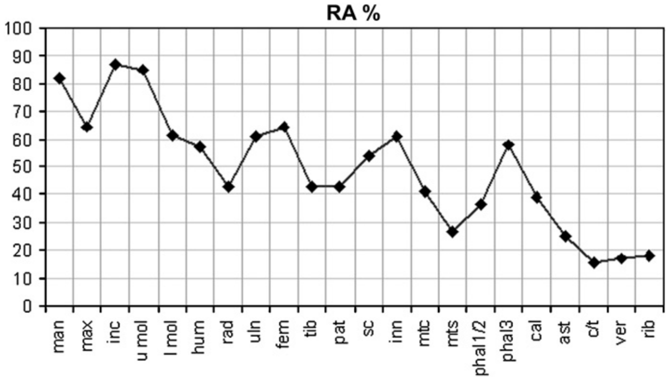

Fig. 1. Relative abundance of different parts of the skeleton. Abbreviations – man: mandible, max: maxilla, inc: incisors, u mol: upper molars, l mol: lower molars, hum: humerus, rad: radius, uln: ulna, fem: femur, tib: tibia, pat: patella, sc: scapula, inn: innominate, mtc: metacarpus, mts: metatarsus, phal 1/2: phalanges 1/2, phal 3: phalanges 3, cal: calcaneum, ast: astragalus, c/t: carpal/tarsal, ver: vertebrae, rib: ribs.

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

- Indices that compare postcranial to cranial elements (PCRT/CR; PCRAP/CR) pointed to a deficiency in the numbers of postcrania;
- This difference became less evident when cranial elements were compared to long bones (PCRLB/CR);
- Comparisons of lower to upper limb elements (AUT/ZE and Z/E) showed loss of the former in a greater proportion;

Table 1
Skeletal elements recovered from Iberian lynx scats

Skeletal element	*N* (1)	*N* (2)	*N* (1 + 2)	*N* (1 + 2)%	MNE	RA%
Mandible	7	38	45	2.95	23	82.1
Cranium (maxilla)	9	50	59	3.87	18[b]	64.3
Incisors	14	59	73	4.79	73	86.9
Upper molars	34	111	145	9.52	143	85.1
Lower molars	15	71	86	5.65	86	61.4
Humerus	6	37	43	2.82	16	57.1
Radius	3	18	21	1.37	12	42.8
Ulna	7	21	28	1.83	17	60.7
Femur	4	32	36	2.36	18	64.3
Tibia	3	23	26	1.7	12	42.8
Patellae	5	7	12	0.78	12	42.8
Scapula	1	21	22	1.44	15	53.6
Innominate	4	45	49	3.21	17	60.7
Metacarpus	10	64	74	4.86	58	41.4
Metatarsus	0	40	40	2.62	30	26.8
Phalanges 1/2	20	185	205	13.46	175	36.8
Phalanges 3	16	130	146	9.59	146	57.9
Calcaneum	0	13	13	0.85	11	39.3
Astragalus	0	7	7	0.45	7	25.0
Carpal/tarsal	11	42	53	3.48	53	15.8
Vertebrae	33	182	215	14.12	103	17.1
Ribs	12	105	117	7.68	60	17.9
Total	214	1301 + 7 = 1308[a]	1515 + 7 = 1522		1087	

N(1): number of skeletal elements in series 1. *N*(2): number of skeletal elements in series 2. *N*(1 + 2): number of skeletal elements in series 1 + 2. *N*(1 + 2)%: skeletal elements in percentage. MNE: minimum number of elements. RA%: relative abundance.

[a] Number of skeletal elements in series 2 was 1301 + 7 fragments of metapodial not classified as mtc or mts.

[b] MNE for cranium was 18 including incisive bone and 15 for maxillae, both counted laterally.

Table 2
Proportions of different parts of the skeleton

Indices %	
PCRT/CR	43.1
PCRAP/CR	45.1
PCRLB/CR	70
AUT/ZE	67.6
Z/E	80.4
AN/PO	343.3

A key to the abbreviations is provided in Section 2.

- The AN/PO index revealed better survival of anterior limb elements than posterior limb bones.

3.2. Breakage

The small size of the recovered remains (more than 80% of them had length values under 10 mm; Fig. 3) is a clear indicator of their high fragmentation state (Fig. 2). Average maximum length of identified skeletal elements was 7.07 mm, with values varying between 1.07 and 30.08 mm (Fig. 3).

The average percentage of complete elements was 43% (Table 6). Although values varied according to bone size, the highest percentages were obtained for the small carpals/tarsals, patellae, molars and phalanges (Table 3; Fig. 4).

Breakage categories (Table 3) show that:

- skulls had generally suffered an advanced degree of breakage and were identified by parts of maxilla (M), zygomatic arch (ZA), incisive bone (IB) and neurocranium (NC);
- mandibles were represented by body fragments (MB) and condylar process (PC) except for a few cases in which the front part (IP) was recovered;

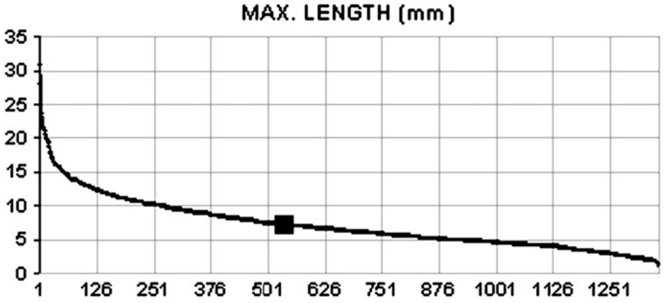

Fig. 3. Maximum length (in mm) of the leporid remains recovered from Iberian lynx scats (vertical axis). The average value is shown emboldened. The horizontal axis shows the number of bones and teeth measured.

