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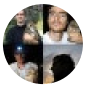

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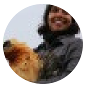

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Understanding the taphonomic signature of Bonelli's Eagle (*Aquila fasciata*)

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ABSTRACT

Bonelli's eagle (*Aquila fasciata*) is a large bird of prey that breeds in warm regions of the Palearctic. In Europe, it is mainly found in the Mediterranean region, in open or partially-open landscapes in mountainous areas. They normally feed on mammals, up to the size of a hare, medium-sized birds and large reptiles.

The remains of Bonelli's eagles have been found at Pleistocene archaeological sites, raising the possibility that they were active bone accumulating agents in caves and shelters, a practice evidenced by contemporary studies that show their nests are usually located on rocky cliffs.

Taphonomic studies on prey remains consumed by these raptors do not exist and their role in bone accumulations at archaeological sites is not understood. We analyse non-ingested bone remains and pellets recovered at well-known Bonelli's eagle nests situated in the south of Spain and Portugal with the aim of characterising their accumulations. Specifically, we detail taxonomic and anatomical representation, bone breakage, beak marks and digestion damage. Results show that European wild rabbit (*Oryctolagus cuniculus*), red-legged partridge (*Alectoris rufa*) and pigeons (*Columba* spp.) are the dominant prey. The taphonomic pattern varies depending on the type of prey and the origin of skeletal materials (non-ingested versus pellets). Comparisons with other agents of bone accumulation (birds of prey and terrestrial carnivores) suggest that the taphonomic signature of Bonelli's eagle differs from most other predators.

1. Introduction

Bonelli's eagles (*Aquila fasciata*) are widespread raptors, with a range extending from the Iberian Peninsula and NW Africa across southern Europe, the Middle East and the Arabian Peninsula through Afghanistan to India, south China and Indonesia. Western Palaearctic populations are distributed mainly in the Mediterranean area, generally in fairly warm and dry regions (Cramp and Simmons, 1980; Ferguson-Lees and Christie, 2001; Real, 2003).

They inhabit open or partially-open landscapes often in hilly areas and prefer short or sparse vegetation, such as garrigue, dry grassland and rocky habitats; however, its habitat can be highly variable including forests and parkland as well as bushes and scrub. It is also often found in open habitats with non-intensive crops, vineyards, olive groves, small woodlands and pastures (Cramp and Simmons, 1980; Tucker and Heath, 1994).

Despite a marked decline in numbers since the early 1980s, Bonelli's eagle is still present in most of the Iberian Peninsula with the exception of the Cantabrian region and in the north-western quarter of Spain (Cabral, 2008; Del Moral, 2006). Pairs are primarily distributed in the Mediterranean regions (from southern Portugal to Catalonia), in the mountainous areas with a Mediterranean climate characterized by hot summers and low precipitation (Muñoz et al., 2005; Ontiveros and Pleguezuelos, 2003; Palma et al., 1996; Real and Mañosa, 1997).

Bonelli's eagles are large birds of prey (55–67 cm in length and a mass of 1.5–2.5 kg [Cramp and Simmons, 1980]) that feed on medium-sized mammals, birds and reptiles. Previous feeding

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studies have shown that rabbits, partridges and pigeons are the preferred game but they also take hares, squirrels, rodents, corvids and lizards among others (Caro et al., 2011; Del Amo et al., 2008; Ontiveros and Pleguezuelos, 2000; Ontiveros et al., 2005; Palma et al., 2006; Real, 1996; Valkama et al., 2005). Rabbits seems to be the favourite prey of the eagle in terms of weight and energetic value, but when they are scarce, the eagle preys upon a wider range of species that are more difficult to capture and offer lower calorific returns (Arroyo and Ferreiro, 1997; Moleón et al., 2009).

While Bonelli's eagles do nest in trees (particularly in south Portugal, although less than 4% of the Spanish population do it), breeding is normally in holes in cliffs rock shelters of variable size (Del Moral, 2006; Palma et al., 2006). Pellets and leftover prey remains accumulate on the surface of the nest and under roosting sites and perches of the surrounding area (Real, 1996). Pleistocene-aged remains of Bonelli's eagles have been found in archaeological deposits at Gruta da Figueira Brava (Portugal), Brechas de la Cantera de l'Altissent (Spain) and Devil's Tower and Gorham's Cave (Gibraltar) (Tyrberg, 2008), raising the possibility that they were active bone-accumulating agents in prehistoric caves and shelters. Their nests can therefore occur in the same spaces frequented by prehistoric hunter-gatherers populations and the food remains of both may become intermingled. Establishing the taphonomic signature of this diurnal raptor is necessary to distinguish between human and eagle accumulations.

In recent years, assessment of the origin of small prey bone accumulations from archaeological sites has become an important line of taphonomic research. In order to identify the agent responsible for accumulations of small prey, several actualistic studies have been conducted for terrestrial carnivores (e.g. Alvarez et al., 2012; Cochard, 2004a; Lloveras et al., 2008a, 2012a; Mallye et al., 2008; Mondini, 2002; Rodríguez-Hidalgo et al., 2013; Sanchis, 2000; Sanchis Serra and Pascual Benito, 2011; Schmitt and Juell, 1994; Stiner et al., 2012) and nocturnal and diurnal raptors (Bochenski, 2005; Bochenski et al., 1997, 1999, 2009; Cochard, 2004b; Hockett, 1989, 1991, 1995; 1996; Laroulandie, 2002; Lloveras et al., 2008b, 2009, 2012b, 2014a; Sanchis, 2000; Sanchis et al., 2013; Schmitt, 1995; among others). Information provided by these taphonomic studies is necessary to understand the formation processes at archaeological and palaeontological sites, and distinguish human and other animal agents of accumulation. The aim of our study is to elucidate the taphonomic patterns of prey remains recovered from modern nests and pellets of Bonelli's eagles and to establish diagnostic features that can be used to evaluate their role as contributors of bone accumulations in archaeological assemblages.

2. Materials and methods

We analysed osteological remains of prey from nine Bonelli's eagle nests located in two areas in the south of the Iberian Peninsula (Fig. 1): six nests from the Algarve and Alentejo regions (south of Portugal) and three nests from the Sistema Bético (south of Spain).

All materials were collected by the authors (AD, RL and JC) between 2007 and 2012 after the breeding season to avoid disturbing the birds. Each sample comprises non-ingested remains and pellets collected on the surface of nests and in the surrounding areas beneath them (Fig. 2). Feeding behaviour studies of Bonelli's eagles show that these raptors usually remove uneaten prey remains from the nest; only a low proportion of remains are left on the surface (Real, 1996). For this reason, most non-ingested bones can be found on perches or on the floor around nests.

Pellets were disaggregated while dry to separate the osteological material and bones and teeth were sorted under a magnifying glass to prepare for analysis. Skeletal remains were anatomically determined, sided, and identified to taxon whenever possible.

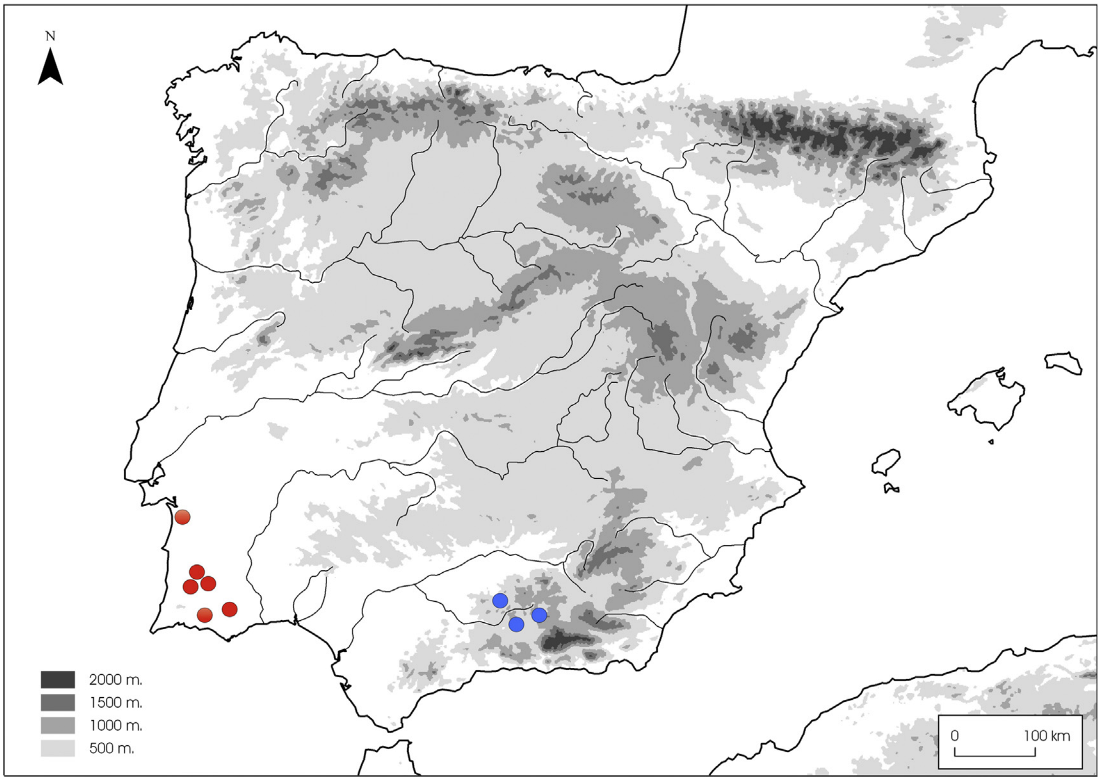

Fig. 1. Locations from which Bonelli's eagles nests samples were collected. In red: Portuguese samples. In blue: Spanish samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. Examples of pellets and non-ingested materials recovered from Bonelli's Eagle nesting areas.

Identifications were carried out using the animal bone reference collection of the School of Archaeology and Ancient History Bone Laboratory, University of Leicester. The Number of skeletal elements (N), Number of Identified Specimens Present (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated as well as relative frequencies.

Determination of the age at death of the prey mammals was only possible for rabbits and was estimated taking into account the epiphyseal fusion state of long bones (humeri, femora and tibiae), metapodials, scapulae, calcanei and innominates (Rogers, 1982; Taylor, 1959). Only two age categories were considered, adult and immature.

