Archaeol Anthropol Sci (2018) 10:449–464
DOI 10.1007/s12520-016-0364-6

ORIGINAL PAPER

When wildcats feed on rabbits: an experimental study to understand the taphonomic signature of European wildcats (*Felis silvestris silvestris*)

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Received: 8 February 2016 / Accepted: 22 July 2016 / Published online: 8 August 2016

Abstract Studies of the feeding ecology of the European wildcat (*Felis silvestris silvestris*) demonstrate that leporids, mostly European rabbit (*Oryctolagus cuniculus*), dominate their diet in regions where they are present. The remains of wildcats have been found at Pleistocene and Holocene archaeological sites, raising the possibility that they actively accumulated leporid bones in caves and shelters shared with other terrestrial carnivores, raptors and humans. We present the first taphonomic study of rabbit remains consumed by this terrestrial carnivore, with the ultimate aim of understanding their role in bone accumulations at archaeological sites. An experimental study was carried out with a wildcat female, who was fed with nine complete rabbit carcasses. Non-ingested remains and scats were recovered for the analysis of anatomical representation, breakage and bone surface modification. This revealed that non-ingested remains and scats of the European wildcat can be discriminated from most other agents of accumulation. The referential framework provided will permit the discrimination of hominids and wildcats as agents of fossil accumulations of rabbits.

Keywords Taphonomy · Wildcat · European rabbit · Small prey · Bone accumulators

Electronic supplementary material The online version of this article (doi:10.1007/s12520-016-0364-6) contains supplementary material, which is available to authorized users.

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Introduction

The wildcat *Felis silvestris* is a medium-sized carnivore that ranges over Africa, Europe and central Asia to India, China and Mongolia. It is the most common and widely distributed wildcat species in the world. In contemporary Europe, the European wildcat (*Felis silvestris silvestris*) presents a rather fragmented geographic distribution, ranging from the Iberian Peninsula to the eastern part of the continent (Stahl and Artois 1991; Sunquist and Sunquist 2002).

Wildcats consume a large diversity of prey from rodents to small ungulates, with a diet that varies geographically and is dependent upon prey availability (Lozano et al. 2006). Diet studies show that throughout its range, small rodents (mice, voles, rats, dormice) are the wildcat's primary prey; however, birds and reptiles may also be consumed. Most studies also evidenced that in areas where abundances of leporids are high, normally, European rabbits (*Oryctolagus cuniculus*) are preferred to other prey, constituting up to 70–90 % of their diet (Condé et al. 1972; Gil-Sánchez et al. 1999; Sunquist and Sunquist 2002; Malo et al. 2004; Lozano et al. 2006; Lozano 2008). Wildcats can use small caves and rock shelters for sheltering and resting (Lozano 2008), and during breeding seasons in particular, they will accumulate prey leftovers and scats (SC) containing prey digested teeth and bone fragments within these dens.

The wildcat is first recorded in the fossil deposits of the Middle Pleistocene 250 ky ago, during the Holsteinian Interglacial period (Wolsan 1993). The remains of wildcats have been found at many Pleistocene and Holocene archaeological sites, raising the possibility that these carnivores were active accumulators of rabbit bones in caves and shelters that they shared with other terrestrial carnivores, raptors and humans. Thus, taphonomic studies on rabbit remains consumed by this terrestrial carnivore are essential in order to identify its role as an agent responsible for rabbit remains assemblages on archaeological sites.

In the last decades, numerous taphonomic studies examining the role of small carnivores as possible agents of bone accumulation in archaeological deposits have been published (Schmitt and Juell 1994; Sanchis 2000; Mondini 2002; Cochard 2004; Gómez and Kaufmann 2007; Lloveras et al. 2008a; Mallye et al. 2008; Sanchis Serra and Pascual Benito 2011; Alvarez et al. 2012; Lloveras et al., 2012a; Stiner et al. 2012; Rodríguez-Hidalgo et al. 2013; Krajcarz and Krajcarz 2014; Amstrong 2016). They are especially relevant to the discussion about subsistence strategies and ways of life of hunter-gatherer communities. Particularly, in areas where European rabbits are present (Iberian Peninsula and Mediterranean regions), this prey is usually the most abundant taxon in the zooarchaeological record (Aura et al., 2002; Hockett and Haws 2002). Distinguishing anthropogenic and other predator accumulations is thus imperative in order to assess the importance of small game exploitation in the past. Despite this fact, taphonomic studies on rabbit remains consumed by the European wildcat do not exist and its role as an agent responsible for bone accumulations at archaeological sites is unknown. The aims of this study are as follows: firstly, to study the taphonomic patterns left by the European wildcat on non-ingested and scats rabbit remains, and secondly, to put forward a series of criteria that can be used in archaeological samples to separate assemblages produced by wildcats from those accumulated by people or other predators.

Materials and method

To achieve our goals, an experimental study was conducted with a wildcat female kept at the Wildlife Recovery Center of Vallcalent (Lleida, Spain), which was fed with nine wild rabbits. The rabbit remains used in this study come from a farm specialized in breeding wild rabbits. The animals chosen were sub-adults with an average weight of approximately 1.5 kg. During February of 2013, the wildcat female, which was isolated in a naturalized enclosure of 150 m^2, was fed with the complete rabbit carcasses. The rabbit leftovers not ingested during feeding as well as the scats were collected and reserved for posterior analysis (Fig. S1).

All scats were rehydrated, water screened and disaggregated in a 1.5-mm mesh. Non-ingested remains were still anatomically connected and attached to the skin of the rabbit so to facilitate removal of any remaining soft tissue, carcasses were boiled and cleaned under running water. The material was then ready for analysis.

The analytical methodology used in this study follows the same criteria applied in previous works that were carried out with leporid assemblages originated by different predators (Lloveras et al., 2008a, b, 2009, 2012a, b, 2014a, b). The variables considered within each of the analytical parameters studied are presented in the following section.

Anatomical representation

The number of identified specimens present (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI) were calculated as well as relative frequencies. Relative abundance was calculated using the formula advocated by Dodson and Wexlar (1979). In addition, proportions of skeletal elements were evaluated using the following ratios (Andrews 1990):

(a) PCRT/CR, which is the total number of postcranial elements (limb elements, vertebrae and ribs) compared with the total number of cranial elements (mandibles, maxillae and teeth).
(b) PCRAP/CR, which is the total number of limb elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals and phalanges) compared with the total number of cranial elements (mandibles, maxillae and teeth).
(c) PCRLB/CR, which is the total number of postcranial long bones (humeri, radii, ulnae, femora and tibiae) compared with the total number of cranial elements (mandibles and maxillae).

Loss of distal limb elements was shown by two indices (Lloveras et al., 2008a):

(d) AUT/ZE, which is autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae);
(e) Z/E, which is zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

(f) AN/PO, which is scapulae, humeri, radii, ulnae and metacarpals compared with innominates, femora, tibiae and metatarsals.

Breakage

The breakage pattern was described by the maximum length of all identified skeletal elements. Percentages of complete elements, isolated teeth and articulated elements were calculated. For immature individuals, the diaphyses of long bones with unfused epiphyses were considered complete elements. Bone fragments were categorized depending on bone type:

- Patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F).
- Phalanges were recorded as C, proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as F.
- Vertebrae were registered as C, vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP).
- Breakage of teeth was calculated separately for isolated and in situ elements (Fernández-Jalvo and Andrews 1992) and they were classified as C or F.

Breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates are fully described and illustrated in Lloveras et al. (2008a, Fig. 1). The presence of long bone cylinders (fragments of long bones with snapped ends resulting from consumption), and V-shaped and helical fractures (Villa and Mahieu 1991) were also recorded.

Bone surface modifications

All of the skeletal remains were examined both macro- and microscopically. Damage to the bone surface was observed under light microscope (×10–40 magnification) with an oblique cold-light source.

Digestion damage

Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo and Andrews 1992; Lloveras et al., 2008a, b, 2014c). Five categories of digestion were distinguished as follows: null (0), light (1), moderate (2), heavy (3) and extreme (4). These were valued separately for bones and dental remains.

Tooth marks

Damage to bone surfaces caused by teeth were noted and counted. Marks were classified as scoring, notches, tooth punctures/tooth pits and crenulated/fractured edges (Haynes 1980; Binford 1981; Brain 1981). Punctures and pits were also classified by their number (isolated or multiple) and distribution (unilateral—i.e. located on one surface—or bilateral) (Sanchis Serra et al. 2014).

Density-mediated attrition

Differential survival in relation to bone density was evaluated using the bivariate *Spearman's rho* correlation (Grayson 1984), taking into account the rabbit bone density data provided by Pavao and Stahl's (1999).

Results

Anatomical representation

Table 1 shows the anatomical composition of the identified remains for both non-ingested (NI) and scat (SC) remains

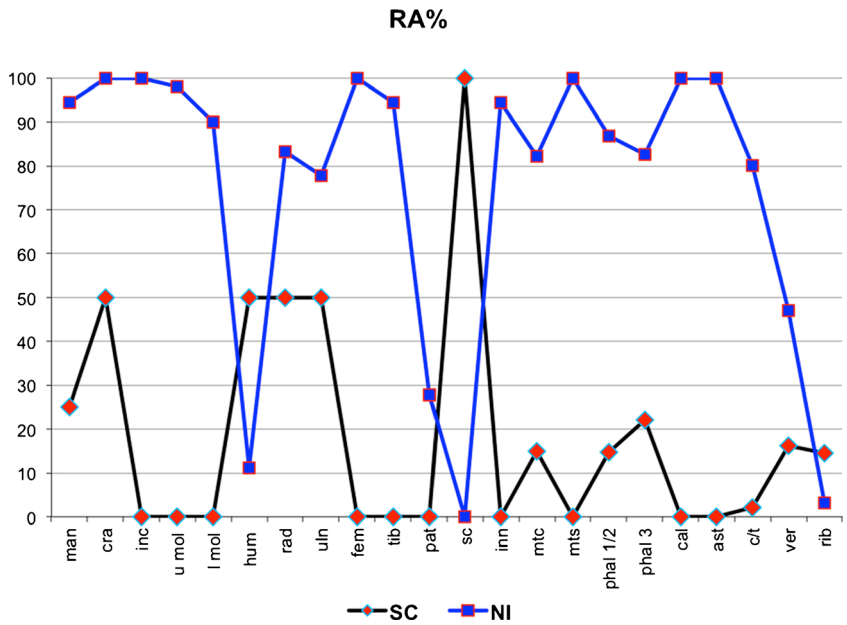

Fig. 1 Relative abundance of the different parts of the skeleton in the scats (SC) and non-ingested (NI) remains samples. *man* mandible, *cra* cranium, *inc* incisors, *u mol* upper molars, *l mol* lower molars, *hum* humerus, *rad* radius, *uln* ulna, *fem* femur, *tib* tibia, *pat* patella, *sc* scapula, *inn* innominate, *mtc* metacarpals, *mts* metatarsals, *phal 1/2* phalanges 1/2, *phal 3* phalanges 3, *cal* calcaneum, *ast* astragalus, *c/t* carpal/tarsal, *ver* vertebrae, *rib* rib

Table 1 Numbers (N), percentages (N%), minimum number of elements (MNE), minimum number of individuals (MNI), and relative abundance proportions (RA%) of rabbit remains recovered from non-ingested and scat samples

	Non-ingested (MNI = 9)				Scats (MNI = 2)				Digestion damage - SC sample										Tooth marks					
									Null		Light		Moderate		Heavy		Extreme		FRE	CRE	SCO	NOT	TPI	TPU
	N	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%						
Mandible	25	1.7	17	94.4	1	1.1	1	25	0	0	0	0	0	0	1	100	0	0	12	1	–	–	–	2
Cranium	26	1.8	9	100	3	3.4	1	50	0	0	0	0	0	0	1	33.3	2	66.6	1	–	–	–	–	–
Incisors	54	3.7	54	100	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Upper molar	106	7.3	106	98.1	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lower molar	81	5.6	81	90	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Humerus	3	0.2	2	11.1	7	8	2	50	0	0	0	0	1	14.3	2	28.6	4	57.1	4	–	–	–	–	–
Radius	31	2.1	15	83.3	3	3.4	2	50	0	0	0	0	0	0	2	66.6	1	33.3	18	–	1	-	2	2
Ulna	29	2	14	77.8	3	3.4	2	50	0	0	0	0	0	0	1	33.3	2	66.6	15	–	–	–	–	–
Femur	36	2.5	18	100	0	0	0	0	–	–	–	–	–	–	–	–	–	–	1	1	2	–	2	–
Tibia	36	2.5	17	94.4	0	0	0	0	–	–	–	–	–	–	–	–	–	–	7	1	–	–	–	–
Patella	5	0.3	5	27.8	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scapula	0	0	0	0	4	4.6	4	100	0	0	0	0	0	0	1	25	3	75	–	–	–	–	–	–
Innominate	23	1.6	17	94.4	0	0	0	0	–	–	–	–	–	–	–	–	–	–	2	1	-	1	1	2
Metacarpus	85	5.8	74	82.2	4	4.6	3	15	0	0	0	0	0	0	3	75	1	25	–	–	–	–	–	–
Metatarsus	87	6	72	100	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phalanges 1/2	268	18.4	266	86.9	11	12.6	10	14.7	0	0	1	9	5	45.5	5	45.5	0	0	–	–	–	–	–	–
Phalanx 3	134	9.2	134	82.7	8	9.2	8	22.2	1	14.3	0	0	1	14.3	3	42.9	2	28.6	–	–	–	–	–	–
Calcaneum	19	1.3	18	100	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astragalus	18	1.2	18	100	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carpal/tarsal	173	11.9	173	80.1	1	1.1	1	2.1	0	0	0	0	0	0	1	100	0	0	–	–	–	–	–	–
Vertebra	211	14.5	195	47.1	35	40.2	15	16.3	0	0	0	0	0	0	6	27.3	16	72.7	13	3	–	–	1	2
Rib	7	0.5	7	3.2	7	8	7	14.6	0	0	0	0	0	0	3	42.9	4	57.1	5	–	–	–	–	–
Total	1457		1312		87		56												78	7	3	1	6	8

Digestion damage numbers and percentage of rabbit bones included in each digestion category, *Tooth marks* numbers and location of tooth marks on rabbit remains, *FRE* fractured edges, *CRE* crenulated edges, *SCO* scoring, *NOT* notches, *TPI* tooth pits, *TPU* tooth punctures

samples. A total of 1544 bones and teeth were determined, 1457 coming from NI samples and 87 from scats.