- isolated teeth (69.6%) and teeth placed ‘‘in situ’’ were almost always complete (96.3%);
- vertebrae fragments were represented mainly by vertebral body (VB) and vertebral epiphysis (VE) while ribs were almost always fragmented;
- ilium fragments (IL) were the most common for the innominates, followed by fragments of acetabulum (A) and ischium (IS);
- scapulae were never complete and most fragments comprised the glenoid cavity (63.6%);
- all breakage categories but that of complete bones were well represented for limb bones;
- metapodials were the best preserved (39.5% were complete);
- calcanea and astragali were equally fragmented;
- on the whole more than 80% of phalanges appeared complete.

The high percentage of isolated teeth (82.2%) and the scarcity of articulated elements (9.7%) attest also to the high degree of breakage in the assemblage.

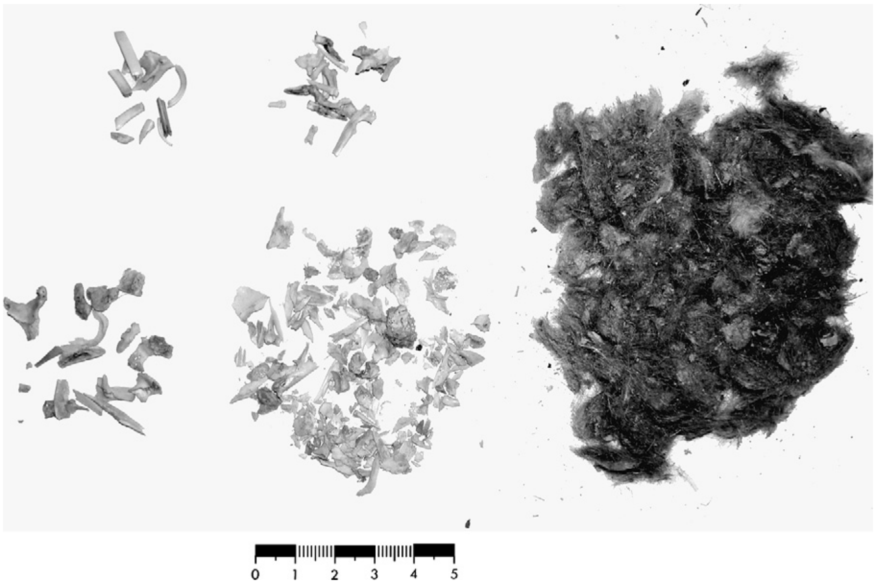

Fig. 2. Bones, teeth and fur recovered from an Iberian lynx scat.

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

Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Humerus	0	0	13	30.2	6	13.9	7	16.3	8	18.6	9	20.9
Radius	2	9.5	3	14.3	10	47.6	2	9.5	0	0	4	19
Ulna	2	7.1	2	7.1	13	46.4	9	32.1	1	3.6	1	3.6
Femur	0	0	19	52.8	3	8.3	3	8.3	0	0	11	30.6
Tibia	0	0	8	30.8	3	11.5	5	19.2	4	15.4	6	23.1
Metacarpus	33	44.6	0	0	18	24.3	0	0	9	12.2	14	18.9
Metatarsus	12	30	0	0	10	25	0	0	5	12.5	13	32.5

Mandible	*N*	%	Cranium	*N*	%	Innominate	*N*	%	Scapula	*N*	%
C	0	0	C	0	0	C	0	0	C	0	0
IP	2	4.4	IB	14	23.7	A	10	20.4	GC	3	13.6
MBI	0	0	IBM	0	0	AIS	2	4.1	GCN	11	50
MB	27	60	M	18	30.5	AISIL	0	0	NF	1	4.5
MBB	0	0	ZA	12	20.3	AIL	4	8.2	F	7	31.8
PC	16	35.6	NC	15	25.4	IS	10	20.4			
						IL	23	46.9			

Vertebrae	*N*	%	Phalanges 1/2	*N*	%	Phalanges 3	*N*	%
C	14	6.5	C	164	80	C	126	86.3
VB	89	41.4	P	26	12.7	P	0	0
VE	92	42.8	D	11	5.3	D	17	11.6
SP	20	9.3	F	4	1.9	F	3	2

Patella	*N*	%	Car/tar	*N*	%	Cal	*N*	%	Ast	*N*	%	Ribs	*N*	%
C	12	100	C	53	100	C	3	23.1	C	2	28.6	C	5	4.3
F	0	0	F	0	0	F	10	76.9	F	5	71.4	F	112	95.7

Teeth	"In situ"						Isolated					
	Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	16	94.1	21	100	15	93.7	40	71.4	80	65.5	54	77.1
F	1	5.9	0	0	1	6.3	16	28.6	44	35.5	16	22.9