To facilitate comparison of the taphocoenosis of Bonelli's eagle with other predators, the analytical methodology follows the same criteria applied in previous works (Lloveras et al., 2008a, 2008b, 2009, 2012a, 2014a):

2.1. Anatomical representation

Relative abundance was calculated using the formula advocated by Dodson and Wexlar (1979):

$$RA_i = MNE_i/MNI \times E_i$$

(RA_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; E_i = the number of element i in the prey skeleton).

In addition, proportions of skeletal elements in mammalian prey were evaluated using the following ratios (Andrews, 1990):

(a) PCRT/CR – 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 – 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 – 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 – autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae);
(e) Z/E – zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

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

The following ratios were calculated for birds:

(a) To assess the differential representation of wings and legs (following Ericson, 1987), the number of wing elements (humeri, ulnae, carpometacarpi) was divided by the sum of wing and leg elements (femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.
(b) To evaluate the presence of proximal and distal elements (Bochenski and Nekrasov, 2001), the number of proximal elements (scapulae, coracoids, humeri, femora, tibiotarsi) was divided by the sum of proximal and distal fragments

(ulnae, radii, carpometacarpi, tarsometatarsi), and expressed as a percentage.

(c) To appraise the proportions of core and limb elements (Bochenski, 2005), the number of core elements (sterna, pelves, scapulae, coracoids) was divided by the sum of core and limb elements (humeri, ulnae, radii, carpometacarpi, femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.

All the ratios were calculated using the MNE.

Chi-square test and *Z*-test were used to evaluate the significance of differences in survivorship of particular skeletal elements or their fragments.

2.2. Breakage

The breakage pattern was described by the maximum length of all identified skeletal elements. Percentages of complete elements, isolated teeth (for mammals) and articulated elements were also calculated (Andrews, 1990). Fragmentation of bones was analysed using separate categories for mammals and birds. For all mammals, bone fragments were categorised depending on bone type:

- Patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F).
- Phalanges were recorded as complete (C), proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as fragment (F).
- Vertebrae were registered as complete (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 complete (C) or fragmented (F).
- Breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates follow those proposed by Lloveras et al. (2008a) and applied in subsequent studies (Lloveras et al., 2008b, 2009, 2012a, 2014a).

Breakage of bird bones was analysed using the methodology proposed by Bochenski et al. (1993). The ratio of proximal and distal portions of long bones (Bochenski, 2005) was calculated to observe the differences between whole bones and proximal and distal parts.

2.3. Digestion

Damage to the bone surface was observed under light microscope (×10–×40 magnification). Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo and Andrews, 1992; Lloveras et al., 2008a, 2008b, 2014b). Five categories of digestion were distinguished: null (0); light (1); moderate (2); heavy (3); and extreme (4).

2.4. Beak/talon marks

Damage to bone surfaces caused by beaks were noted and counted. Following the methodology used in previous studies (Lloveras et al., 2008a, 2008b, 2009, 2012a, 2014a) beak marks were classified as scoring, notches, tooth punctures/tooth pits and crenulated/fractured edges (Andrews, 1990; 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., 2013).

3. Results

A total of 826 skeletal fragments was analysed, 321 from south Portugal and 505 from south Spain. For analytical purposes the data from all nest sites have been combined and analysed as a single assemblage. Since the accumulating agent is the same for each sample it was assumed that the taphonomic pattern would be identical.

3.1. Taxonomic representation

The taxa recovered from the samples are presented in Table 1. The leporid sample was exclusively European wild rabbit (*Oryctolagus cuniculus*). Two unidentified small mammal bone fragments were also present. The birds included red-legged partridge (*Alectoris rufa*), pigeon (*Columba* spp.), dove (*Streptopelia* spp.), Eurasian jay (*Garrulus glandarius*), yellow-legged gull (*Larus michahellis*) and unidentified corvids, Ciconiiformes and passerine remains. Fish were represented by a single specimen attributed to Cyprinidae (carps, true minnows, and their relatives).

The most abundant taxon was European rabbit, which made up 53% of the total sample, followed by birds (46.6% – red-legged partridge (21.5%), pigeon (16.3%) and dove (3.4%)), small mammals (0.2%) and fish (0.1%) (Table 1, Fig. 3). The most abundant taxa when quantified by MNI were European rabbit (9), red-legged partridge (8) and pigeon (7).

Table 1 separates the taxonomic abundance for the Portuguese and Spanish samples. In both regions rabbits, red-legged partridges and pigeons were clearly the most numerous species. However, rabbits and pigeons were better represented in the Spanish sample. Partridges were more common in the Portuguese sample, which also included a greater diversity of taxa.

3.2. Age at death

Age at death was only estimated for rabbits and revealed a preponderance of immature individuals ($N = 34$, 58.6%).

3.3. Taphonomic analysis

All body parts were represented in the samples, though their presence and frequency varied by taxonomic group. Observation of

Table 1
NISP (Number of Identified Specimens), MNE (Minimum Number of Elements) and MNIs (Minimum Number of Individuals) by taxon recovered in Portuguese and Spanish samples.

	Portuguese sample		Spanish sample		Whole sample			
TAXA	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**MNE**	**MNIs**
Leporids								
Oryctolagus cuniculus	140	43.6	298	59	438	53	385	9
Small mammals								
Unidentified	–	–	2	0.4	2	0.2	2	1
Birds								
Alectoris rufa	116	36.1	62	12.3	178	21.5	147	8
Columba spp.	31	9.7	104	20.6	135	16.3	125	7
Streptopelia spp.	–	–	28	5.5	28	3.4	28	2
Garrulus glandarius	7	2.2	–	–	7	0.8	7	1
Corvidae	1	0.3	–	–	1	0.1	1	1
Ciconiiformes	12	3.7	–	–	12	1.5	12	1
Larus michahellis	5	1.6	–	–	5	0.6	5	1
Passeriformes	7	2.2	–	–	7	0.8	7	1
Unidentified	1	0.3	11	2.2	12	1.5	12	1
Fish								
Cyprinidae	1	0.3			1	0.1	1	1
Total	321		505		826		732	

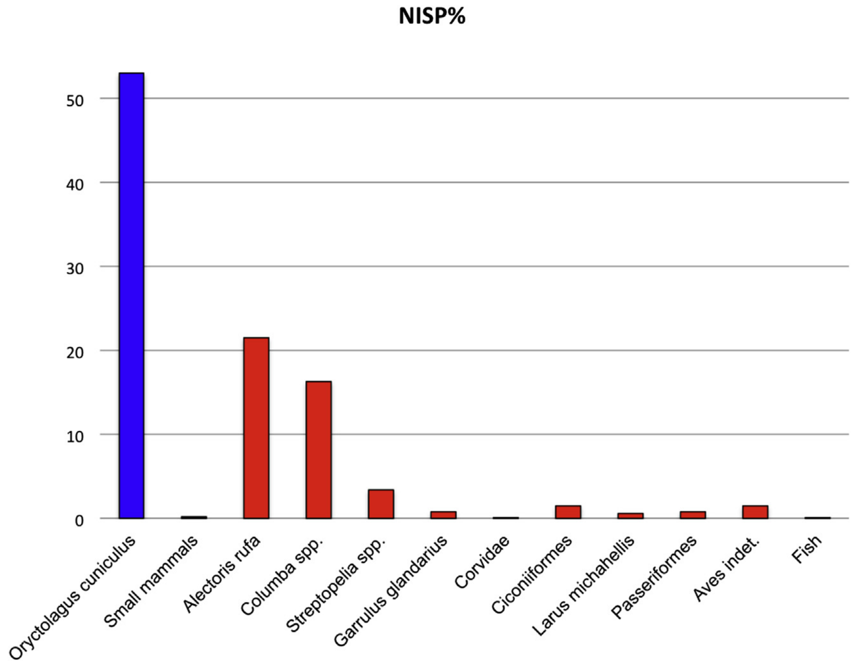

Fig. 3. Relative abundance of prey taxa (%NISP).

breakage patterns reveals that prey remains were moderately fragmented with an average percentage of complete bones of 62.6%. Additionally, a total of 43.4% of the remains measured less than 10 mm in length, 38.7% of bones were articulated and 62.7% of teeth remained *in situ*. Damage from digestion affected 44.7% of the remains and most (49.2%) showed a heavy degree of corrosion. Beak or talon marks occurred on 34 remains (4.1%), crenulated edges (41.9%) and beak punctures (27.9%) were the most common form.

Henceforth, the taphonomic analysis for leporids and birds is treated separately given the potential for different groups of taxa to exhibit different taphonomic signatures.

3.3.1. *Leporids*

The total number of recovered leporid remains was 438, 245 were non-ingested remains and 193 were extracted from pellets.

3.3.1.1. Anatomical representation. The anatomical composition of the identified remains in the leporid sample is presented in Table 2. The entire skeleton was represented – upper molars (22.4%), vertebrae (18%), phalanges (15.1%) and cranial remains (8.9%) were the most numerous elements (N%). The relative abundance of skeletal elements (RA%) is also shown in Table 2 and Fig. 4. The mean value (28.5%) was very low indicating an important loss of

Table 2

Leporid skeletal elements recovered from Bonelli's Eagle nest accumulations. Key: *N* – number of skeletal elements; *N*% – percentage of skeletal elements; MNE – minimum number of elements; RA% – relative abundance. Abbreviations: cra – cranium; man – mandible; inc – incisors; u mol – upper molar; l mol – lower molar; sc – scapula; hum – humerus; rad – radius; uln – ulna; mtc – metacarpal; inn – innominate; fem – femur; pat – patella; tib – tibia; mts – metatarsal; cal – calcaneum; ast – astragalus; c/t – carpal/tarsal; phal – phalanges; ver – vertebrae; rib – rib.