In the NI sample, the estimated minimum number of individuals (MNI) was nine. The entire skeleton was represented except for the scapula. In absolute numbers, phalanges (27.6 %), vertebrae (14.5 %), carpal/tarsal bones (11.9 %) and upper molars (7.3 %) were the most numerous elements (N%). The relative abundance of skeletal elements (RA%) is also shown in Table 1 and Fig. 1. The mean value (75.2 %) was high, indicating a low loss of bones in the assemblage. The best-represented elements were the cranium, metatarsus, calcaneum, astragalus, femur and incisors; all of which displayed values of 100 %. Most skeletal elements (77.3 %) showed RA values over 75 %. Scapula, ribs and humerus were less well represented (0, 3.2 and 11.3 %, respectively).

The relative proportions of skeletal elements are shown in Table 2. Results indicate that there was a deficiency in the numbers of postcranial compared to cranial remains. Among the long bones, parts of the lower appendicular skeleton were more numerous than upper limb bones, with 1.3 times more elements from the hands and feet than the upper parts. The same goes for the relationship among zygopodium and stilopodium limb bones: there were 1.5 as many radii/ulnae/tibiae than humeri/femora. Posterior limb elements survived better than anterior elements.

In the SC sample the estimated minimum number of individuals (MNI) was only two individuals, indicating a loss of 77.8 % of the individuals originally consumed. The best-represented elements were the scapula, forelimb bones and cranial remains (Table 1). Some vertebrae, ribs, metacarpals and phalanges were also registered; other skeletal elements were absent. The relative abundance of skeletal elements (RA%) is also shown in Table 1 and Fig. 1. The mean value (15.2 %) was very low indicating an important loss of bones in the assemblage. The best-represented elements were the scapula (100 %), humerus/radius/ulna (50 % each) and cranium (50 %).

Proportion indices reveal that the scat sample contain more postcranial than cranial remains, more long bones than autopodium and more forelimb than hindlimb bones (Table 2); this pattern is the reverse of that seen in non-ingested remains.

Table 2 Proportions of different parts of the skeleton in non-ingested (NI) and scat (SC) samples. Abbreviations are explained in the "Material and Method" section

Indices %	NI	SC
PCRT/CR	75.9	523.6
PCRAP/CR	88.6	449.1
PCRLB/CR	96.1	960
AUT/ZE	130.2	44.9
Z/E	153.3	133.3
AN/PO	65.9	–

Breakage

Breakage was limited in the NI sample, with 65 % of specimens recorded over 10 mm in length. The percentage of complete bones was 92 %, and almost 24 % of long bones were complete. The ulna, radius and humerus were the elements most affected by breakage (Fig. 2). Breakage categories are shown in Table 3.

- The most common complete long bones were the femur (47.2 %) and the tibia (36.1 %), while the humerus was never complete. The shaft plus distal epiphysis was most common among the fractured portions of humerus, radius and ulna. On the contrary, femur and tibia fragments were mostly represented by proximal epiphysis portions. Most long bone fractures were mechanical, V-shaped and helical. Diaphyseal cylinders were not recorded in the assemblage.
- Metapodials were well preserved, 85.9 % of the metacarpals and 83.9 % of the metatarsals were complete. All the recovered fragments were parts of distal epiphysis.
- Of the skulls, 19.2 % survived complete and the most common fragments were parts of the neurocranium and maxillary bone.
- Mandibles were recovered fully intact in 48 % of cases. Condylar process and body fragments with the incisive part had a higher rate of survival than other fragments.
- Of the innominates, 73.9 % were complete. Among the fragments, only parts of the ischium were recovered.
- Scapulae fragments were not recovered.
- Most of the vertebrae were complete (82.9 %). Fragments were represented mainly by the vertebral body and vertebral epiphyses.
- The ribs were scarce, they were intact in 57.1 % of the cases.
- Carpals, tarsals and phalanges were complete in percentages above 94 % in all cases.
- All teeth were placed "in situ" and they were always complete.

In the SC assemblage, breakage was very high. This sample comprised mainly very small fragments, only 1.2 % of bones displayed length values over 10 mm and only 11.5 % of bones were complete. In addition, no complete long bones were recovered. In fact, the only complete bones were some phalanges and carpals (Fig. 2). Breakage categories are shown in Table 4.

- The long bones were only represented by fragments of humerus, radius and ulna. The proximal epiphysis was the most common among the fractured portions recovered.
- Metapodials were scarce and they were never complete.