Long bones, metacarpal and metatarsal bones were classified as: complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal epiphysis (SDE) and distal epiphysis (DE). Mandible as: complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB) and condylary process (CP). Cranium as: complete (C), incisive bone (IB), incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC).Innominate as: complete (C), acetabulum (A), acetabulum + ischium (AIS), acetabulum + ischium + ilium (AISIL), acetabulum + ilium (AIL), ischium (IS) and ilium (IL). Scapula as: complete (C), glenoid cavity (GC), glenoid cavity + neck (GCN), neck + fossa (NF) and fossa (F). Vertebrae as: complete (C), vertebral body (VB), vertebral epiphisis (VE) and spinous process (SP). Phalanges as: complete (C), proximal fragment, (P), distal fragment (D) and fragment (F). Patella, carpal/tarsal, calcaneum, astragalum, ribs and teeth as: complete (C) and fragment (F).

3.3. Digestion

Different degrees of digestion were observed on the surface of 96.9% of the bones. Most bone remains presented a heavy degree of digestion (Figs. 5 and 6a–g; Table 4). The different bones were altered in similar proportions although calcaneum, astragalus and vertebrae remains appeared to be slightly more damaged. Phalanges were the best preserved. Teeth showed a bias towards stronger degrees of digestion corrosion (Figs. 5 and 7; Table 5) with 98.3% of the remains altered by the effects of digestion. No important differences between incisors, upper and lower molars were observed.

Other traces caused by lynx on bone surfaces were very rare. Only four bone fragments (0.26%): innominate (body of the ischium), ulna (shaft; Fig. 6h), incisive bone and scapula (fossa), displayed tooth puncture marks.

4. Discussion

All predators modify the bones of their prey to a certain extent. Mammal terrestrial carnivores, as described above in the analysis of recent scats of Iberian lynx, produce a substantial amount of bone destruction. In order to assess if the previous results can be used to identify lynx as the responsible agent for a particular leporid bone assemblage it turns necessary to compare them with those reported for other predators, such as other terrestrial carnivores, diurnal and nocturnal birds of prey.

4.1. Lynx and other terrestrial carnivores

The work done with modern scatological samples containing leporid remains from lynx similar-sized species of carnivores is that concerned with coyote (*Canis latrans*) (Schmitt

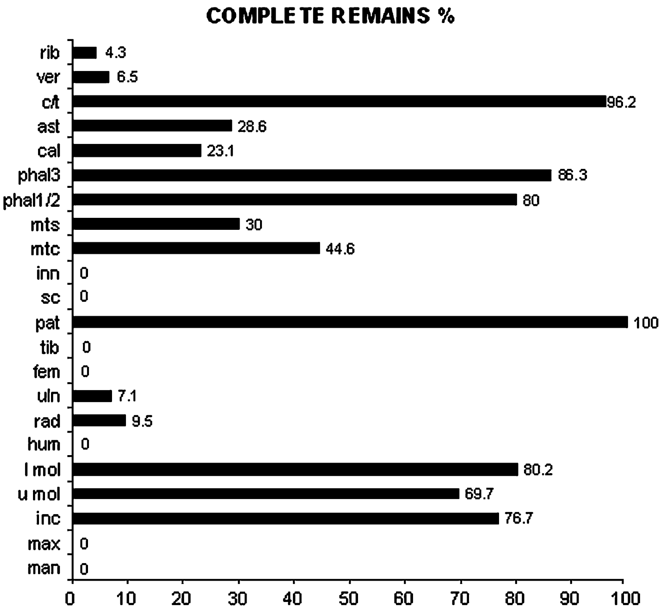

Fig. 4. Percentage of complete bones and teeth. For abbreviations see the caption of Fig. 1.

and Juell, 1994) and fox (*Vulpes vulpes*) (Cochard, 2004; Sanchis Serra, 2000).

As far as anatomical representation is concerned, it has been noted that vertebrae, ribs, teeth, skull/mandibles and phalanges are, in this order, the skeletal elements best represented in coyote scats (Schmitt and Juell, 1994). Table 1 shows that these are also the most frequent remains in the lynx scats although they rank differently. Multiple proportion test for anatomical representation showed significant differences between these two species ($\chi^2 = 201.05$; df = 17; $p < 0.005$) that might be due to, on one hand, the highest frequency of phalanges ($N\% = 23.05$) and teeth ($N\% = 19.96$) and, on the other hand, the scarcity of ribs ($N\% = 7.68$) and cranial fragments ($N\% = 6.82$) in the lynx sample.

It stands out that anterior and posterior limb bone elements were present in very different proportions in lynx scats (Table 2). The value obtained for AN/PO index (343.3, Table 2) shows that anterior limb bones are 3.43 times more abundant than those of the back leg. The difference lies mainly in the low number of metatarsals vs. metacarpals since the upper limb bones of front and hind legs are present in very similar proportions (Table 1). It is probably due to the fact that the lynx usually does not consume the rabbit posterior feet which remain articulated and are abandoned with the leporid skin attached (Calzada and Palomares, 1996). Similar behaviour has also been observed in coyote and fox if prey are abundant (Aldama and Delibes, 1990; Schmitt and Juell, 1994). However, no striking differences as those noted here were recorded for these other terrestrial carnivores.