LEPORIDS	Whole sample (MNI = 9)					Non-ingested (MNI = 8)				Pellets (MNI = 4)			
	N	*N*%	MNE	RA%	MNI	*N*	*N*%	MNE	RA%	*N*	*N*%	MNE	RA%
cra	39	8.9	9	100	9	15	6.1	7	87.5	24	12.4	2	50
man	4	0.9	4	22.2	2	0	0	0	0	4	2.1	4	50
inc	24	5.5	24	44.4	5	19	7.8	19	39.6	5	2.6	5	20.8
u mol	98	22.4	98	90.7	9	61	24.9	61	63.5	37	19.2	37	77.1
l mol	10	2.3	10	11.1	1	0	0	0	0	10	5.2	10	25
sc	6	1.4	4	22.2	2	3	1.2	2	12.5	3	1.6	2	25
hum	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
rad	6	1.4	5	27.8	3	2	0.8	2	12.5	4	2.1	3	37.5
uln	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
mtc	4	0.9	4	4.4	1	0	0	0	0	4	2.1	4	10
inn	18	4.1	16	88.9	8	14	5.7	13	81.3	4	2.1	3	37.5
fem	8	1.8	7	38.9	4	6	2.4	5	31.3	2	1	2	25
pat	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
tib	7	1.6	4	22.2	3	4	1.6	3	18.8	3	1.6	1	12.5
mts	19	4.3	15	20.8	2	8	3.3	8	16.7	11	5.7	7	21.9
cal	3	0.7	3	16.7	2	2	0.8	2	12.5	1	0.5	1	12.5
ast	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
c/t	23	5.3	23	10.6	2	10	4.1	10	5.2	13	6.7	13	13.5
phal1/2	42	9.6	42	13.7	2	16	6.5	16	5.9	26	13.5	26	19.1
phal3	24	5.5	24	14.8	2	8	3.3	8	5.6	16	8.3	16	22.2
ver	79	18	73	17.6	2	62	25.3	62	16.8	17	8.8	11	6
rib	12	2.7	10	4.6	1	7	2.9	6	3.1	5	2.6	4	4.2
Total	438		385			245		232		193		153	

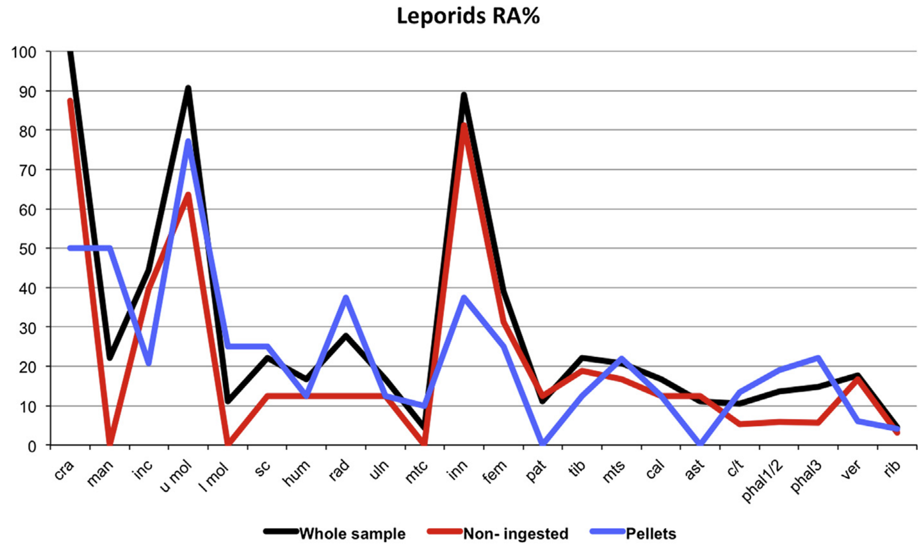

Fig. 4. Relative abundance of different parts of the skeleton for leporid remains. For abbreviations see the caption for Table 2.

bones in the assemblage. The best-represented elements were the cranium (100%), upper molars (90.7%) and the innominate (88.9%), whilst metacarpals and ribs were rare (4.4% and 4.6% respectively).

Relative proportions of skeletal elements are shown in Table 3. Results indicate that there was a deficiency in the numbers of:

- postcranial compared to cranial remains;
- lower compared to upper limb elements, indicating an important loss of distal elements (specially the smallest ones, i.e., third phalanges and carpal/tarsal bones) and;
- anterior compared to posterior limb elements.

Analysis of the leporids by the origin of remains (non-ingested and pellets), reveals that the absolute numbers of cranial remains, metapodials and phalanges were higher in pellets, whereas vertebrae and innominates were better-represented in non-ingested remains (Table 2). Relative abundance profiles were similar in both samples (Table 2, Fig. 4), but long bones, mandibles and phalanges were more abundant in pellets, and crania and innominates predominated in non-ingested remains. This difference is statistically significant ($\chi^2 = 187.9$, $P < 0.01$, df = 21).

3.3.1.2. Breakage. The size of leporid bone fragments ranges between 1.7 and 89.6 mm; the average maximum length was 19.7 mm and 54.9% of the rabbit remains had length values under 10 mm. The percentage of complete elements was 74.7%. Values vary according to bone size, with the highest percentages obtained for the smallest bones: carpals/tarsals; patellae; calcanei; astragali; phalanges; and teeth (Table 4). Long bones were complete in 51.7% of cases.

A total of 172 (39.3%) remains within the entire leporid sample were articulated and 63.6% of teeth were recovered *in situ.*

Table 3
Proportions of different parts of the skeleton for leporids.

Indices %	Leporids sample
PCRT/CR	32.1
PCRAP/CR	30.4
PCRLB/CR	48.6
AUT/ZE	57.7
Z/E	80
AN/PO	35.2

Breakage categories (Table 5) show that:

- crania were complete in only 2.6% of cases and their fragments were mostly identified by parts of the neurocranium (NC) and maxilla (M);
- mandibles were never complete, their fragments were represented by body portions (including MB and MBB);
- teeth located *in situ* were always complete and isolated teeth were complete in 91.8% of cases;
- vertebrae were complete in 79.7% of cases, their fragments were mainly represented by the vertebral body (VB); there were a few instances of vertebral epiphyses (VE) and spinous processes (SP);
- innominates were complete in 55.6% of cases, fragments were represented by portions containing the acetabulum (AISIL, AIL, AIS);

Table 4
Numbers (*C*) and percentages (*C*%) of complete skeletal remains of leporids. For abbreviations see the caption for Table 2.

LEPORIDS	Whole sample		Non-ingested		Pellets	
	C	*C*%	*C*	*C*%	*C*	*C*%
cra	1	2.6	1	6.7	0	0
man	0	0	–	–	0	0
inc	23	95.8	19	100	5	80
u mol	97	99	61	100	36	97.3
l mol	8	80	–	–	9	90
sc	0	0	0	0	0	0
hum	2	50	2	100	0	0
rad	3	50	2	100	1	25
uln	2	50	2	100	0	0
mtc	4	100	–	–	4	100
inn	10	55.6	10	71.4	0	0
fem	5	62.5	4	66.7	1	50
pat	2	100	2	100	–	–
tib	3	42.9	3	75	0	0
mts	12	63.2	8	100	4	36.4
cal	3	100	2	100	1	100
ast	2	100	2	100	–	–
c/t	23	100	10	100	13	100
phal1/2	40	95.2	16	100	23	88.5
phal3	24	100	8	100	16	100
ver	63	79.7	61	98.4	2	11.8
rib	0	0	0	0	0	0
Total	327	74.7	213	86.9	115	59.6

Table 5

Numbers and percentages of parts of the skeleton included in each breakage category for leporids. **Long bones**, **metacarpal** and **metatarsal** bones were classified as: complete (C); proximal epiphysis (PE); proximal epiphysis + shaft (PES); shaft (S); shaft + distal epiphysis (SDE); and distal epiphysis (DE). **Mandible** as: complete (C); incisive part (IP); mandible body + incisive part (MBI); mandible body (MB); mandible body + branch (MBB); and condylar process (CP). **Cranium** as: complete (C); incisive bone (IB); incisive bone + maxilla (IBM); maxilla (M); zygomatic arch (ZA); and neurocranium (NC). **Innominate** as: complete (C); acetabulum (A); acetabulum + ischium (AIS); acetabulum + ischium + ilium (AISIL); acetabulum + ilium (AIL); ischium (IS); and illium (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 epiphysis (VE); and spinous process (SP). **Phalanges** as: complete (C); proximal fragment (P); distal fragment (D); and fragment (F). **Patella, carpal/tarsal, calcaneum, astragalus, ribs and teeth** as: complete (C); and fragment (F).

Leporids sample – breakage categories

Long bones and metapodial	**C**		**PE**		**PES**		**S**		**SDE**		**DE**	
	N	**%**	***N***	**%**	***N***	**%**	***N***	**%**	***N***	**%**	***N***	**%**
Humerus	2	50	1	25	0	0	1	25	0	0	0	0
Radius	3	50	0	0	0	0	0	0	1	25	1	25
Ulna	2	50	0	0	0	0	0	0	1	16.7	2	33.3
Femur	5	62.5	1	12.5	1	12.5	0	0	1	12.5	0	0
Tibia	3	42.9	1	14.3	0	0	2	28.6	0	0	1	14.3
Metacarpus	4	100	0	0	0	0	0	0	0	0	0	0
Metetarsus	12	63.2	0	0	0	0	0	0	3	15.8	4	21.1

Mandible	***N***	**%**	**Cranium**	***N***	**%**	**Innominate**	***N***	**%**	**Scapula**	***N***	**%**
C	0	0	C	1	2.6	C	10	55.6	C	0	0
IP	0	0	IB	2	5.1	A	1	5.6	GC	0	0
MBI	0	0	IBM	3	7.7	AIS	1	5.6	GCN	2	33.3
MB	3	75	M	8	20.5	AISIL	3	16.7	NF	2	33.3
MBB	1	25	ZA	3	7.7	AIL	2	11.1	F	2	33.3
PC	0	0	NC	22	56.4	IS	0	0			
						IL	1	5.6			

Vertebrae	***N***	**%**	**Ribs**	***N***	**%**	**Phalanges 1/2**	***N***	**%**	**Phalanges 3**	***N***	**%**
C	63	79.7	C	0	0	C	40	95.2	C	24	100
VB	10	12.7	F	12	100	P	2	4.8	F	0	0
VE	2	2.5				D	0	0			
SP	4	5.1									

Patella	***N***	**%**	**Car/tar**	***N***	**%**	**Cal**	***N***	**%**	**Ast**	***N***	**%**
C	2	100	C	23	100	C	3	100	C	2	100
F	0	0	F	0	0	F	0	0	F	0	0

Teeth	**"in situ"**						**Isolated**					
	Incisors		**Upper molars**		**Lower molars**		**Incisors**		**Upper molars**		**Lower molars**	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	19	100	64	100	1	100	5	83.3	33	97.1	7	77.8
F	0	0	0	0	0	0	1	16.7	1	2.9	2	22.2

- scapulae were never complete and most fragments comprised the glenoid cavity (GC, GCN);
- all breakage categories were found on the limb bones, which were mostly complete; the majority of radius and ulna fragments included the distal epiphysis;
- metapodials were well preserved; metacarpals and metatarsals were complete in 100% and 63.2% of cases respectively.

