



Assessing the variability in taphonomic studies of modern leporid remains from Eagle Owl (*Bubo bubo*) nest assemblages: the importance of age of prey

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ABSTRACT

The Eagle Owl (*Bubo bubo*) is an important leporid remains accumulator at archaeological sites. Taphonomical studies of modern leporid remains from nest assemblages of this nocturnal raptor aim to establish the main characteristics that define the taphonomic signature of Eagle Owls in order to distinguish them from that of other leporid predators, namely diurnal raptors, terrestrial carnivores and humans. However, analyses carried out so far have shown that the identification of diagnostic features of Eagle Owls leporid nest accumulations is not a straightforward issue – variability has been observed. Age and size of prey are pointed among others as accountable factors but little research has been done on the study of these variables. Here we present the analysis of two samples of modern leporid remains recovered from Eagle Owls nests with the aim of contributing new data to this subject. The high presence of juvenile individuals in both samples enables us to assess anatomical representation, breakage and digestion patterns of immature leporid remains and also to compare them with other assemblages richer in adult prey. Results show that the main characteristic features noted in previous works which recognise Eagle Owls as agents of leporid bones accumulations in the fossil record, are not significantly affected by the age of prey. Less variability than originally thought occurs which means other variables need to be further investigated.

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1. Introduction

Due to the importance that leporid remains and specifically European rabbit (*Oryctolagus cuniculus*) have in most prehistoric sites from the Iberian Peninsula and the Mediterranean region, in the last decades several taphonomic studies of modern leporid remains accumulated by different kinds of predators (nocturnal or diurnal raptors and mammalian terrestrial carnivores) have been carried out (Cochard, 2004a; Guennouni, 2001; Guillem and Martínez-Valle, 1991; Hockett, 1989, 1991, 1995, 1996; Lloveras et al., 2008a, 2008b, 2009, 2011; Sanchís, 2000; Sanchís and Pascual, 2011; Schmitt, 1995; Schmitt and Juell, 1994; Yravedra, 2004). Such studies attempt to gain some knowledge on the patterns produced by each of those predators on prey anatomical representation, breakage and bone surface modifications (digestion, beak – tooth marks) so as to distinguish responsible agents of leporid assemblages in the archaeological record. Some of these

works that deal with multiple samples for the same predator record certain degree of variability in the results for the different parameters observed (Cochard, 2004a, 2008; Hockett, 1995; Lloveras et al., 2009, 2011). Behind such variability the reasons may be manifold. Perhaps, the origin of the assemblage is the most explored. In the case of raptors, it has been argued that leporid remains derived either from regurgitated pellets or non-ingested leftovers, either from nests or roost sites, show different patterns as regards anatomical representation and bone damage (Cochard, 2008; Hockett, 1995; Lloveras et al., 2009). Equally, material from scats of terrestrial carnivores differs from that of unconsumed prey waste (Cochard, 2004a, 2004c; Lloveras et al., 2008b, 2011; Sanchís, 2000; Schmitt and Juell, 1994). Availability of prey, season of the year and consequently age of prey are factors that tend to be carefully monitored in biological studies interested in the dietary habits of avian and carnivore predators (Calzada, 2000; Delibes et al., 1975; Donázar, 1987, 1989; Donázar and Ceballos, 1989; Fernández and Purroy, 1990; Goszczynski, 1974; Hiraldo et al., 1975; Rau et al., 1987; Serrano, 1998). On the contrary, they appear to have been usually ignored in taphonomic analyses. The part they might have played in the intra-specific variability pointed out in those studies remains unknown to a great extent.

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This paper focuses on the analysis of one of the most specialized rabbit predators among large European raptors (Delibes and Hiraldo, 1981; Donázar, 1987) and one of the most studied from a taphonomic perspective (Cochard, 2004a; Guennouni, 2001; Guillem and Martínez-Valle, 1991; Hockett, 1995; Lloveras et al., 2009; Sanchís, 2000; Yravedra, 2004) since it has great potential as an accumulator of faunal remains at an archaeological level – the Eagle Owl (*Bubo bubo*). In particular, our aim is to evaluate if the variable ‘age of prey’ is worth considering when interpreting intra-specific variability among leporid remains derived from Eagle Owl nest accumulations and more specifically, to assess which taphonomical parameters (i.e., anatomical representation, breakage and bone surface modification) may show more variability due to ‘age of prey’. It is hoped that the results will be useful to enhance our interpretations of fossil leporid assemblages.

2. Material and methods

The leporid remains analysed come from two Eagle Owls nests (Nest 1P and Nest 2P) located in the Portuguese region of Alentejo (Fig. 1). This geographical area is characterized by a hot, dry Mediterranean climate (Rivas-Martínez et al., 2002). The landscape is dominated by plains and low hills. Agricultural fields (cereal steppes, olives groves and vineyards) alternate with Mediterranean scrublands, pastoral woodlands of holm oak (*Quercus rotundifolia*) and cork oak (*Quercus suber*). Both nests were located in protected shelters, approximately 3.5 km apart. Nest 1P was a few metres away from a swamp.