Unfortunately, the literature published for fox analyze mixed scatological and no scatological samples (Cochard, 2004; Sanchis Serra, 2000) so that no detailed comparisons could be made with these results. As noted for other predators, the pattern of anatomical representation between digested and non-digested remains might be different (Bochenski and Tomek, 1997; Hockett, 1995).

It appears that bone breakage indices are very high for both the coyote and the lynx. In this study and the work reported by Schmitt and Juell (1994), nearly 80% of leporid remains are smaller than 10 mm in size (Fig. 3). The length of recovered remains is similar for both predators (Table 6). However, as shown by the percentage of complete bones (7% in the coyote sample vs. 43% in the lynx sample), coyote seems to produce more damage than lynx (Table 6).

Both carnivores cause high degrees of digestion corrosion on almost all the recovered leporid remains (Table 6). Those remains ingested by coyotes were not classified in different categories of damage (Schmitt and Juell, 1994), so no direct comparisons with the lynx results (Tables 4 and 5) could be made.

Finally, the low percentage of punctured bones both carnivores produced is noteworthy. In the lynx sample, only four tooth marks or 0.26% of the assemblage were recorded, whereas, a slightly higher frequency (0.95%) was noted for coyote (Schmitt and Juell, 1994). This may be related to different behaviour at ingesting prey bones or to higher bone destruction caused by lynx digestive enzymes which could mask the evidence of puncture marks.

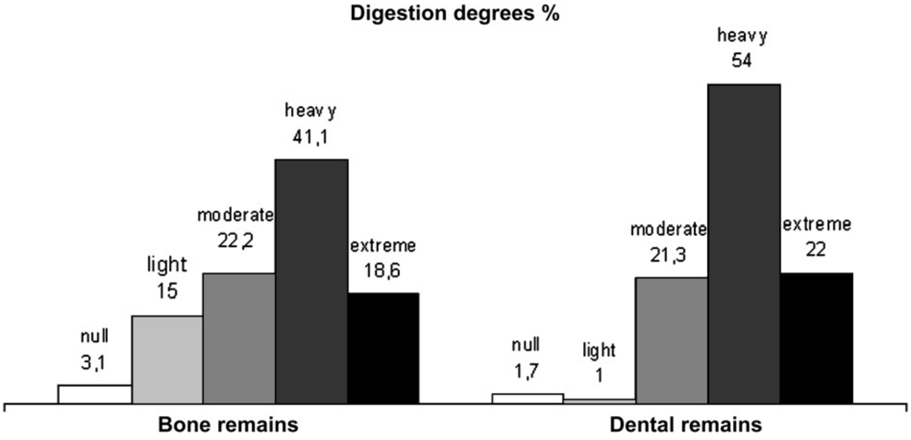

Fig. 5. Percentage of bone remains and teeth included in each digestion category.