Non-ingested remains were clearly less affected by breakage than bones from pellets. The size of the leporid remains differs noticeably; in the non-ingested remains sample the average maximum length was 43.1 mm and only 6.8% of the rabbit remains had length values under 10 mm, whereas those in the pellets had an average maximum length of 8.3 mm and 78.1% of remains had length values under 10 mm. The percentage of complete elements was also distinct: 86.9% in non-ingested remains compared with 59.6% in pellets. Differences were mostly concentrated in large skeletal elements (Table 4) such as: long bones (88.3% *vs* 15%); innominates (55.6% *vs* 0%); and metatarsi (100% *vs* 36.4%).

3.3.1.3. Digestion and beak/talon marks. Digestion damage was present in 31.2% of the overall leporid sample (Fig. 5). Different degrees of digestion damage were observed on the surface of rabbit remains; specifically, 2.3% of the skeletal elements were altered by a light degree, 7.9% by a moderate degree, 14.4% by a heavy degree and 6.5% by an extreme degree of corrosion.

No digested remains were recovered in the non-ingested sample. Considering the pellet sample, the percentage of remains affected by digestion was considerably higher (72%). In this sample, the percentage of elements included in each degree of digestion damage was: 5.4% light, 18.3% moderate, 33.3% heavy and 15.1% extreme (Fig. 6 and Table 6). Different skeletal elements were altered in different proportions: vertebrae, scapulae, skull remains, humerus and tibia were more corroded than the remains of autopodia (carpals/tarsals, metapodials and phalanges) (Table 6). Whole surfaces of bones were often affected by digestive corrosion, the most altered areas were fractured or articular surfaces. A high proportion of teeth (92%) were corroded (Table 6).

Beak marks were observed on ten specimens (2.3% of the sample); all occurred on non-ingested remains (4.1% of the sample) and were mostly situated on the innominates (5) and scapulae (2), although crania (1), vertebrae (1) and femora (1) were also affected. The most common form of damage was crenulated edges (36.4%), followed by notches (27.3%), punctures (18.2%), pits (9.1%) and fractured edges (9.1%) (Fig. 5). Pits and punctures were always isolated and limited to a single surface (i.e. not opposed). Some of the recorded marks may have been inflicted by talons, however, there are no reliable criteria by which these might be separated.

3.3.2. Birds

The total number of recovered bird remains was 385, of which 57 came from non-ingested remains and 328 were from pellets.

3.3.2.1. Anatomical representation. All parts of the avian skeleton were recovered (Table 7). Phalanges (36.9%) showed the highest values. Vertebrae (7%), crania (6.2%), tarsometatarsi (4.9%),

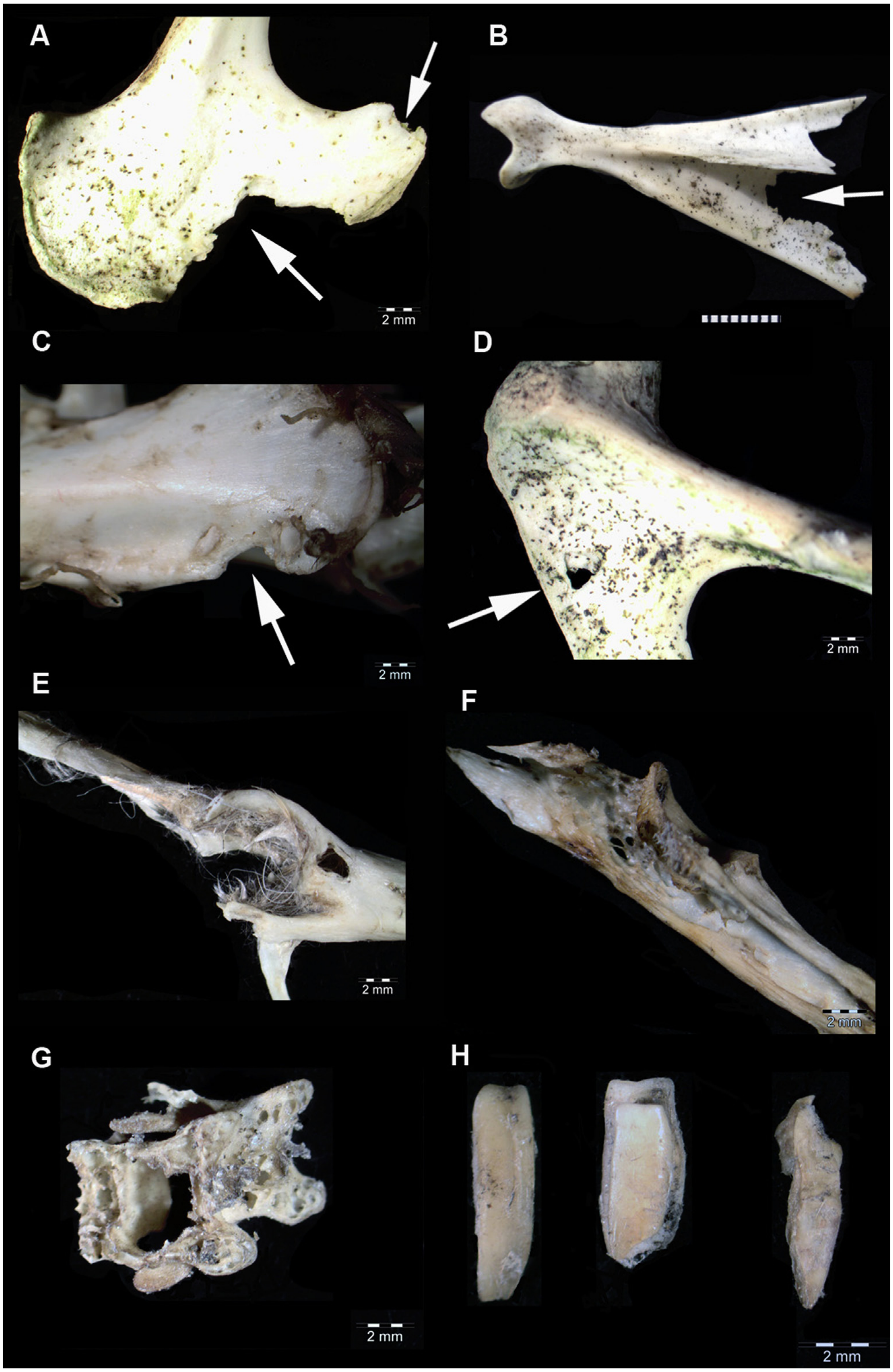

Fig. 5. Examples of leporid bones and teeth displaying beak marks (A–D) and digestion damage with extensive corrosion ($E = 4$, $F = 3$, $G = 4$ and $H = 3$) caused by Bonelli's eagles.

tibiotarsi (4.4%) and scapulae (4.2%) were also common. Relative abundance varied by skeletal element (Table 7, Fig. 7): fragments of the trunk (sternum and pelvis) were the best represented (100% and 91.7% respectively) followed by cranial remains (75%). Pectoral arch (scapula, coracoid and clavicle), wing and leg bones were also well represented: most displayed values over 50% (Table 7, Fig. 7). Vertebrae and ribs showed the lowest percentages (6.9% and 3.1% respectively).

Relative abundance was calculated separately for *Columba* spp. and red-legged partridge because these were the best represented taxa. Results show that anatomical representation is similar in both taxa; however, the pelves and crania were the most frequent elements for red-legged partridge whereas sterna and scapulae dominated the *Columba* spp. assemblage (Table 7, Fig. 7). Differences in the relative abundance of both taxa were statistically significant ($\chi^2 = 213.4$, $P < 0.01$, $\mathrm{df} = 16$).

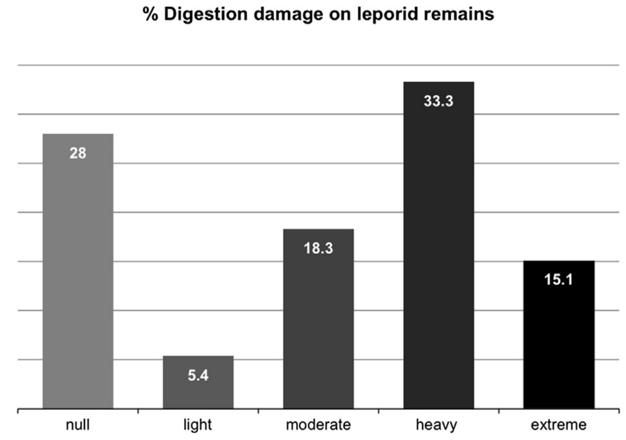

Fig. 6. Percentage of leporid remains from the pellets sample included in each digestion category.

Wing bones account for 45.8% of the sum of wing and leg bones evidencing a slightly higher representation of leg bones. The deviation from the expected 50% (1:1 proportion) is not statistically significant ($Z = 0.53$, $p > 0.05$). The ratio of proximal to distal portions was almost equal (53.2%). Deviation from the expected percentage (50%) is not statistically significant ($Z = 0.05$, $p > 0.05$). The ratio of the core to limb elements was 36.6%, the predominance of limb elements is highly statistically significant ($Z = 2.54$, $p < 0.01$).

Separate analysis of the sample by origin (non-ingested *vs* pellets) reveals that sterna and pelves were the most common elements in the non-ingested sample, with poor representation or absence of other elements. In contrast, crania, pectoral arch and most wing and leg bones (including phalanges) were abundant in pellets and sterna and pelves were rare, demonstrating that Bonelli's eagles do not normally ingest these skeletal elements. Vertebrae and ribs were very scarce indicating almost total loss of these elements (Table 7, Fig. 7). Differences in anatomical representation in both samples were statistically highly significant ($\chi^2 = 424.8$, $P < 0.01$, df = 12).

Table 6
Numbers and percentage of leporid bones and teeth included in each digestion category. For abbreviations see the caption for Table 2. The number of bones considered was 186, a total of 7 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.