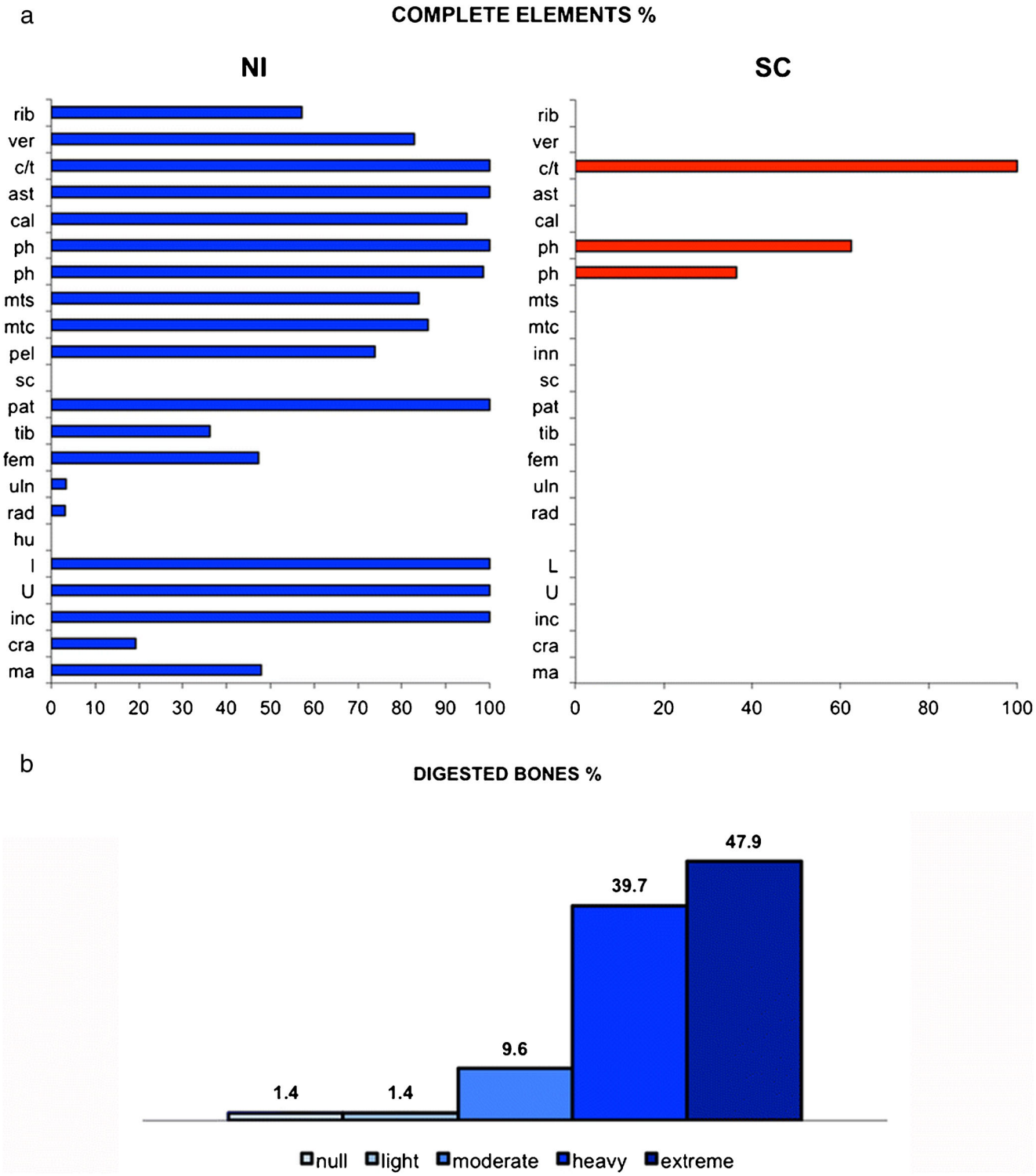

Fig. 2 **a** Percentage of complete rabbit remains in the scats (SC) and non-ingested (NI) remains samples. For abbreviations, see caption for Fig. 1. **b** Percentage of skeletal remains included in each digestion category

- The skull was only represented by parts of the neurocranium.
- For the mandible, only one fragment of the condylar process was recovered.
- Scapulae fragments always comprised the glenoid cavity (GC and glenoid cavity + neck (GCN)).
- The vertebrae were never complete. Fragments were mainly represented by vertebral body and spinous process.
- The ribs were fragmented in all cases.
- More than 47 % of phalanges appeared complete. Only one complete carpal was recovered.

Table 3 Numbers and percentages of parts of the skeleton included in each breakage category for the non-ingested remains sample

NI sample – breakage categories												
Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
humerus	0	0	0	0	0	0	1	33.3	2	66.6	0	0
radius	1	3.2	0	0	1	3.2	5	16.1	14	45.2	10	32.2
ulna	1	3.4	0	0	1	3.4	1	3.4	14	48.3	12	41.4
femur	17	47.2	10	27.8	1	2.8	0	0	0	0	8	22.2
tibia	13	36.1	9	25	3	8.3	5	13.9	4	11.1	2	5.5
metacarpus	73	85.9	0	0	0	0	0	0	0	0	12	14.1
metetarsus	73	83.9	0	0	0	0	0	0	0	0	14	16.1
Mandible	*N*	%	Cranium	*N*	%	Innominate	*N*	%	Scapula		*N*	%
C	12	48	C	5	19.2	C	17	73.9	C		0	0
IP	3	12	IB	0	0	A	0	0	GC		0	0
MBI	4	16	IBM	0	0	AIS	0	0	GCN		0	0
MB	1	4	M	4	15.4	AISIL	0	0	NF		0	0
MBB	0	0	ZA	1	3.8	AIL	0	0	F		0	0
PC	5	20	NC	16	61.5	IS	6	26.1				
						IL	0	0				
Vertebrae	*N*	%	Ribs	*N*	%	Phalanges 1/2	*N*	%	Phalanx 3		*N*	%
C	175	82.9	C	4	57.1	C	234	98.3	C		134	100
VB	20	9.5	F	3	42.8	P	4	1.7	F		0	0
VE	11	5.2				D	0	0				
SP	5	2.4										
Patella	*N*	%	Car/tar	*N*	%	Cal	*N*	%	Ast		*N*	%
C	5	100	C	173	100	C	18	94.7	C		18	100
F	0	0	F	0	0	F	1	5.3	F		0	0
Teeth	"in situ"						Isolated					
	incisors		upper molars		lower molars		incisors		upper molars		lower molars	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	54	100	106	100	81	100	0	0	0	0	0	0
F	0	0	0	0	0	0	0	0	0	0	0	0

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). Mandibles as C, incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB) and condylary process (CP). Crania as C, incisive bone (IB), incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). Innominates as C, acetabulum (A), acetabulum + ischium (AIS), acetabulum + ischium + illium (AISIL), acetabulum + illium (AIL), ischium (IS) and illium (IL). Scapulae as C, glenoid cavity (GC), glenoid cavity + neck (GCN), glenoid cavity + neck + fossa (GCNF), neck + fossa (NF) and fossa (F). Vertebrae as C, vertebral body (VB), vertebral epiphysis (VE) and spinous process (SP). Phalanges as C, proximal fragment, (P), distal fragment (D) and fragment (F). Patellae, carpals/tarsals, calcanea, astragali, ribs and teeth as C and F

Bone surface modifications

Digestion damage

In the SC sample 98.6 % of remains presented digestion damage with 47.9 % exhibiting "extreme" digestion and 39.7 % exhibiting "heavy" digestion damage; light digestion damage was recorded rarely (1.4 %, Fig. 2 and Table 1). Different bones were altered in similar proportions although vertebrae were damaged to a slightly greater extent. Normally, the entire surface of the bones was affected by digestion corrosion (Fig. 3) as a result of the high degree of breakage.

Tooth marks

In the NI sample, tooth marks were observed on 87 specimens (6 % of the sample). The most common form of damage was fractured edges (*N* = 79, 76.7 %), followed by punctures (*N* = 8, 7.8 %); pits (*N* = 6, 5.8 %); crenulated edges (*N* = 6, 5,8 %) and scoring (*N* = 4, 3.9 %) (Table 1, Fig. 4). On the whole, 1.2 % of bones displayed tooth pits and/or punctures.

Tooth marks were mostly documented in the radius (25.2 %) and vertebrae (18.4 %). Tooth pits and punctures were recorded on the mandible fossa; the shaft and distal

Table 4 Numbers and percentages of parts of the skeleton included in each breakage category for the scats remains sample. For abbreviations, see Table 3

SC sample – breakage categories

Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
humerus	0	0	3	42.9	0	0	3	42.9	0	0	1	14.3
radius	0	0	1	33.3	1	33.3	0	0	1	33.3	0	0
ulna	0	0	2	66.6	0	0	1	33.3	0	0	0	0
femur	0	0	0	0	0	0	0	0	0	0	0	0
tibia	0	0	0	0	0	0	0	0	0	0	0	0
metacarpus	0	0	0	0	1	25	0	0	2	50	1	25
metetarsus	0	0	0	0	0	0	0	0	0	0	0	0
Mandible	*N*	%	Cranium	*N*	%	Innominate	*N*	%	Scapula		*N*	%
C	0	0	C	0	0	C	0	0	C		0	0
IP	0	0	IB	0	0	A	0	0	GC		2	50
MBI	0	0	IBM	0	0	AIS	0	0	GCN		2	50
MB	0	0	M	0	0	AISIL	0	0	NF		0	0
MBB	0	0	ZA	0	0	AIL	0	0	F		0	0
PC	1	100	NC	3	100	IS	0	0				
						IL	0	0				
Vertebrae	*N*	%	Ribs	*N*	%	Phalanges 1/2	*N*	%	Phalanx 3		*N*	%
C	0	0	C	0	0	C	4	36.4	C		5	62.5
VB	15	42.9	F	7	100	P	1	9.1	F		3	37.5
VE	5	14.3				D	6	54.5				
SP	15	42.9										
Patella	*N*	%	Car/tar	*N*	%	Cal	*N*	%	Ast		*N*	%
C	0	0	C	1	100	C	0	0	C		0	0
F	0	0	F	0	0	F	0	0	F		0	0
Teeth	"in situ" incisors		upper molars		lower molars		isolated incisors		upper molars		lower molars	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	0	0	0	0	0	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0	0	0	0	0	0

epiphysis of the radium; the proximal epiphysis of the femur; the acetabulum and ilium of the innominate; and the vertebral body. In many cases, different types of tooth marks were documented in the same specimen. In the SC sample, as a consequence of the high degree of breakage and digestion damage, tooth marks were not found.