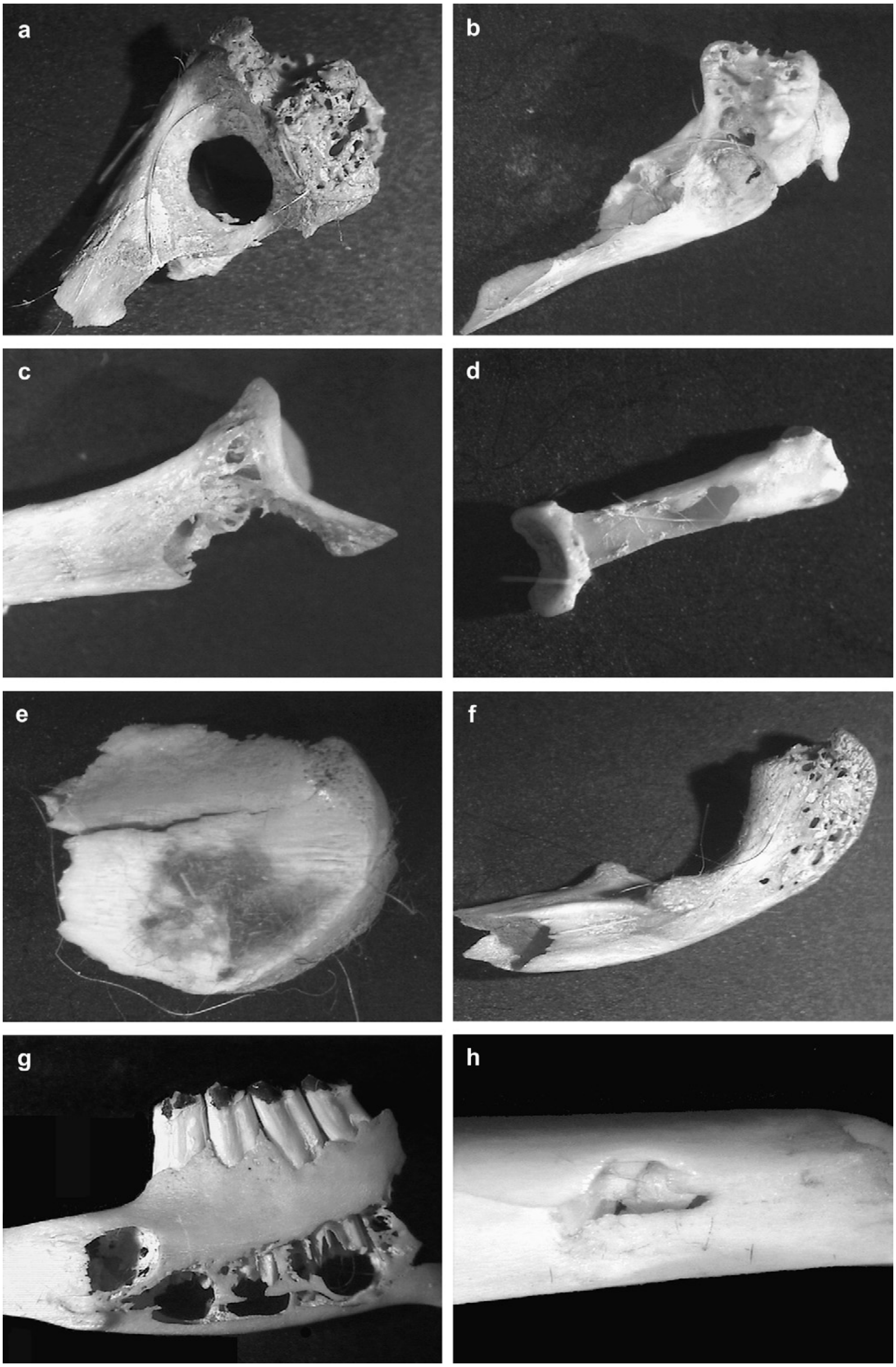

Fig. 6. Different leporid bones affected by digestion. Bone destruction, pitting, staining, splitting and strong rounding of edges can be observed. (a) Distal humerus (×10) with heavy digestion; (b) distal humerus (×12) affected by an extreme degree of digestion; (c) glenoid cavity from a scapula with heavy digestion (×12); (d) bone destruction on a phalange (×12) caused by heavy digestion; (e) fragment of ilium (×12) with a moderate degree of digestion; (f) proximal ulna (×10) affected by moderate digestion; (g) fragment of mandible with four molars "in situ", important bone destruction caused by heavy digestion; and (h) fragment of shaft (×18) with a punctured mark caused by the predator teeth.

4.2. Lynx and diurnal raptors

A study of a small sample of leporid remains obtained from Golden Eagle (*Aquila chrysaetos*) pellets (Hockett, 1996) showed that body parts representation and breakage differ from those observed in this study. On one hand, Golden Eagles do not usually eat the head of their prey (Hockett, 1996) so that cranial remains are scarce. In general, vertebrae and

Table 4
Numbers and percentage of leporid bones included in each digestion category

Digestion	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
Mandible	0	0	8	17.8	13	28.9	19	42.2	5	11.1
Maxilla	0	0	6	10.2	16	27.1	35	59.3	2	3.4
Humerus	0	0	5	11.6	4	9.3	26	60.5	8	18.6
Radius	0	0	2	9.5	5	23.8	12	57.1	2	9.5
Ulna	0	0	3	10.7	7	25	14	50	4	14.3
Femur	0	0	1	2.8	7	19.4	20	55.5	8	22.2
Tibia	0	0	2	7.7	3	11.5	15	57.7	6	23.1
Patellae	0	0	0	0	3	25	6	50	3	25
Scapula	0	0	3	13.6	2	9.1	8	36.4	9	40.9
Innominate	0	0	0	0	6	12.2	34	69.4	9	18.4
Metacarpus	0	0	14	19.4	18	25	23	31.9	17	23.6
Metatarsus	2	5	2	5	14	35	16	40	6	15
Phalanges 1/2	24	11.8	69	33.8	57	27.9	36	17.6	18	8.8
Phalanges 3	7	20	8	22.8	10	28.6	7	20	3	8.6
Calcaneum	0	0	0	0	3	23.1	5	38.5	5	38.5
Astragalus	0	0	0	0	0	0	2	28.6	5	71.4
Carpal/tarsal	0	0	8	15.1	12	22.6	28	52.8	5	9.4
Vertebrae	1	0.5	9	4.3	30	14.3	94	45	75	35.9
Ribs	0	0	24	20.5	32	27.3	48	41	13	11.1

hind limb bones (femur, tibia and calcaneus) occur most abundantly. Schmitt (1995) also reports that leporid bone accumulations associated with nests and perches are represented predominantly by posterior body parts, especially tibiae and hind feet. On the other hand, leporid remains present in pellets of Golden Eagles are larger and less fragmented than those recorded for Iberian lynx (Table 6). Hockett (1996) recovered a complete tibia of 80 mm, whereas the maximum length measured in this study was 30.08 mm (Table 6). Also the percentage of complete long bones is much higher in Golden Eagles (66.6%) than in lynx (2.5%). The same difference is observed between lynx and Northern Harrier (*Circus cyaneus*) (Hockett, 1991) with 72.5% of complete long bones (Table 6).

Bochenski et al. (1999) notice that Golden Eagles are able to cause extensive corrosion on ingested bird bones, in contrast Hockett (1996) found that in the same sample there could be corroded and well preserved leporid remains. As shown in Table 6 it appears that higher degrees of digestion corrosion are visible in leporid bones consumed by lynx.