Digestion damage on leporid remains (pellets sample)										
	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	0	0	0	0	7	29.2	10	41.7	7	29.2
man	0	0	0	0	0	0	2	66.6	1	33.3
inc	0	0	0	0	2	40	2	40	1	20
u mol	4	11.4	4	11.4	11	31.4	14	40	2	5.7
l mol	0	0	2	20	1	10	7	70	0	0
sc	0	0	0	0	0	0	1	33.3	2	66.7
hum	0	0	0	0	0	0	1	50	1	50
rad	2	50	0	0	1	25	1	50	0	0
uln	1	50	0	0	1	50	0	0	0	0
mtc	4	100	0	0	0	0	0	0	0	0
inn	0	0	0	0	0	0	4	100	0	0
fem	1	50	0	0	0	0	1	50	0	0
pat	0	0	0	0	0	0	0	0	0	0
tib	0	0	0	0	0	0	3	100	0	0
mts	5	45.5	1	9.1	2	18.2	3	27.3	0	0
cal	0	0	0	0	0	0	1	100	0	0
ast	0	0	0	0	0	0	0	0	0	0
c/t	11	84.6	0	0	0	0	2	15.4	0	0
phal1/2	17	65.4	3	11.5	4	15.4	1	3.8	1	3.8
phal3	7	58.3	0	0	2	16.7	3	25	0	0
ver	0	0	0	0	1	5.9	4	23.5	12	70.6
rib	0	0	0	0	2	40	2	40	1	20
TOTAL	52	28	10	5.4	34	18.3	62	33.3	28	15.1

The ratio of wing to leg elements varied in both samples (88.9% in non-ingested and 39.7% in pellets) indicating that leg bones were very scarce in non-ingested remains. The ratio of proximal to distal bones did not show great differences (58.8% and 46.4%), but the ratio of the core to limb elements (65.9% and 22.7%) pointed to a major presence of core elements in the non-ingested remains sample. Differences in survivorship of particular skeletal elements in both types of samples are statistically significant ($\chi^2 = 8.43$, $P = 0.014$, df = 2).

3.3.2.2. Breakage. The size of the recovered avian remains ranged between 2.3 mm and 90.4 mm (average maximum length 17.6 mm) and 35.4% of bones had length values under 10 mm.

The degree of fragmentation was moderate; on average 49.9% of the elements were complete, with the small bones such as carpals, ribs and phalanges being the least fragmented (Table 8). The tarsometatarsi and coracoids were the best preserved (26.3% and 23.1% respectively) limb/core bones, whereas the femur and tibiotarsus were never complete.

A notable number of skeletal remains was articulated ($N = 148$, 38.4%); most being leg bones (tarsometatarsi and phalanges, 55.4%).

Breakage categories (Table 9) show that:

- all breakage categories occurred on long bones, scapulae and coracoids; few bones were complete (14.4%), but proximal and distal ends and shaft (with missing articular ends) were well represented (35.6%, 22% and 28% respectively);
- most scapula, coracoid, radius and femur fragments were proximal ends; the best represented fragments of humeri and tarsometatarsi were distal ends; the tibiotarsi and ulnae were mostly shaft fragments and most carpometacarpi were complete;
- skulls were generally represented by brain case and beak fragments;
- most mandibles were represented by fragments of *pars symphysialis*;
- most pelves fragments included the synsacrum and ilium–ischium–pubis bones (50%), fragments of ilium-ischium-pubis bones were also abundant (35.7%);
- a high percentage of sternae fragments included the rostrum (91.6%), but most were less than half complete (58.3%).

Non-ingested remains were less affected by breakage than those from pellets. The average maximum length of uneaten remains was 43.9 mm and all bones were over 10 mm in length; the average maximum length in the pellets sample was 14.9 mm and 40.1% of remains had length values under 10 mm. The percentage of complete elements was very similar in both samples (around 50%, Table 8) because of the presence of high numbers of small elements (phalanges, carpals) in the pellets sample, which were normally complete. When long bones are considered in isolation, the percentage of complete elements decreases to 47.1% (in non-ingested remains) and 9.5% (in pellets).

3.3.2.3. Digestion and beak/talon marks. Digestion corrosion was evident in 60.4% of the whole bird sample (Fig. 8). Most bones showed heavy corrosion (30.8%) whereas it was light on only 3.3% of the elements. The percentage of elements recorded as being

Table 7

Bird skeletal elements recovered from Bonelli's Eagle nests. Key: N – number of skeletal elements; N% – percentage of skeletal elements; MNE – minimum number of elements; MNI – minimum number of individuals; RA% – relative abundance. Abbreviations: cra – cranium; man – mandible; fur – furcula; sc – scapula; cor – coracoid; hum – humerus; rad – radius; uln – ulna; cmc – carpometacarpus; c – carpal (carpi radial, carpi ulnare); di – wing digit; fem – femur; tbt – tibiotarsus; tmt – tarsometatarsus; str– sternum; pel – pelvis; phal – leg phalanges; ver – vertebrae; rib – rib.

BIRDS	Whole sample (MNI = 12)					*Columba* spp. (MNI = 7)				*Alectoris rufa* (MNI = 8)				Non-ingested (MNI = 10)				Pellets (MNI = 8)			
	N	*N%*	MNE	RA%	MNI	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%
cra	24	6.2	9	75	9	2	1.5	2	28.6	21	11.8	6	75	1	1.8	1	10	22	6.7	8	100
man	4	1	4	33.3	4	0	0	0	0	3	1.7	3	37.5	1	1.8	1	10	3	0.9	3	37.5
fur	4	1	4	33.3	4	2	1.5	2	28.6	1	0.6	1	12.5	1	1.8	1	10	3	0.9	3	37.5
sc	16	4.2	14	58.3	8	10	7.4	8	57.1	3	1.7	3	18.8	3	5.3	3	15	13	4	11	68.8
cor	13	3.4	12	50	8	7	5.2	7	50	4	2.2	3	18.8	4	7	4	20	9	2.7	8	50
hum	10	2.6	7	29.2	7	3	2.2	2	14.3	5	2.8	3	18.8	3	5.3	3	15	8	2.4	4	25
rad	14	3.6	13	54.2	9	4	3	4	28.6	7	3.9	6	37.5	1	1.8	1	5	13	4	12	75
uln	12	3.1	11	45.8	8	3	2.2	3	21.4	6	3.4	5	31.3	2	3.5	2	10	10	3	9	56.3
cmc	17	4.4	15	62.5	9	3	2.2	3	21.4	9	5.1	7	43.8	3	5.3	3	15	14	4.3	12	75
c	11	2.9	11	–	4	1	0.7	1	–	5	2.8	5	–	3	5.3	3	–	8	2.4	8	–
di	9	2.3	9	–	3	0	0	0	–	5	2.8	5	–	4	7	4	–	5	1.5	5	–
fem	14	3.6	12	50	8	5	3.7	4	28.6	4	2.2	3	18.8	0	0	0	0	14	4.3	12	75
tbt	17	4.4	14	58.3	11	8	6	7	50	7	3.9	5	31.3	0	0	0	0	17	5.2	14	87.5
tmt	19	4.9	13	54.2	8	8	6	5	35.7	9	5.1	6	37.5	1	1.8	1	5	18	5.5	12	75
str	12	3.1	12	100	12	7	5.2	7	100	3	1.7	3	37.5	10	17.5	10	100	2	0.6	2	25
pel	14	3.6	11	91.7	11	1	0.7	1	14.3	11	6.2	8	100	12	21.1	10	100	2	0.6	1	12.7
phal	142	36.9	142	42.3	10	63	46.7	63	32.1	51	28.7	51	22.8	0	0	0	0	142	43.3	142	63.4
ver	27	7	25	6.9	2	6	4.4	4	1.9	21	11.8	21	8.8	5	8.8	5	1.7	22	6.7	20	8.3
rib	6	1.6	6	3.1	1	2	1.5	2	1.8	3	1.7	3	2.3	3	5.3	3	1.9	3	0.9	3	2.3
TOTAL	385		344			135		125		178		147		57		55		328		289	

affected by a moderate and extreme degree was 14.8% and 11.5% respectively.

No bones exhibiting digestion damaged were recorded in the non-ingested sample. Considering only the pellets sample, the percentage of digested remains was 71.4%. Heavy corrosion (36.4%) predominated, followed by moderate (17.5%) and extreme (13.6%) (Fig. 9 and Table 10).; light digestion was very low (3.9%).

Most skeletal remains exhibited substantial damage with long bones,, specifically humeri, ulnae, femora and tibiotarsi, exhibiting the highest degree of alteration (Table 10). Phalanges appeared to be less damaged, probably because they were ingested in anatomical connection and protected by the skin of the feet. Sterna and pelves were the least affected by digestion because these skeletal elements do not seem to be ingested regularly by Bonelli's eagles.

Traces left by beaks were observed on 24 bones, 6.2% of the sample (Fig. 8). Most of them occurred on the pelves (10) and sterna (9). The rest were located on crania (1), coracoids (1), scapulae (1), humeri (1) and femora (1). Crenulated edges (41.2%) were the most common form of damage, followed by punctures (32.3%), pits (20.6%) and fractured edges (5.9%). One coracoid and two pelves displayed two simultaneous pit/puncture marks; pits and punctures were isolated in all other specimens and they were always unilateral (not opposed).

Most elements affected by beak marks came from the non-ingested sample (*N* = 20; 35.1%), marks occurred on only four bone fragments from the pellets (1.2%).

4. Discussion

The prey taxa identified in our samples is characteristic of Bonelli's eagles. In most feeding studies, leporids and birds are the most abundant prey, with European rabbit, red-legged partridge and pigeons playing a major dietary role (Caro et al., 2011; Del Amo et al., 2008; Moleón et al., 2009; Ontiveros et al., 2005; Palma et al., 2006; Resano et al., 2011). Our observations support the reported diet of Bonelli's eagle, which appears to be adapted to the most abundant prey available in each region, with rabbits always predominating in regions where they are present (Moleón et al., 2009). This variation is evident in the slightly different relative composition of prey in each of our study areas. It is apparent, therefore, that prey diversity must be taken into account when analysing archaeological samples.

Body part representation at the Bonelli's eagle nests varied with taxonomic group or species. Real's (1996) study of prey consumption behaviour at nests of these raptors showed that the lowest weight class prey (red squirrel (*Sciurus vulgaris*), ocellated lizard (*Timon lepidus*), or corvids), were consumed whole in most cases and no remains were left in the nest. In the case of rabbits and pigeons, more than half of the individuals were not completely eaten. However, while rabbit remains were frequently removed from the nest by the eagles, one third of the pigeons were left. This behaviour undoubtedly affects the relative frequencies and anatomical representation of different prey types.

Our study shows that Bonelli's eagles often fragment the bones of their prey, although the degree of fragmentation varies markedly among prey species. The percentage of complete elements and complete long bones was clearly higher for rabbits (74.7% and 51.7%) than for birds (49.9% and 14.4%). Differences between taxa were also found in bone surface alterations. For example, birds were more affected by digestion corrosion than rabbits (60.4% vs 31.2%), which is related to the fact that fewer parts of the rabbit carcass were ingested by Bonelli's eagles. Beak marks were also more common on bird remains (6.2% vs 2.3%). It is manifest that the taphonomic pattern obtained is strongly related to the prey/predator size, to the type of prey and to the feeding behaviour of the predator.