Density-mediated attrition

There was no statistically significant correlation between bone mineral density and the frequency of rabbit skeletal portions recovered in the NI and SC samples (rho = 0.21, $p = 0.429$ and rho = 0.1, $p = 0.703$, respectively). This indicates that preservation of rabbit remains accumulated by the wildcat are generally unaffected by structural density-mediated attrition (after Pavao and Stahl's 1999).

Discussion

The taphonomic signal of the European wildcat has not been characterized in previous works. Results obtained in this study show that this small carnivore only removes a specific number of skeletal elements during feeding, with large parts of prey remaining unconsumed. Such behaviour can generate important accumulations of non-ingested bones that according to the data collected in the present study are characterized by the lack or scarcity of scapulae, humeri and axial skeletal remains; the prevalence of cranial elements and greater survival of hindlimbs over forelimbs; high frequencies of whole bones and scarcity of tooth pit/punctured bones.

The scat sample comprised only 87 identifiable remains, bones from scats were scarce and difficult to identify. Although the sample is small, bone assemblages accumulated from wildcats scats appear to be characterized by an abundance

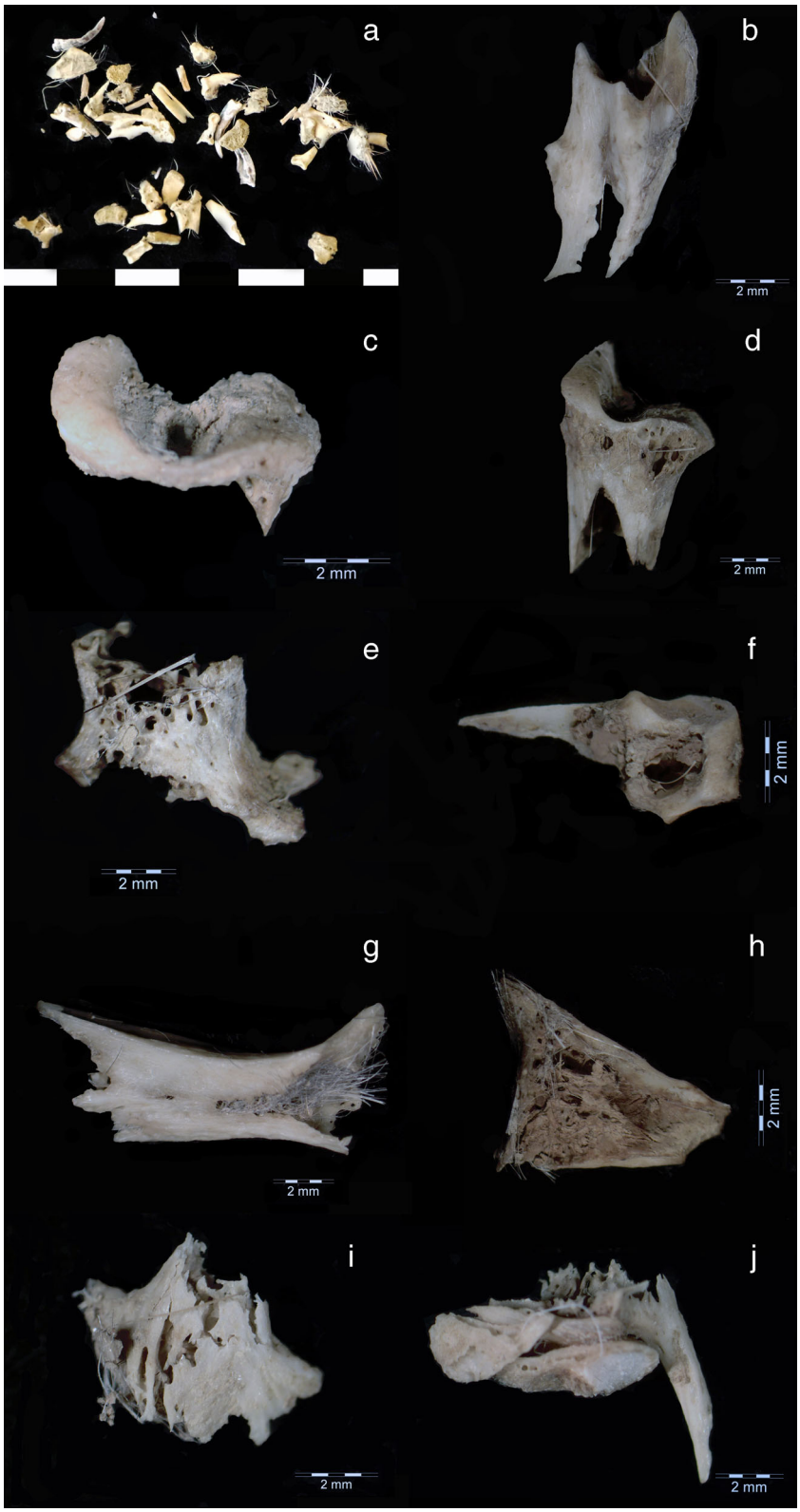

Fig. 3 Examples of very fragmented and digested rabbit bones recovered from wildcat scats (**a**). Fragments of ulna (**b**), radius (**c**, **d**), humerus **(e**), matapodial (**f**), scapula (**g**, **h**) and vertebrae (**i**, **j**) affected by extensive digestion corrosion damage

of scapulae and forelimb bones; a prevalence of postcranial elements and greater survival of forelimbs over hindlimbs; high frequencies of small-sized fragmented bones; and almost 90 % of remains affected by extreme and heavy digestion corrosion without the presence of tooth pit/punctured bones. This evidence demonstrates that wildcat rabbit accumulations may differ significantly, depending on the origin of the assemblage (Tables 1 and 2). The fact that skeletal remains in wildcat scats

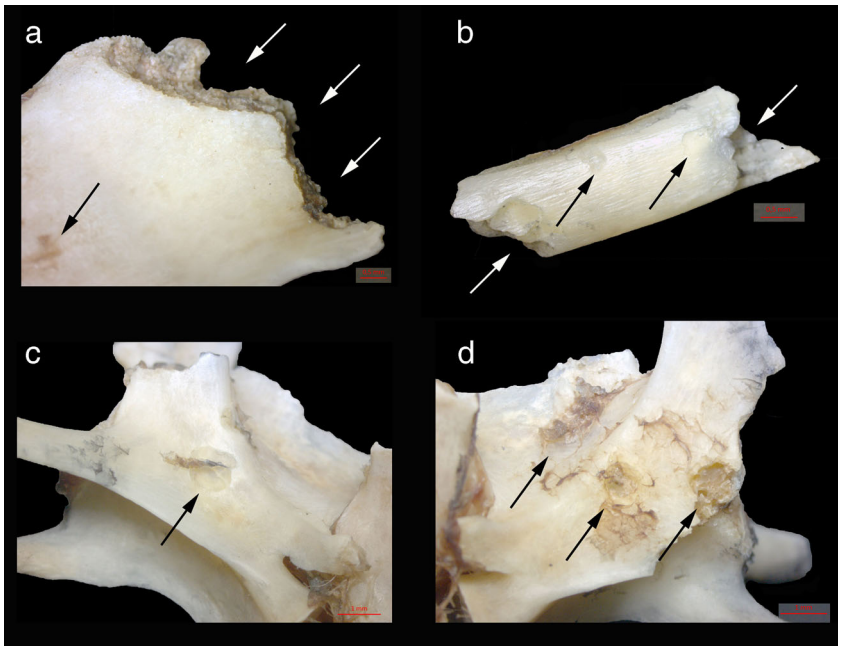

Fig. 4 Examples of tooth marks on rabbit bones recovered from wildcat non-ingested remains sample. Crenulated edges (**a**), fractured edges (**b**), pits and punctures (**a**, **b**, **c**, **d**)

are rare and highly fragmented reduces the likelihood that they will be recovered archaeologically.