Both samples were collected by one of us (LL) in July 2007 at the end of the breeding season. Chicks had abandoned the nests at the end of June. In Nest 1P only one chick was raised whilst in Nest 2P the number of chicks was two. Remains accumulated in both nests corresponded to a unique breeding season occupation and they did not display any sign of weathering or to have been manipulated by scavengers. All material accumulated on the surface of the nests (i.e., degraded pellets, unswallowed bones and debris such as feathers, eggshell fragments, sand and pebbles) was carefully hand-picked to be sure that all remains were recovered (Fig. 2) and later carefully dry-sieved through a 0.5 mm mesh in order to recover all prey remains. Leporid bones and teeth were selected and stored apart.

The age of the rabbits consumed at both nests was estimated taking into account the epiphyseal fusion state of long bones (humerus, femur and tibia), metapodials, scapula, calcaneum and innominate. They were classified as young, sub-adult and adult (Hale, 1949; Rogers, 1982; Taylor, 1959). However, only two categories were used during the analysis, adults and immature individuals. The latter includes young and sub-adult specimens.

Hare remains were identified using both the criteria described by Callou (1997) and the reference collection from the Archaeozoology Lab of the IGESPAR (Lisbon, Portugal).

The taphonomical analysis follows the methodology carried out in previous studies (Lloveras et al., 2008a, 2008b, 2009, 2011) for the sake of clarity it is summarized next.

2.1. Anatomical representation

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

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

(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 were evaluated using three indices for postcrania in relation to crania (Andrews, 1990):

- PCRT/CR – total numbers of postcranial (limb elements, vertebrae and ribs) compared with total numbers of cranial elements (mandibles, maxillae and teeth);



Fig. 1. Map of Portugal showing the area of the Alentejo where the Eagle Owl nests here studied are located.

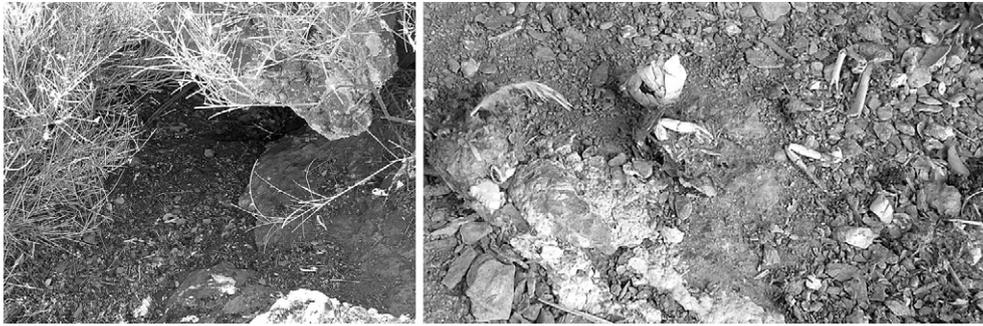


Fig. 2. Material accumulated on the surfaces of Nest 1P and Nest 2P before being collected.

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

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

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

A further index compared anterior to posterior limb elements: AN/PO – humerus, radius, ulna and metacarpals compared with femur, tibia and metatarsals.

2.2. Breakage

The breakage pattern was described by the maximum length of all the identified skeletal elements. Additionally, statistical *T*-Student test was applied to the maximum length of the determined remains to assess any differences in the size of fragments between the two nests. Percentages of complete elements, isolated teeth and articulated elements were also calculated. For immature individuals, diaphyses of long bones with unfused epiphyses were considered as complete elements. Unfused proximal or distal epiphyses were classified as fragments of long bones. Different breakage categories were used 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 distinguishing between proximal or distal was not possible, they were recorded just 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 used for long bones, metapodials, mandibles, cranium, scapula and innominate are presented in Table 3. They are fully described and illustrated in Lloveras et al. (2008a).

2.3. Digestion

Damage to bone surface was observed under light microscope ($\times 10$ to $\times 40$). Based on the methodology used for micromammals by Andrews (1990) and Fernández-Jalvo and Andrews (1992), different categories of digestion damage were applied to leporid bones and teeth (Lloveras et al., 2008a, 2008b). Five degrees of digestion were distinguished: null (0), light (1), moderate (2), heavy (3) and extreme (4). These were valued separately for bones and dental remains.

2.4. Puncture marks

Finally, damage to the bone surfaces caused by the predator's beak or talons were also noted and counted.

3. Results

The total number of leporid remains recovered was scarce compared to other nest assemblages from Iberia (see for example Lloveras et al., 2009; Sanchís, 2000). Birds, rodents (rats, mice...), reptiles, amphibians and in the case of Nest 1P, situated in the vicinity of a swamp, fish and crab remains were much more abundant than leporids. Both nests produce rabbit (*O. cuniculus*) and hare (*Lepus granatensis*) remains, although the latter was much scarcer. In Nest 1P the number of leporid bones and teeth identified to skeletal element was 237 (of which 20 correspond to hare) while in Nest 2P they totalled 638 (of which 36 were identified as hare). The minimum number of individuals was based on femur counts for Nest 1P (MNI = 8) and on innominate bones for Nest 2P (MNI = 16).