4.1. The taphonomic signature of Bonelli's eagle on leporid remains

To facilitate comparisons, we present a summary of results obtained from different leporid predators, where the data have been collected using the same methods (Table 11). In relation to the age at death, we found that the majority of rabbits (58.6%) were immature. Palma et al. (2006) in their study of the feeding habits of Bonelli's eagle found that 86.2% of rabbits were adult. This suggests that the percentage of adult individuals can be variable. Lloveras et al. (2012b), observed a similar phenomena in their study of

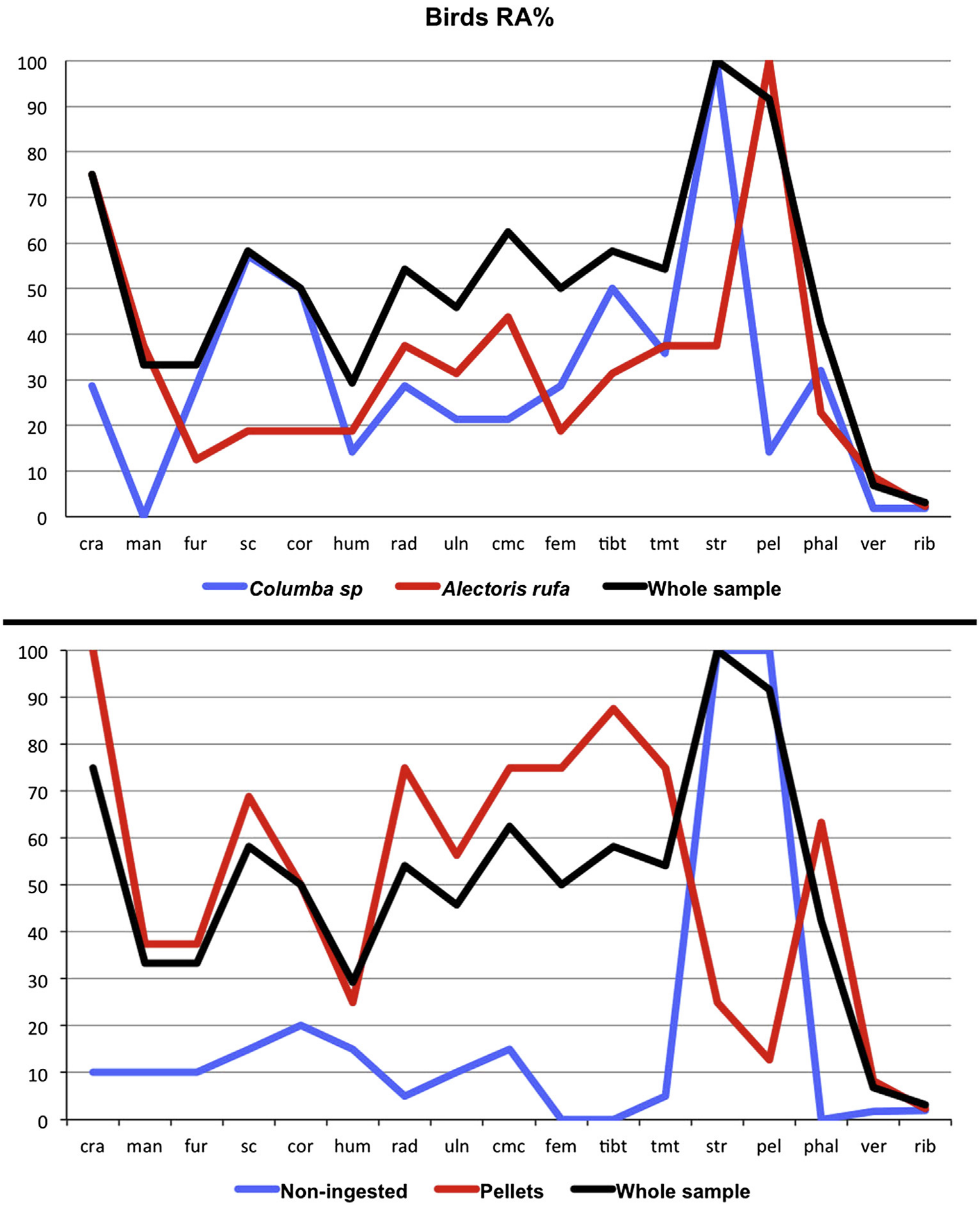

Fig. 7. Relative abundance of different parts of the skeleton in the bird remains samples. For abbreviations see the caption for Table 7.

eagle owl prey at nests. The implication is that leporid age may be an insufficiently distinctive character to separate accumulations generated by Bonelli's eagle and potentially other predators as well.

The main taphonomic features observed in the leporid sample point to anatomical representation characterized by an abundance of cranial remains and innominates, a low frequency of axial elements and autopodia and a greater presence of hindlimbs relative to forelimbs. While some differences were observed between non-ingested remains and pellets, these traits prevailed in both samples. Comparisons with other diurnal raptors reveal that the taphonomic signature of Bonelli's eagle leporid accumulations is distinctive. Hockett (1995, 1996) and Schmit (1995) reported that the most common skeletal elements in leporid assemblages accumulated by golden eagles (*Aquila chrysaetos*) were hindlimb bones, specifically tibiae and associated elements (calcanei and astragali) followed by femora. Cranial remains and innominates were also represented in their samples but in lower frequencies. In contrast, femora outnumbered tibiae in the Bonelli's eagle whole sample, whilst calcanei and astragali were rare. Comparison with the taphonomic signature of Spanish imperial eagle (*Aquila adalberti*) pellet samples also shows clear differences. This eagle tends to accumulate large numbers of tibiae, calcanei and phalanges (Lloveras et al., 2008b); all of which were scarce in our Bonelli's eagle pellet sample. Greater differences are found with nocturnal raptors, such as the European eagle owl (*Bubo bubo*), in which the anatomical profile is characterized by high percentages of postcranial remains, specifically long bones, innominates and autopodia (Cochard, 2004b; Lloveras et al., 2009; Sanchis, 2000). With regards to terrestrial carnivores, both Iberian lynx (*Lynx pardinus*) and red fox (*Vulpes vulpes*) leporid assemblages of non-ingested remains are characterised by low frequencies of cranial remains, with long bones and autopodia much more abundant than in our study (Lloveras et al., 2008a, 2012a; Rodríguez-Hidalgo et al., 2013). The scat accumulations of both carnivores display high percentages of cranial remains;

Table 8
Numbers (*C*) and percentages (*C%*) of complete skeletal remains of birds. For abbreviations see the caption for Table 7.

BIRDS	Complete elements					
	Whole sample		Non-ingested		Pellets	
	C	*C%*	*C*	*C%*	*C*	*C%*
cra	1	4.2	1	100	0	0
man	1	25	1	100	0	0
fur	1	25	1	100	0	0
sc	1	6.3	0	0	1	7.7
cor	3	23.1	3	75	0	0
hum	1	10	1	33.3	0	0
rad	1	7.1	1	100	0	0
uln	2	16.7	1	50	1	10
cmc	6	35.3	2	66.7	4	28.6
c	11	100	3	100	8	100
di	6	66.7	4	100	2	40
fem	0	0	–	–	0	0
tbt	0	0	–	–	0	0
tmt	5	26.3	0	0	5	27.8
str	0	0	0	0	0	0
pel	2	14.3	2	16.7	0	0
phal	135	95.1	–	–	135	95.1
ver	10	37	5	100	5	22.7
rib	6	100	3	100	3	100
Total	192	49.9	28	49.1	164	50

nevertheless long bones are far more abundant than in the Bonelli's eagles samples, especially those of the forelimbs (Lloveras et al., 2008a, 2012a).

As far as breakage patterns are concerned, the percentage of complete elements was surprisingly high in our study. Diurnal raptors have been defined as important bone destroyers compared to owls (Andrews, 1990). However, the 74.7% of complete bones recorded in the Bonelli's eagle whole sample is clearly higher than the 38–32.3% obtained with golden eagle accumulations (Schmit, 1995) and the 53.9–45.9% found in European eagle owl nest assemblages (Lloveras et al., 2009). In the pellets sample, the percentage of complete bones and complete long bones was 59.6% and 15.4%, again higher than the values recorded for Spanish imperial eagles (27% and 0%) or for terrestrial carnivore scat accumulations (Table 11). These results indicate that leporid bones accumulated by Bonelli's eagles are less-fragmented than those generated by other predators. This could be related to the size of the raptor, and more specifically to its beak size. Bonelli's eagle beaks are smaller than those of Spanish imperial eagles, golden eagles and European eagle owls (Cramp and Simmons, 1980), and are thus less capable of breaking the bones of large prey, such as rabbits and hares.

The percentage of digested remains in our Bonelli's eagle samples is lower than those recorded for other predators. Values obtained for the pellets sample (72%) are lower than those recorded for Spanish imperial eagle pellets (98%) and for Iberian lynx and fox scat accumulations (97.2% and 99.5%). Even in eagle owl nest accumulations, the percentage of digested remains is higher (Table 11). However, digested remains in our samples were damaged to a very high degree. This clearly distinguishes Bonelli's eagles from European eagle owls, which are characterised by high percentages of light corrosion. Digestion damage was also more pronounced than in Spanish imperial eagle pellets, where high percentages of moderate corrosion were recorded. The values for Bonelli's eagles are similar to those of terrestrial carnivores (Fig. 10).

The percentage of bones with beak marks is similar to those recorded in European eagle owl nest accumulations but clearly lower than those obtained for other raptors such as the Egyptian vulture (*Neophron percnopterus*), which reached values of 7.5%–10.4% (Lloveras et al., 2014a; Sanchis Serra et al., 2013). Beak marks were not found in pellet remains, but this type of damage was also rare in other raptors such as Spanish imperial eagles (0.5%, Table 10). Iberian lynx produces much less damage in non-ingested remains (0.9%), while the percentage of tooth damage in red fox leporid accumulations was much higher (9.5%). Nevertheless, the lack of gnawing and location of the puncture marks is not typical of the action of carnivores but of birds of prey (Sanchis Serra et al., 2013).