It is clear that working with captive animals permit a major control of different variables affecting experimentation. However, it has been pointed before for other larger carnivores, that captivity may influence predator behaviour and how they modify faunal assemblages (Gidna et al. 2013). To take into account the context in which assemblages are originated is essential. Taking this in mind, we are aware that some bias may be produced concerning our results as they derive from a captive wildcat. Also, the small size of the scats sample implies the need to be cautious with the results from ingested elements. Nevertheless, this research is the first in wildcat modifications and these results are a first approach that may be very useful to researchers analysing archaeological leporid assemblages.

The wildcat and other predators

The results of this research demonstrate that the taphonomic pattern left by wildcats on rabbits differs from other predators. To facilitate comparisons, Table 5 presents a summary of results obtained from different European rabbit predators, where the data have been collected using the same methods.

Comparisons of anatomical representation profiles

Values of anatomical representation indices obtained for the wildcat differ from nocturnal and diurnal raptors. In the wildcat NI remains sample, most skeletal elements display higher relative abundance than in all the raptors samples (Fig. 5). However, there are a few skeletal elements (e.g. the humerus and scapula) that are less well represented in the wildcat sample, than in raptor assemblages. In contrast, in the wildcat SC sample, most skeletal elements are less well represented than in the raptor assemblages with the exception of scapulae and forelimb long bones, which are more abundant in the wildcat accumulation (Lloveras et al., 2008b, 2009, 2014b).

Comparisons with other terrestrial carnivores also show differences in anatomical representation such as the higher representation of cranial remains in the NI wildcat sample (Fig. 6). Long bones, particularly the femur, were also much better represented. Profiles of RA for wildcat, lynx and fox show that wildcats consume little of the rabbit skeleton, whereas the red fox destroys most bones and the Iberian lynx is situated in an intermediate position. While inter-specific differences are less clear in the scat sample, they are still evident (Fig. 6). Lloveras et al. (2012a) reported that red fox accumulations were characterised by high values for the relative abundance of cranial remains and upper limb bones from both anterior and posterior limbs. All these elements are visibly scarcer in the wildcat SC sample. Chi-square test of independence were used for comparing survivorship of skeletal elements or their fragments showing that differences in the relative abundance of both taxa are statistically significant ($\chi^2 = 117.9$, $P < 0.01$, df = 12). Comparison with the taphonomic signature of Iberian lynx scat samples also shows significant differences ($\chi^2 = 268.1$, $P < 0.01$, df = 12). Lynxes tend to accumulate larger numbers of cranial remains, innominate and hindlimb bones (Lloveras et al. 2008a). The scapula is the only skeletal element that is noticeably better represented in the wildcat scat accumulation.

These differences observed in the anatomical representation profiles of wildcat prey reflect the feeding behaviour of this carnivore. When feeding on rabbits, wildcats start consuming the meat located around the axial skeleton, forelimb bones and

Table 5 Anatomical representation, breakage, digestion and teeth/beak marks for leporid remains accumulated by different types of predators compared with the results obtained for European wildcats in the present study

Rabbit predator comparisons	Eagle owl *Bubo bubo*	S. Imperial eagle *Aquila adalberti*	Bonelli's eagle *Aquila fasciata*	Fox *Vulpes vulpes*		Iberian lynx *Lynx pardinus*		European wildcat *Felis silvestris*	
Reference	Lloveras et al. 2009	Lloveras et al. 2008b	Lloveras et al. 2014b	Lloveras et al., 2012a		Lloveras et al. 2008a	Rodríguez-Hidalgo et al. 2013	Present study	
Origin	Nest	Pellets	Nest	Scats	Non-ingested	Scats	Non-ingested	Scats	Non-ingested
N	1808	824	438	265	639	1522	9564	87	1457
RA% > values	cal-inn-fem	phal 3-u mol-tib	cr-u mol-inn	long bone-sc	mts-ast-tib	man-teeth-cra	tib-cal-mts	sc-hu-ra-ul-cr	cr-fe-mts-cal
RA% < values	mtc-c/t	rib-fem-rad	mtc-rib	mtc-c/t-inn	cr-sc-rib	c/t-ver-rib	sc-ver-hum	teeth-hindlimb	sc-rib-hu-ver
PCRT/CR	+postcranial	+cranial	+cranial	=	+postcranial	+cranial	+postcranial	+postcranial	+cranial
P/D	+proximal	+distal	+proximal	+proximal	+distal	+proximal	+distal	+proximal	+distal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+forelimb	+hindlimb	+forelimb	+hindlimb
Complete elements %									
Mean value long bones	14.6	0	51.7	0	5.4	2.5	37.6	0	23.7
Mean value total	53.9	27	74.7	12	89.4	43	73–78	11.5	92.3
Length (in mm)									
Minimum	2.3	1.8	1.7	3	4	1.1	3	2	2
Maximum	86.3	36.1	89.6	26.8	86.2	30.1	69	11.4	138.2
% <10 mm	49	73	54.9	61	28	80	19.7	98.8	35
% Digested remains	68.8	98	31.2	99.5	–	97.2	–	98.6	–
% Digested long bones	88.9	100	31	100	–	100	–	100	–
Degree									
Null	31.2	2	68.8	0	–	2.8	–	1.4	–
Light	40.2	18.2	2.3	6	–	12	–	1.4	–
Moderate	19.8	46.8	7.9	26	–	22	–	9.6	–
Heavy	8	27.4	14.4	43	–	43.8	–	39.7	–
Extreme	0.7	5.6	6.5	25	–	19.3	–	47.9	–
Teeth/beak pits and punctures	2	0.5	0.8	3	9.5	0.3	0.9	0	1.2
Age - % of adults	50	–	41.4	87	–	21.4	–	–	–