Among diurnal raptors in the Iberian Peninsula, the Spanish Imperial Eagle (*Aquila adalberti*) is another important leporid predator. As with lynx, taphonomic studies related to this bird of prey are scarce. Results from a pilot study with pellets from captive individuals (Lloveras et al., in press) showed that phalanges, teeth, vertebrae and cranial remains were the most abundant elements like in Iberian lynx scats. However, statistical analysis showed significant differences in their anatomical representation ($\chi^2 = 422.96$; df = 21; $p < 0.005$). One observed difference is that while the third phalanges were much more abundant in the assemblage created by Spanish Imperial Eagle, cranial elements, vertebrae and ribs were more abundant in lynx scats (Fig. 8). Also, the index that compares the anterior and posterior leporid limb bones indicates that the former were very abundant in lynx scats (343.3; Table 3), whereas, the opposite situation is recorded in the pellets of this bird of prey. The value of 43.75 indicates a clear preponderance of hind limb bones (Lloveras et al., in press).

As far as breakage patterns are concerned, the length mean values were slightly higher for Spanish Imperial Eagle. Results of a Student's *T*-test applied to the maximum length of the identified remains (1358 measures from lynx and 549 measures from Spanish Imperial Eagle) showed significant differences for the size of the recovered fragments ($\bar{x}_{\mathrm{lynx}} = 7.07$; $\mathrm{SD}_{\mathrm{lynx}} = 3.807$; $\bar{x}_{\mathrm{eagle}} = 8.36$; $\mathrm{SD}_{\mathrm{eagle}} = 5.302$; $p = 0.000$*). However, completeness indices were higher in lynx (43%) than in eagle (27.9%; Lloveras et al., in press). Multiple proportion test applied to different kinds of long bone fragments and metapodials also showed significant differences ($\chi^2 = 31.17$; df = 5; $p < 0.005$). These are mainly due to higher numbers of shafts and scarcer numbers of complete bones in the eagle sample.

Some corroded scat bones from coyote may be indistinguishable from Golden Eagle pellet bones (Schmitt, 1995) and this could also be the case between Iberian lynx scat bones and Spanish Imperial Eagle pellet bones. In both samples damage caused by digestion appears to be extensive but the percentage of bones recorded within the heavy/extreme degree of corrosion is higher in lynx (59.5%) than in Spanish Imperial Eagle (33%; see Table 6). Whereas differences for bones are significant ($\chi^2 = 147.00$; df = 4; $p < 0.005$) those for teeth are not ($\chi^2 = 3.63$; df = 4; $p = 0.1$).

4.3. Lynx and nocturnal raptors

Differences between leporid remains from lynx scats and those obtained from owl pellets are clear and evident. A comparison of results obtained in this study with those published on Eagle Owl (*Bubo bubo*) (Cochard, 2004; Hockett, 1995; Sanchis Serra, 2000) and Barn Owl (*Tyto alba*) (Hockett,