In summary, leporid assemblages accumulated by the Bonelli's eagles are characterised by:

- a body part representation with an abundance of cranial remains, upper molars and innominates, very few axial and autopodium elements and a greater abundance of hindlimbs relative to forelimbs;
- a moderate degree of breakage, with high percentages of complete bones;
- a moderate percentage of digested remains but mostly heavy and extreme corrosion;
- a large number of beak/talon marked bones;

Table 9
Numbers and percentages of parts of the skeleton included in each breakage category for birds.

Birds sample – breakage categories											
Mandible	*N*	%	Skull	*N*	%	Pelvis	*N*	%	Sternum	*N*	%
Whole	1	25	whole	1	4.2	Synsacrum + ilium–ischii–pubis	7	50	more 1/2 with rostrum	4	33.3
One branch	0	0	beak + brain case without back part	1	4.2	Ilium–ischii–pubis	5	35.7	less 1/2 with rostrum	7	58.3
Articular part	0	0	brain case without back part	0	0	synsacrum	1	7.1	fragment without rostrum	1	8.3
Pars symphysialis	3	75	brain case	15	62.5	acetabulum	1	7.1			
Middle part branch	0	0	beak	7	29.2						

	Whole		Proximal part		Distal part		Shaft			Complete		Fragment	
	N	%	*N*	%	*N*	%	*N*	%		*N*	%	*N*	%
Scapula	1	6.3	13	81.3	0	0	2	12.5	Phalanges	135	95.1	7	4.9
Coracoid	3	23.1	9	69.2	1	7.7	0	0	Vertebrae	10	37	17	63
Humerus	1	10	3	30	5	50	1	10	Ribs	6	100	0	0
Radius	1	7.1	7	50	1	7.1	5	35.7					
Ulna	2	16.7	1	8.3	2	16.7	7	58.3					
Carpometacarpus	6	35.3	4	23.5	2	11.8	5	29.4					
Femur	0	0	6	42.9	4	28.6	4	28.6					
Tibiotarsus	0	0	2	11.8	6	35.3	9	52.9					
Tarsometatarsus	5	26.3	2	10.5	8	42.1	4	21.1					

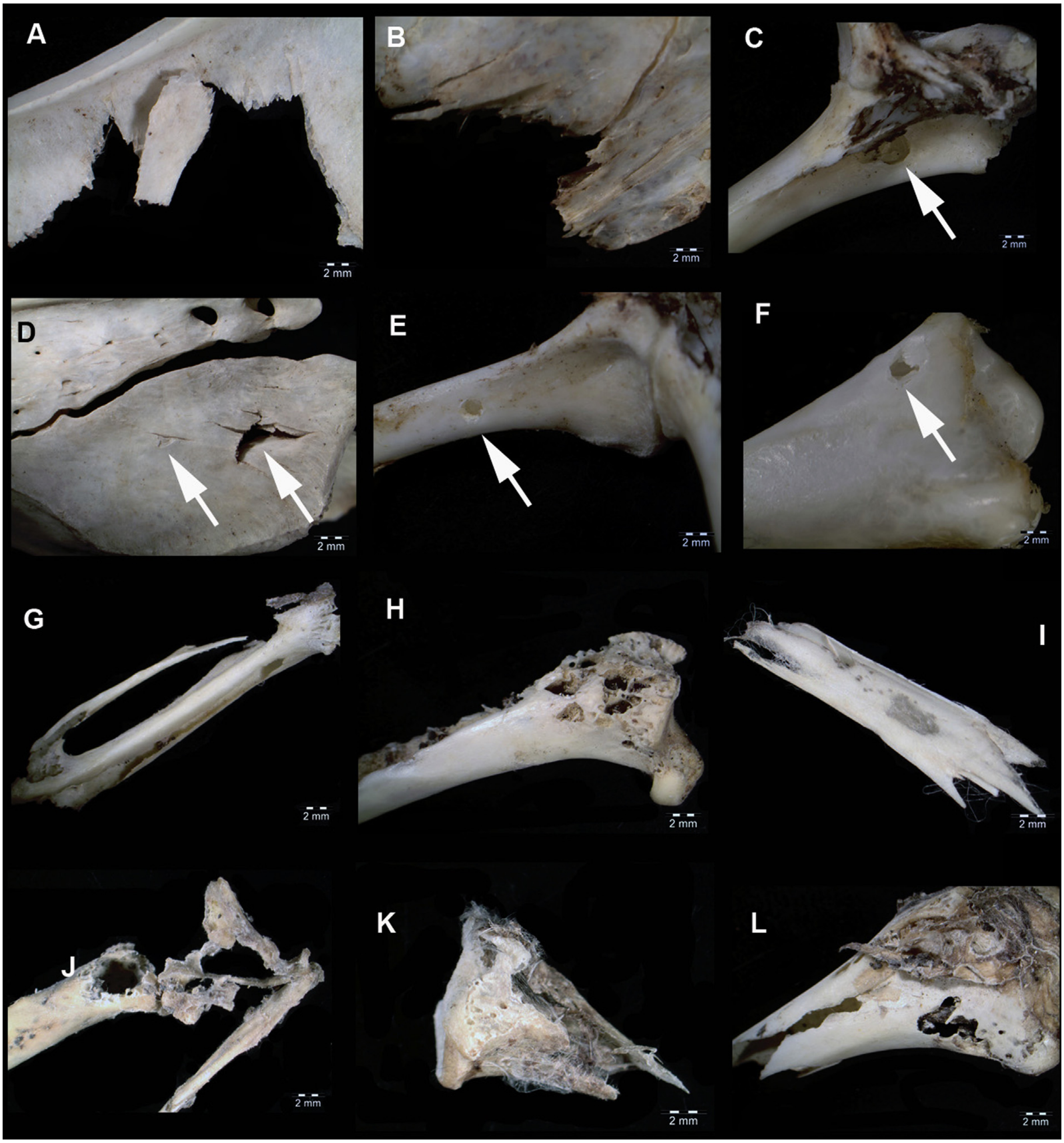

Fig. 8. Examples of bird bones displaying beak marks (A–F) and digestion damage with extensive corrosion (*G* = 3, H = 3, I = 4, *J* = 4, *K* = 4, *L* = 3) produced by the Bonelli's eagle.

Taken separately these features can be shared with other leporid predators, but together they form a distinctive taphonomic signature for Bonelli's eagle.

4.2. *The taphonomic signature of Bonelli's eagle on bird remains*

Among the bird remains recovered, sterna and pelves were the most abundant elements in the non-ingested sample. The sternum was also the best represented element in non-ingested assemblages from diurnal raptors such as Spanish imperial eagle, golden eagle, gyrfalcon (*Falco rusticolus*), crested caracara (*Caracara plancus*) and Egyptian vulture (Bochenski, 2005; Bochenski et al., 1998, 1999, 2009; Lloveras et al., 2014a; Montalvo et al., 2011; Sanchis Serra et al., 2013). In these studies, pelves were also abundant but they do not reach the values we found. Coracoids, scapulae, humeri and carpometacarpi were the best-represented long bones. Coracoids and humeri are the most frequent elements in non-ingested remains of diurnal raptors (Bochenski, 2005). In contrast, the tarsometatarsi or crania (or both) are the best-represented bones in pellet assemblages of diurnal and nocturnal raptors (Bochenski, 2005; Laroulandie, 2002). A similar pattern has been recorded for Bonelli's eagles; however, femora and radii were also abundant in our study whereas in other raptor assemblages they were consistently rare (Bochenski, 2005).

Results from the wing/leg ratio indicated a higher abundance of wing elements in non-ingested remains. When comparing these data with other studies (Bochenski, 2005; Bochenski et al., 1997, 1999; Laroulandie, 2002; Montalvo et al., 2011), it is clear that this is a feature shared with assemblages accumulated by other diurnal raptors. The preponderance of leg bones in the pellet

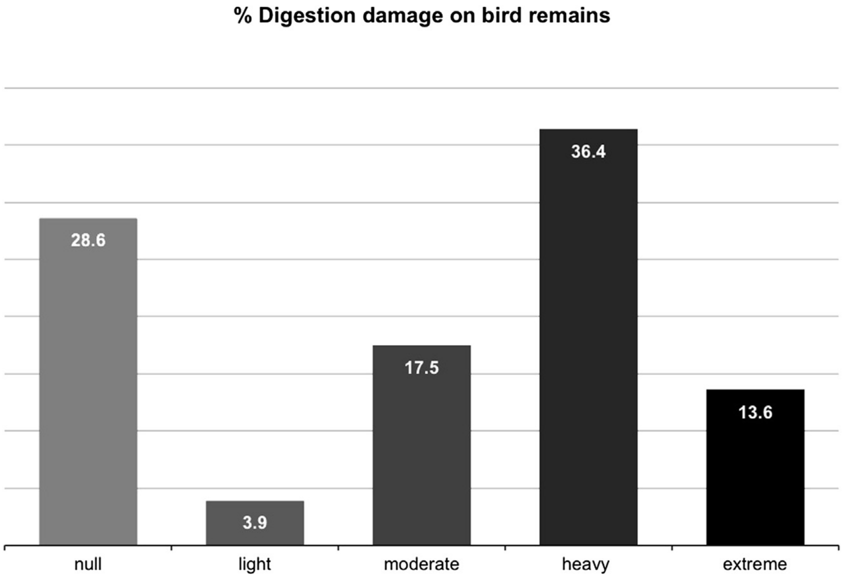

Fig. 9. Percentage of bird remains from the pellets sample included in each digestion category.

sample has only been recorded for Spanish imperial eagles (Bochenski et al., 1997). The ratio of proximal to distal elements permits the distinction of three groups of avian predators, namely: (I) pellets of diurnal birds of prey; (II) pellets of owl species and non-ingested remains of some diurnal raptors; and (III) non-ingested remains of golden eagles (Bochenski, 2005; Bochenski and Nekrasov, 2001). The present material falls into group II, in which proximal elements make up about 60% of the remains (Bochenski et al., 2009). The predominance of limb elements (versus core) observed in pellets has also been recorded for various owls and diurnal birds of prey. The abundance of core elements detected in non-ingested food remains is only shared with golden eagles (Bochenski, 2005; Bochenski et al., 1999).