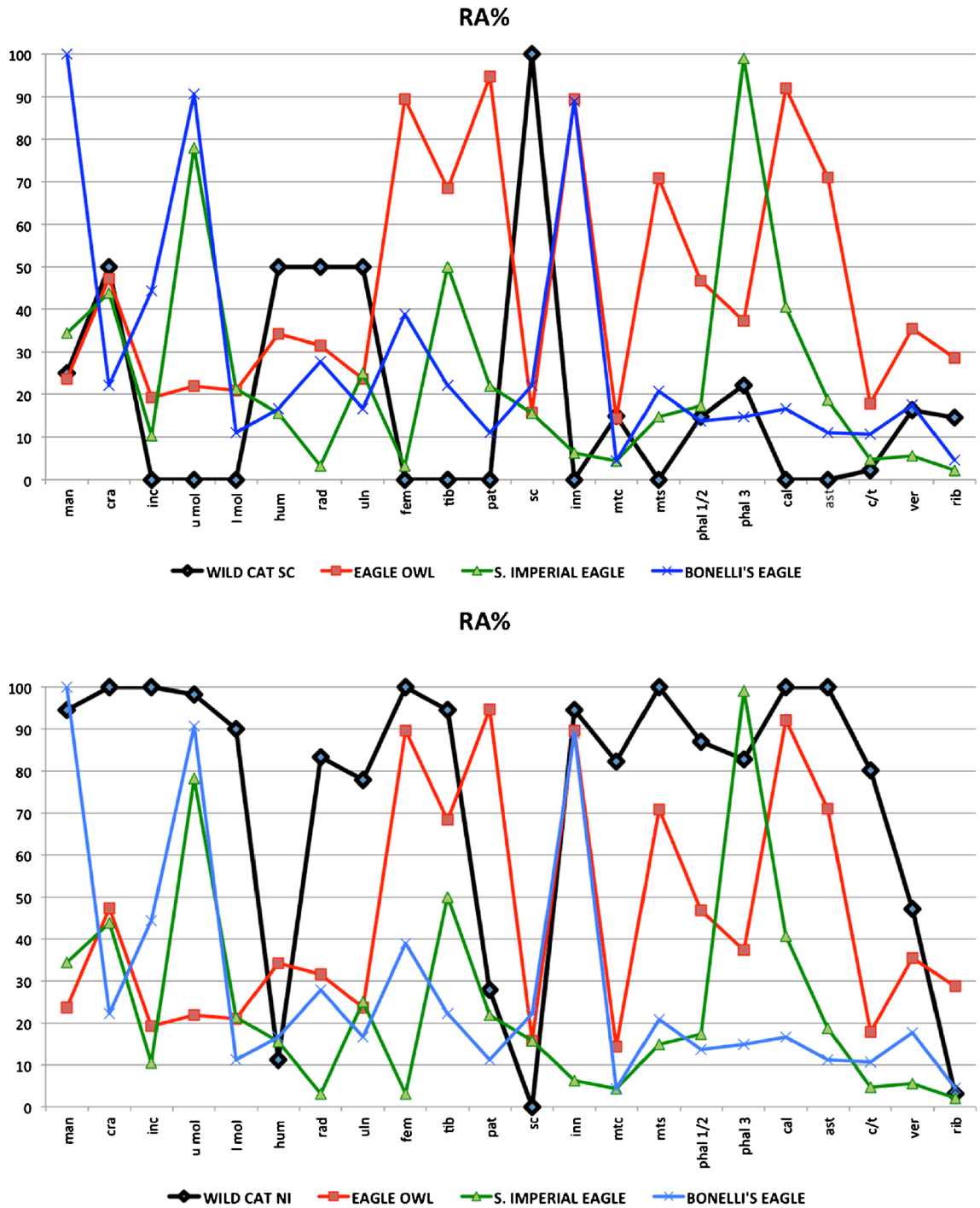

Fig. 5 Comparisons of relative abundance of different parts of the skeleton in raptors and wildcat (non-ingested and scats) samples. For abbreviations, see the caption for Fig. 2

crania, and only a few fragments of bones are ingested (observed by researchers from Wildcat Breeding Center of Vallcalent).

Comparisons of breakage patterns

Observation of breakage patterns reveal a low degree of fragmentation in the wildcat NI sample: 65 % of remains were over 10 mm and the percentage of complete bones was 92 %. These values indicate that the wildcat fragmented non-ingested remains less than diurnal and nocturnal raptors nests, where the percentage of remains over 10 mm were 45–50 % and the percentage of complete bones 38–75 % (Schmitt 1995; Lloveras et al. 2009, 2012b, 2014b; Table 5). However, this trend is reversed with forelimb long bones. The ulna, radius and humerus were the elements most affected by breakage (the humerus was never recovered complete) in the wildcat sample with an average of 2.2 % of

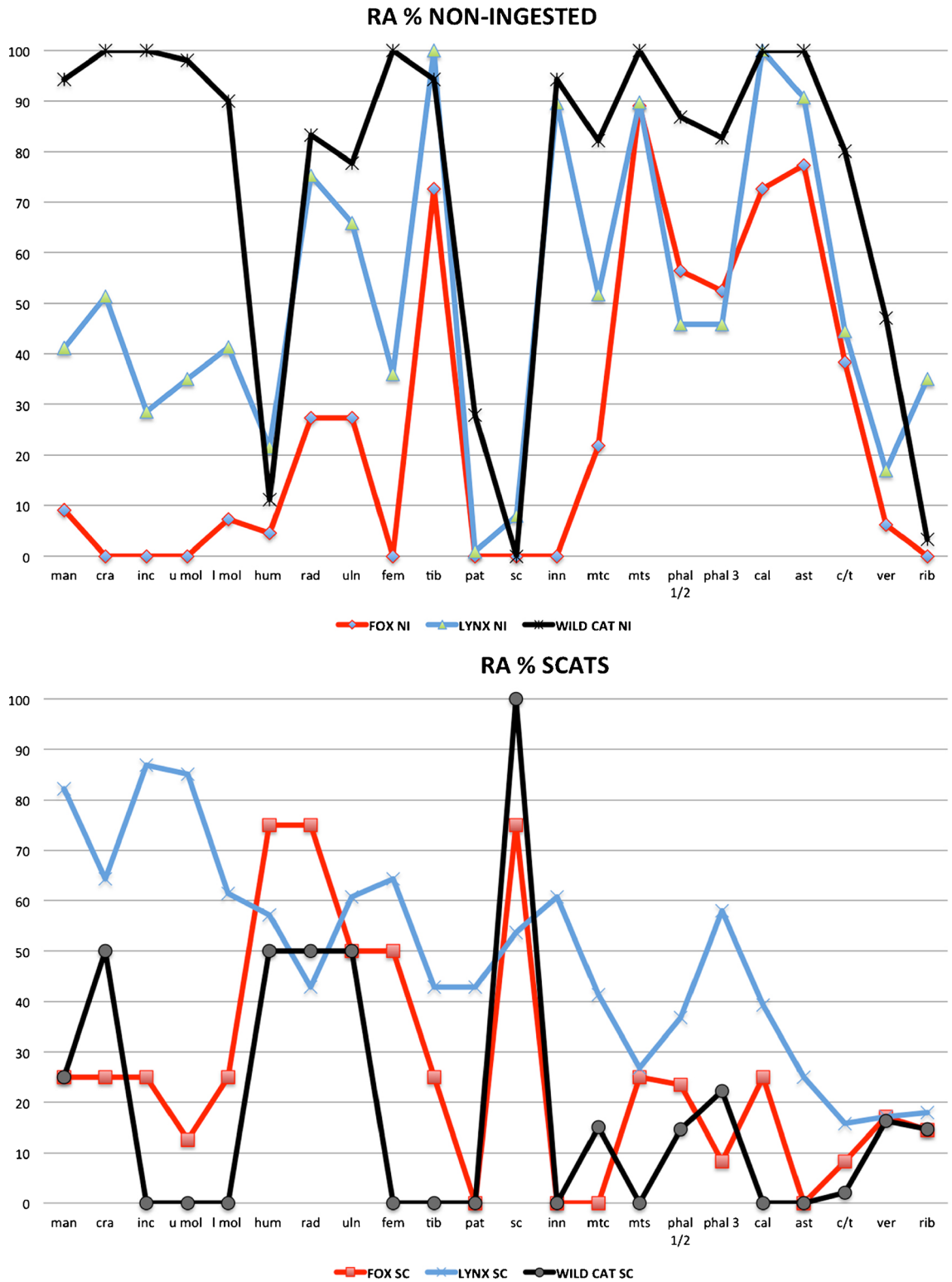

Fig. 6 Comparisons of relative abundance of different parts of the skeleton in red fox, Iberian lynx and wildcat (non-ingested and scats) samples. For abbreviations, see the caption for Fig. 2