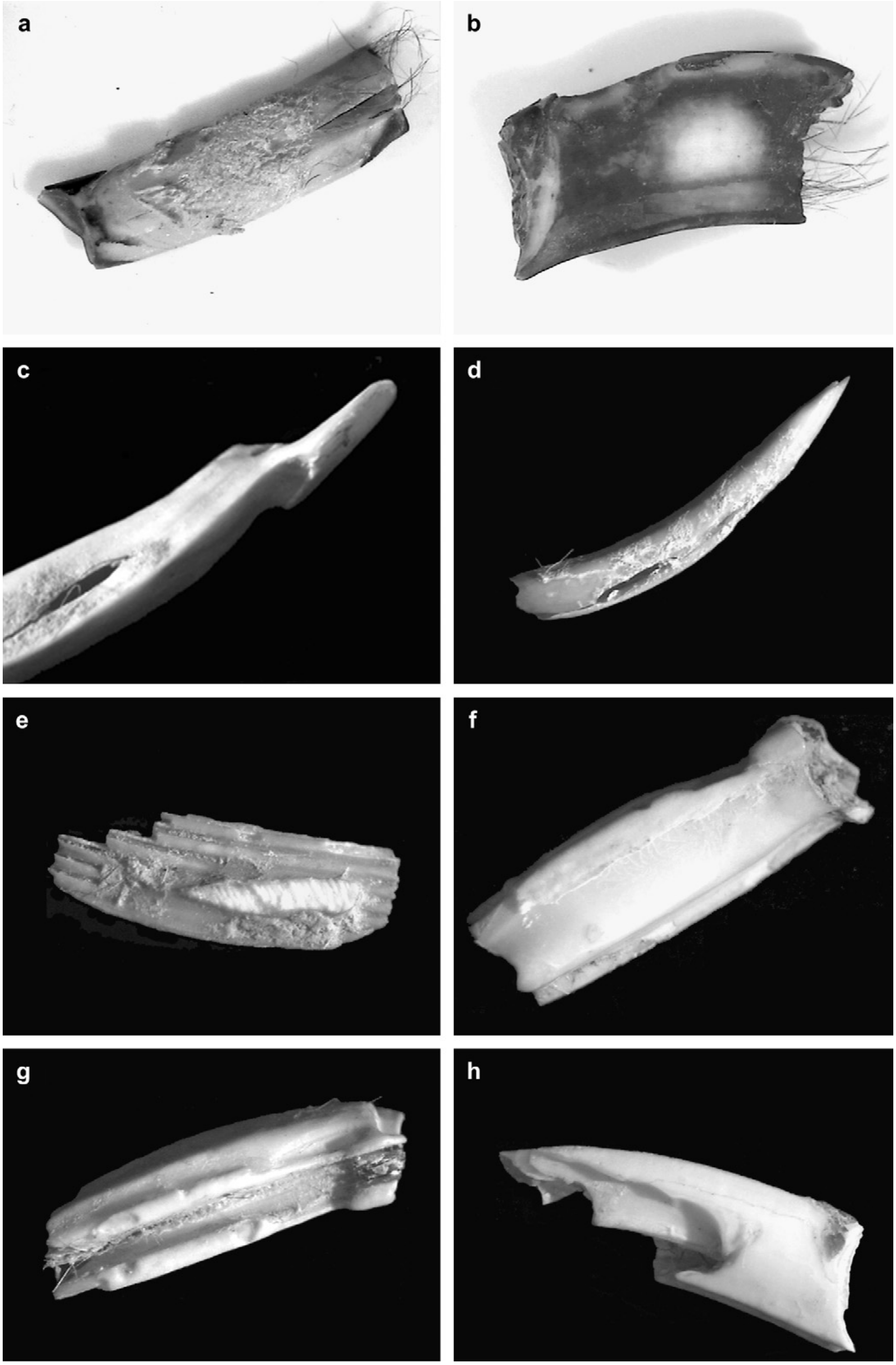

Fig. 7. Different rabbit teeth affected by heavy degree of digestion corrosion. Enamel is extensively removed, dentine is exposed and also affected by wearing, staining, splitting cracking and strong rounding of edges can also be observed. (a) Upper molar (×12); (b) upper molar (×12); (c) lower incisor (×12); (d) lower incisor (×10); (e) upper molar (×14); (f) lower molar (×14); (g) lower molar (×12); and (h) upper molar (×12).

1991, 1995) showed that leporid bones contained in pellets of these nocturnal raptors were always much less fragmented and corroded than those present in lynx scats. Not only is the percentage of whole bones obtained from our study lower than that recorded for these predators (see Table 6), but also the percentage of digested bones was clearly higher (97.2% vs. 81%). Moreover, digested leporid remains from lynx scats were affected by higher degrees of digestion and the whole surface of the bone was damaged (Fig. 6a–g). In contrast, corrosion usually affects only specific parts of the surface of

Table 5
Numbers and percentages of leporid teeth included in each digestion category

Digestion	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
Incisors	1	1.4	1	1.4	21	30	40	57.1	7	10
Upper molars	4	2.7	2	1.4	23	15.9	70	48.3	46	31.7
Lower molars	0	0	0	0	20	23.5	52	61.2	13	15.3

those remains contained in Eagle Owl pellets (Cochard, 2004; Sanchis Serra, 2000). This might be related to the small size of the fragments that are being digested by the Iberian lynx whereas owls tend to swallow whole portions of their prey (Sanchis Serra, 2000).

In Eagle Owl pellets (Cochard, 2004), all leporid body parts were present but the maximum values were for the postcranial elements, the innominate (81%) and vertebrae (48%) respectively, with the cranial elements being less abundant (15%). This contrasts to the situation already noted in lynx scats (RA% for cranial remains between 61.4 and 86.9%; Table 1). Further, as reported above for diurnal raptors, posterior limb bones were also more frequent than forelimb bones (Cochard, 2004; Guillem Calatayud and Martínez Valle, 1991; Sanchis Serra, 2000). This may indicate the preference of Eagle Owl to consume that anatomical part. Curiously, as reported by Hockett (1995) this kind of behaviour does not seem to be applicable to American Eagle Owl (*Bubo virginianus*) or maybe the variability observed could be related to other factors such as the abundance and age profile of the prey.

It is also noteworthy that marks caused by the beak of nocturnal raptors are relatively abundant (Table 6), particularly in leporid remains recovered from Eagle Owl pellets (3.8%) (Cochard, 2004; Sanchis Serra, 2000) whilst modifications (i.e., tooth puncture marks) caused by Iberian lynx are almost insignificant (0.26%; Table 6).

5. Conclusion

This work is the first taphonomic study of leporid remains contained in Iberian lynx scats. The fact that this species is, at present, the most endangered feline of the world (Delibes et al., 1998) might partly explain the little research that has been carried out following this methodological approach. As attested by the archaeological record, the geographical distribution of Iberian lynx was not reduced to small areas in southern Spain, as it is nowadays, but it was present all over the Iberian Peninsula (Altuna, 1972). Rabbits comprise the main component of their diet so that one would expect lynx played a role, together with other competing predators (i.e., wolf, fox, diurnal and nocturnal raptors), in the accumulation of leporid remains recovered from Iberian archaeological sites. Taphonomic studies on some of these other predators have been carried out worldwide (Hockett, 1989; Sanchis Serra, 2000). Their results are frequently applied to explain the formation of archaeological faunal assemblages all over the world, ignoring sometimes that local parameters such as environmental conditions or prey and predator ecological settings might differ from one region to another (Hockett and Haws, 2002). For this reason, this paper has tried to describe some of the taphonomic traces, such as anatomical representation, breakage pattern and digestion damage, evident on leporid bones recovered from modern Iberian lynx scats. Comparison of these preliminary results with those published for other leporid predators present in the Iberian Peninsula was favoured in order to begin to understand the taphonomic signature of this Iberian feline.