Bonelli's eagles fragment bird bones to a similar extent to other diurnal birds of prey. However, the percentage of complete long bones was 47.1% for uneaten remains, which is comparable with values above 60% reported by Bochenski (2005) for diurnal raptors. This indicates that Bonelli's eagles break their victims' bones somewhat more frequently. In pellets, only 9.5% of long bones were complete. This percentage is consistent with the pattern exhibited in the pellets of diurnal raptors in which less than 30% of complete bones were registered (Bochenski, 2005). Particular skeletal elements differ in the degree of fragmentation: scapulae and tibiotarsi are the most affected and carpometacarpi, tarsometatarsi and coracoids are the best preserved. This is a feature related to the physical properties of these skeletal elements and it is common to all predators (Bochenski, 2005).

Table 10
Numbers and percentage of bird bones included in each digestion category. For abbreviations see the caption for Table 7. The number of bones considered was 308, a total of 20 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.

Digestion damage on bird remains (pellets sample)

	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	3	14.3	0	0	3	14.3	12	57.1	3	14.3
man	1	33.3	0	0	2	66.7	0	0	0	0
fur	0	0	0	0	1	33.3	2	66.7	0	0
sc	0	0	0	0	3	25	7	58.3	2	16.7
cor	0	0	0	0	2	28.6	2	28.6	3	42.9
hum	0	0	0	0	1	14.3	5	71.4	1	14.3
rad	0	0	0	0	5	38.5	7	53.8	1	7.7
uln	0	0	0	0	0	0	9	90	1	10
cmc	0	0	0	0	2	13.3	10	66.7	3	20
c	3	37.5	0	0	3	37.5	1	12.5	1	12.5
di	0	0	0	0	0	0	4	80	1	20
fem	0	0	0	0	1	7.1	10	71.4	3	21.4
tbt	0	0	0	0	1	5.9	10	58.8	6	35.3
tmt	1	5.6	2	11.1	3	16.7	9	50	3	16.7
str	1	50	0	0	0	0	0	0	1	50
pel	0	0	0	0	0	0	2	100	0	0
phal	73	57.9	10	7.9	26	20.6	14	11.1	3	2.4
ver	4	18.2	0	0	0	0	8	36.4	10	45.5
rib	2	66.7	0	0	1	33.3	0	0	0	0
TOTAL	88	28.6	12	3.9	54	17.5	112	36.4	42	13.6

Few data exist on the digestion of bird remains (Bochenski, 1997; Bochenski et al., 1998; Laroulandie, 2002; Lloveras et al., 2014a; Montalvo et al., 2011). In Bonelli's eagle pellets more than 70% of total remains and practically 100% of long bones were digested. These values are clearly higher than those recorded for the European eagle owl (Laroulandie, 2002), Snowy owl (*Bubo scandiacus*) (Bochenski et al., 1997), crested caracara (Montalvo et al., 2011), Egyptian vulture (Lloveras et al., 2014a) and gyrfalcon (Bochenski et al., 1998). Moreover, most remains were digested with a heavy degree of damage (category 3 of damage defined by Bochenski (2005)).

The percentage of remains affected by beak marks was lower for Bonelli's eagle (6.2%) than for Egyptian vulture (28.3%, Lloveras et al., 2014a). The location of most beak marks on pelves (71.4%) and sterna (75%) is replicated on non-ingested assemblages left by other diurnal birds of prey. Bochenski et al. (2009) found punctures on 70% of sterna and 38% of pelves in white-tailed eagle (*Haliaaetus albicilla*) assemblages and punctures were observed on 39% of sterna, 51% of pelves in golden eagles. Our results show that Bonelli's eagles are closer to white-tailed eagles than golden eagles (Bochenski et al., 2009). Coracoids, scapulae, humeri and femora were the most affected long bones in our study. Similar results have also been recorded for other raptors (Bochenski et al., 2009).

In summary, the taphonomic signature observed on bird remains accumulated by Bonelli's eagles is characterised by:

- an abundance of sterna and pelves in non-ingested remains; and crania, pectoral arch and most of the wing and leg bones (including phalanges) in pellets;

Table 11
Anatomical representation, breakage, digestion and teeth/beak marks for leporid remains accumulated by different types of predators compared with the results obtained for Bonelli's eagles in the present study.

Leporid comparisons	Eagle owl		S. imperial eagle	Iberian lynx		Fox		Bonelli's eagle		
Reference	*Bubo bubo*		*Aquila adalberti*	*Lynx pardinus*		*Vulpes vulpes*		*Aquila fasciata*		
	Lloveras et al., 2009		Lloveras et al., 2008b	Lloveras et al., 2008a	Rodríguez-Hidalgo et al., 2013	Lloveras et al., 2012a		Present study		
Origin	Nest	Nest	Pellets	Scats	Non-ingested	Scats	Non-ingested	Whole sample	Non-ingested	Pellets
N	1808	1932	824	1522	9564	265	639	438	245	193
RA% >values	cal-inn-fem	cal-inn-tib	phal 3-u mol-tib	man-teeth-cra	tib-cal-mts	long bone-sc	mts-ast-tib	cra-u mol-inn	cra-inn-u mol	u mol-cra-man
RA% <values	mtc-c/t	rad-c/t-mtc	rib-fem-rad	c/t-ver-rib	sc-ver-hum	mtc-c/t-inn	cr-sc-rib	mtc-rib	man-l mol-mtc	ast-pat-rib
PCRT/CR	+postcranial	=	+cranial	+cranial	+postcranial	=	+postcranial	+cranial	+cranial	+cranial
P/D	+proximal	+proximal	+distal	+proximal	+distal	+proximal	+distal	+proximal	+proximal	+proximal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+forelimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb
Complete elements %										
Mean value long bones	14.6	10.8	0	2.5	37.6	0	5.4	51.7	81.3	15.4
Mean value total	53.9	45.9	27	43	73.2	12	89.4	74.7	86.9	59.6
Length (in mm)										
Minimum	2.3	2.5	1.8	1.1	3	3	4	1.7	2.8	1.7
Maximum	86.3	90	36.1	30.1	69	26.8	86.2	89.6	89.6	78.7
%<10 mm	49	40	73	80	19.7	61	28	54.9	6.8	78.1
% Digested remains	68.8	65.6	98	97.2	–	99.5	–	31.2	–	72
% Digested long bones	88.9	83.9	100	100	–	100	–	31	–	69.2
Degree										
Null	31.2	34.4	2	2.8	–	0	–	68.8	–	28
Light	40.2	40.2	18.2	12	–	6	–	2.3	–	5.4
Moderate	19.8	19.8	46.8	22	–	26	–	7.9	–	18.3
Heavy	8	5.3	27.4	43.8	–	43	–	14.4	–	33.3
Extreme	0.7	0.15	5.6	19.3	–	25	–	6.5	–	15.1
Teeth/beak marks	2	1.34	0.5	0.26	0.9	3	9.5	2.3	4.1	0
Age – % of adults	50	50	–	21.4	–	87	–	41.4	–	–

- a moderate degree of breakage of non-ingested remains, with around 50% complete bones. A high degree of long bone breakage in pellets (less than 10% complete bones);
- a high percentage of digested remains, most of them to a heavy and extreme degree;
- a significant percentage of beak marked bones, most on pelves, sterna and long bones.

Comparisons show clear differences to nocturnal birds of prey. Although many features are shared with other diurnal raptors,

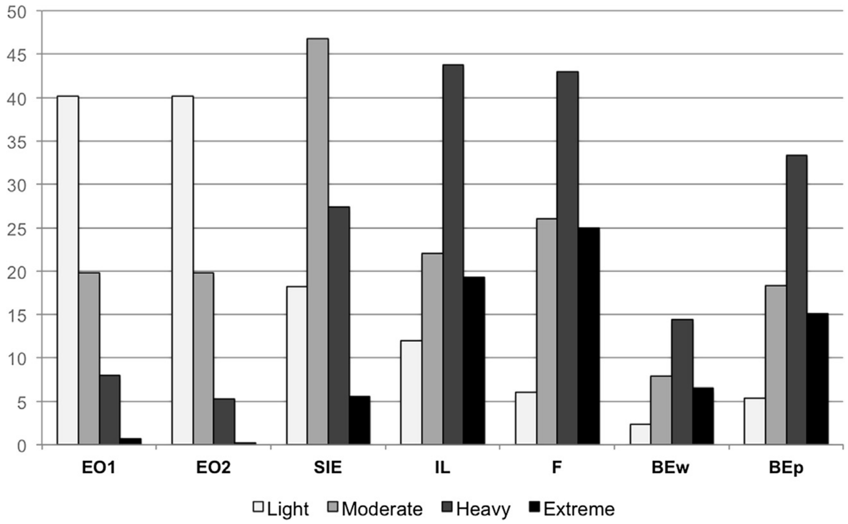

Fig. 10. Comparison of percentage of leporid remains included in each digestion category in accumulations produced by eagle owls (EO1 and EO2, Lloveras et al., 2009), Spanish imperial eagle (SIE; Lloveras et al., 2008b), Iberian lynx (IL; Lloveras et al., 2008a), red fox (F; Lloveras et al., 2012a) and Bonelli's eagle whole and pellets sample (BEw, BEp; present study).

especially with Spanish imperial eagles, differences are, apparent nevertheless. Some of the differences recorded could relate to different prey species accumulated in the samples analysed. Taphonomic data about avian prey accumulations are still scarce, especially regarding some variables such as digestion damage. Future studies are needed to provide more data that permit a deeper understanding of this variability.

5. Conclusions

This study provides the first detailed taphonomic observations on leporid and bird bones accumulated by Bonelli's eagles. Results from our analysis help to identify and classify the most important characteristics of bones accumulated by this raptor. Where rabbits, partridges and pigeons are abundant, they constitute a very high percentage of their diet. Both, non-ingested elements and bones from pellets are found in nest assemblages.

The observations and results obtained through this study showed that damage caused by Bonelli's eagles on leporids and birds differ sufficiently from other predators. Differences also exist in the character of leporid depending on the origin of the assemblage (i.e. non-ingested remains compared with pellets). The skeletal elements most abundant in non-ingested remains were scarce in the pellets and vice versa. The other taphonomic patterns observed also show divergent results. Non-ingested remains were less fragmented and beak/talons marks were more common, whereas pellet remains were affected by heavy and extreme digestion corrosion.

On archaeological grounds, assemblages of mixed origin are the most likely to be encountered. The criteria presented in this study for mixed samples can reveal the presence of this predator; however, results may vary depending on the relative proportion of remains derived from non-ingested accumulations and pellets. The use of the criteria presented in this study together with data on the geographical and biological background (i.e. location of the site and prey species composition of the deposit) can help to assess the potential contribution of Bonelli's eagles in accumulating small prey remains on archaeological sites.

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