complete elements (Table 3). This average was much higher in all raptor nest assemblages: 40 % for eagle owl; 50 % for Bonelli's eagle and 33.4 % for golden eagle (Schmitt 1995; Lloveras et al. 2009, 2012b, 2014b).

The scat sample was more affected by breakage than raptor accumulations, even than those originating from pellets which are always constituted of more fragmented elements. The percentage of complete bones and complete long bones obtained

in the present study (11.5 and 0 %) is lower than the values recorded for Bonelli's eagles (59.6 and 15.4 %) and Spanish imperial eagles (27 and 0 %) pellets.

With regards to terrestrial carnivores, wildcat, Iberian lynx and red fox leporid assemblages of NI remains are characterised by a low degree of fragmentation. The percentage of remains over 10 mm, complete elements and complete long bones are similar for all carnivores. In fact, given that these completeness values can vary slightly as consequence of intraspecific variables (age of the prey, age of the predator, rabbit abundance, etc.) (Lloveras et al. 2012a; Rodríguez-Hidalgo et al. 2013, 2015), values obtained for different carnivores could overlap, making any distinction difficult.

Breakage patterns are also similar in wildcat, fox and lynx scat assemblages. Rabbit fragments from wildcat scats are slightly smaller than in scats of Iberian lynx and fox. Equally, the percentage of complete elements is higher in the lynx sample but practically the same in the red fox (Table 5). However, more studies of wider wildcat scat samples are required to confirm these subtle differences.

Comparisons of bone surface modifications

Different types of predators produce similar kinds of teeth/beak damage when feeding on rabbit carcasses. This study shows that in the NI sample, the percentage of bones with tooth damage (6 %) is similar to those recorded in raptor nest accumulations such as the Bonelli's (4.1 %) eagle or the Egyptian vulture (7.5–10.4 %) (Lloveras et al. 2014a, 2014b; Sanchis Serra et al. 2014). The percentage of tooth pits/punctures (1.2 %) is lower than the beak pits/punctures registered in European eagle owl nest accumulations (2 %) but higher than values obtained for Bonelli's eagle (0.8 %). However, values are too close to distinguish predators. The innominate, vertebrae, femora and mandibles were commonly affected by surface modifications in these studies. These bones were also affected in the wildcat sample, but most marks were documented on the radius (25.2 %). The presence of different types of tooth marks registered in the same specimen (related to gnawing damage) is uncommon in raptor accumulations.

Distinguishing the damage produced by different terrestrial carnivores is more challenging. The percentage of tooth pits/punctures has been defined as one of the best characteristics to discriminate between Iberian lynx and red fox leporid accumulations Different studies show that lynxes produce much less damage (0.8–1.8 %) than foxes (9.5–19 %) (Cochard 2004; Lloveras et al. 2008a, 2012a; Sanchis Serra and Pascual Benito 2011; Rodríguez-Hidalgo et al. 2013, 2015).

On the whole, in the wildcat NI sample, 1.2 % of bones displayed tooth pits and/or punctures. This low percentage also places the wildcat far from the red fox but in the same range of damage expected for the Iberian lynx. One possible difference to explore between both carnivores could be the location of tooth marks. As noted earlier, in the wildcat, most of the marks were documented in the radius (25.2 %) and vertebrae (18.4 %); however in the lynx samples, the tooth marks occurred most commonly in innominates (26 %) and tibiae (20 %).

Regarding digestion damage, the percentage of digested remains in the wildcat SC sample (98.6 %) is higher than values obtained for raptor nest accumulations (i.e. 68.8 % for Eagle owl, 31.2 % for Bonelli's eagle, Table 5), but similar to the percentage of digested bones in some raptor pellets (i.e. 98 % for Spanish imperial eagle) and other terrestrial carnivore scat assemblages (where almost 100 % of remains exhibit digestion damage). However, in the wildcat sample, digestion damage is clearly more pronounced than in the raptor samples, with a higher percentage of remains affected by an extreme degree of damage (47.9 vs 5.6 %). Digestion corrosion damage is also stronger in the wildcat sample than in the red fox and Iberian lynx scat accumulations (47.9 vs 25 and 19.3 %, Table 5).

Conclusions

In this study we provide the first detailed taphonomic observations on rabbit remains accumulated by the European wildcat. The results obtained help to identify and classify the most important characteristics of rabbit bone assemblages created by this carnivore. Identifiable rabbit remains are scarce in scats. Non-ingested material is characterized by the lack/scarcity of the scapula, humerus and axial skeleton remains, whereas the scapula and forelimb bones are the most abundant elements in scats. Non-ingested remains are much less fragmented and show a high percentage of complete bones. Rabbit remains in scats are affected by extreme and heavy digestion corrosion. Tooth marks are scarce and only evident on non-ingested remains.

Comparisons between the taphonomic signature of European wildcat and other rabbit predators showed that there are great similarities especially between wildcats and other terrestrial carnivores. Nevertheless, damage caused by wildcats on rabbits differ sufficiently from modifications produced by foxes and Iberian lynxes. The biggest difference lies in the anatomical representation profile. The frequency of tooth marks also differs from foxes, which can generate much larger numbers of tooth pits/punctures than the wildcat, although it is close to the values obtained for the Iberian lynx.

On archaeological sites, assemblages dominated by non-ingested remains are the most likely to be encountered; however, results may vary depending on the relative proportion of remains derived from scats. In fact, archaeological assemblages most often result in complex palimpsests of depositional history, mixing debris from prehistoric human occupations with those from other processes, both geological and faunal (Enloe 2012). The use of the reference data obtained in this

study and others of the kind, is one way of deciphering portions of complex depositions. The taphonomic pattern obtained with fossil assemblages will rarely match exactly to the taphonomic signature here described, precisely as a consequence of the existence of palimpsests that mix signatures originated by different agents. However, the criteria presented in this study for both types of accumulations (scats and non-ingested) can help to assess the potential contribution of European wildcats in accumulating fossil rabbit remains on archaeological sites.

Acknowledgments Ll. Lloveras was funded by postdoctoral fellowships BP-A 00334 2011 and BPB-00140-2014 from the Secretaria d'Universitats i Recerca del Departament d'Economia i Coneixement de la Generalitat de Catalunya and COFUND programme (Marie Curie Actions). Financial support from research projects HAR2014-55131 from the Ministerio de Ciencia e Innovación (MICINN) and SGR2014-108 from the Generalitat de Catalunya are gratefully acknowledged.

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