Results of body part representation showed that phalanges, teeth and vertebrae were the most frequent elements but relative proportions of postcranial to cranial elements suggested a deficiency of the former. In addition, bones of the fore-limb are 3.4 times more abundant than those from the hind-limb. This disproportion accounts for the scarcity of metatarsals. The lack of comparable information regarding terrestrial carnivores of similar size reveals the need to do more work, especially with fox, and other, scatological samples. Strictly speaking, the results reported for coyote, a non-European mammal species, are not directly analogous with the Iberian felid. Even so, the data are illuminating as both predators appear to produce similar patterns. Greater differences in anatomical representation were evident with leporid remains contained in pellets of diurnal and nocturnal birds of prey, particularly as far as the more abundant occurrence of hind limb bones and the scarcity of cranial remains are concerned.

Breakage patterns estimated from the average length of identified bone fragments indicated similar values for coyote and lynx but completeness indices suggested coyote caused more damage than lynx. Some divergences were noted on these parameters among results recorded for Golden Eagle and Spanish Imperial Eagle. Leporid remains in the pellets of the latter species resemble size-wise those contained in lynx scats but they showed a lower percentage of complete bones, suggesting the effects of this diurnal raptor could be stronger than those caused by lynx. Data from Eagle Owl demonstrated that leporid remains accumulated in their pellets are more distinctive since they are less fragmented.

Finally, degrees of digestion corrosion seem to indicate that digestive enzymes of lynx cause more extensive damage on rabbit bones surfaces than those recorded for diurnal raptors or nocturnal birds of prey, which generally appear to be corroded only in specific parts.

In summary, differences in the taphonomic signatures of leporid competing predators within the Iberian Peninsula are starting to be identified and documented. The results obtained are encouraging and show that there are some characteristics which considered together may distinguish lynx-accumulated leporid remains from remains accumulated by other predators.

Table 6
Breakage, digestion and beak/teeth mark comparisons on leporid remains from pellets and scats of different kinds of predators

Breakage, digestion and beak/teeth mark comparisons	Spanish Imperial Eagle *Aquila adalberti*	Golden Eagle *Aquila chrysaetos*	Northern Harrier *Circus cyaneus*	Eagle Owl *Bubo bubo*		Great Horned Owl *Bubo virginianus*	Barn Owl *Tyto alba*		Coyote *Canis latrans*	Iberian lynx *Lynx pardinus*
	Lloveras et al., in press	Hockett, 1996	Hockett, 1991	Cochard, 2004	Sanchis Serra, 2000	Hockett, 1995	Hockett, 1991	Hockett, 1995	Schmitt and Juell, 1994	
Complete elements %										
Mean value long bones	0	66.6	72.5	58	48	–	7.1	–	0	2.5
Mean value total	27	–	–	85	49	–	–	–	7	43
Length (mm)										
Maximum	36.1	80	–	–	–	–	55	–	35	30.1
Minimum	1.8	–	–	–	–	–	5	–	–	1.1
Average	8.36	–	–	–	–	–	–	–	–	7.1
% <10	73	–	–	–	–	–	–	–	75	80
Digestion										
% Digested remains	98	Majority	–	81	–	–	–	–	100	97.2
Degree										
Null	2	–	–	19	–	–	–	–	–	2.8
Light	18.2	–	–	38 X	X	–	–	–	–	12
Moderate	46.8 X	X	–	18	X	–	–	–	–	22 X
Heavy	27.4 X	X	–	25	–	–	–	–	–	43.8 X
Extreme	5.6	–	–	–	–	–	–	–	–	19.3 X
Beak/teeth marks %										
	0.5	–	–	3.8	Abundant	1	0.5	1.4	0.9	0.26

X Digestion categories where authors place most leporid remains analyzed.

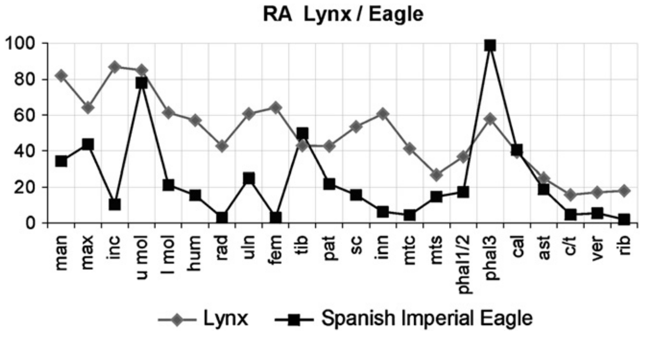

Fig. 8. Comparison between relative abundances of bone and teeth assemblages accumulated by Iberian lynx and Spanish Imperial Eagle. For abbreviations see the caption of Fig. 1.

This study is still in progress, more samples will be analysed and other variables such as season of the year, abundance and age profile of the prey will be taken into account. Nevertheless, faunal analysts working in this geographical region should be aware of the possibility that highly corroded and fragmented archaeological leporid assemblages in caves and rock-shelters may derive from the action of the Iberian lynx, a predator that certainly was a significant component of the Iberian Peninsula landscape in the past.

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