Taking into account the fusion stage of long bone and metapodial epiphyses, scapula, calcaneum and innominate, the percentage of immature leporid remains in each sample was very high: 95.2% in Nest 1P and 86% in Nest 2P.

3.1. Anatomical representation

Table 1 shows the anatomical composition of the identified remains for each nest. The entire skeleton is represented – vertebrae, ribs, phalanges 1/2, metatarsals, tibia/femur and innominate are the most numerous elements in both samples (N%). Cranial remains are slightly more abundant in Nest 1P than in Nest 2P. In both samples metacarpals are much less abundant than metatarsals. Relative abundance of skeletal elements (RA%) is also shown in Table 1 and Fig. 3. The mean values (20.3% for Nest 1P and 25.8% for Nest 2P) are very low indicating an important loss of prey bones in both nest assemblages.

Table 1

Leporid skeletal elements recovered from Eagle Owl (*Bubo bubo*) nests 1P and 2P. N: number of skeletal elements. N%: skeletal elements in percentage. MNE: minimum number of elements. RA: relative abundance. *Number of skeletal elements in Nest 2P was 632 + 6 fragments of metapodials (not classified as metacarpals or metatarsals).

Skeletal element	Nest 1P				Nest 2P			
	N	N%	MNE	RA%	N	N%	MNE	RA%
Mandible	5	2.1	3	18.8	3	0.5	2	6.3
Cranium	8	3.4	1	12.5	8	1.2	2	12.5
Incisors	3	1.3	3	6.3	3	0.5	3	3.1
Upper molars	4	1.7	4	4.2	1	0.2	1	0.5
Lower molars	10	4.2	10	12.5	11	1.7	11	6.9
Humerus	3	1.3	2	12.5	11	1.7	6	18.8
Radius	3	1.3	3	18.8	5	0.8	4	12.5
Ulna	6	2.5	4	25	5	0.8	4	12.5
Femur	20	8.4	12	75	66	10.3	17	53.1
Tibia	24	10.1	10	62.5	57	8.9	26	81.2
Patellae	2	0.8	2	12.5	7	1.1	7	21.9
Scapula	1	0.4	1	6.3	6	0.9	4	12.5
Innominate	17	7.2	8	50	51	8	29	90.6
Metacarpus	4	1.7	2	2.5	2	0.3	2	1.3
Metatarsus	28	11.8	21	32.8	108	16.9	93	72.7
Phalanges 1/2	29	12.2	28	10.3	75	11.7	74	13.6
Phalanges 3	5	2.1	5	3.5	14	2.2	14	4.9
Calcaneum	11	4.6	10	62.5	23	3.6	22	68.8
Astragalus	0	0	0	0	14	2.2	14	43.8
Carpal/tarsal	2	0.8	2	1	34	5.3	34	8.9
Vertebrae	25	10.5	21	9.7	78	12.2	62	14.4
Ribs	27	11.4	15	7.8	50	7.8	27	7
Total	237	99.8	167		632 + 6 = 638*	99.7	458	

The best represented elements are those of the hindlimb, including the innominate whilst metacarpals and third phalanges are always very scarce.

Relative proportions of skeletal elements are shown in Table 2. Results show that in both samples there is a great deficiency in numbers of:

- i) cranial remains compared to postcranial (particularly visible in Nest 2P);

Table 2

Proportions of different parts of the skeleton. A key to the abbreviations is provided in the methods section.

Indices %	Nest 1P	Nest 2P
PCRT/CR	134.8	448.1
PCRAP/CR	147.0	517.1
PCRLB/CR	472.4	960
AUT/ZE	19.5	48.4
Z/E	80.9	98.6
AN/PO	18.3	9.4

- ii) lower compared to upper limb elements. That means an important lost of distal elements, specially the smallest ones, i.e., third phalanges and carpal/tarsal bones;
- iii) anterior compared to posterior limb elements.

3.2. Breakage

The degree of fragmentation was similar for both samples. The size of the recovered remains varies with values of maximum length between 2.7 and 64.7 mm in Nest 1P and between 2.9 and 71.1 mm in Nest 2P. Average maximum length was 15.9 mm in Nest 1P and 17.7 mm in Nest 2P. More than 71% of the rabbit remains recovered in both nests had length values over 10 mm (Fig. 4). T-Student test applied to the maximum length of the determined remains (230 measures from Nest 1P and 602 measures from Nest 2P) show that differences for the size of the recovered fragments in both collections bordered on statistical significance ($\bar{x}_1 = 15.8922$; $SD_1 = 9.32$; $\bar{x}_2 = 17.6525$; $SD_2 = 11.83$; $p = 0.043$), indicating that both samples could be considered similar.

The average percentage of complete elements is 43.5% in Nest 1P and 47% in Nest 2P. Values vary according to bone size. The highest percentages were obtained for the small carpal/tarsals, patellae, astragali, calcaneum and phalanges (Tables 3 and 4; Fig. 5). Long bones are complete in 7.1% in Nest 1P and 6.9% in Nest 2P. Multiple proportion test applied to long bones completeness show no significant differences between these two samples ($\chi^2 = 2.78$; $df = 3$; $p = 0.4268 > 0.05$).

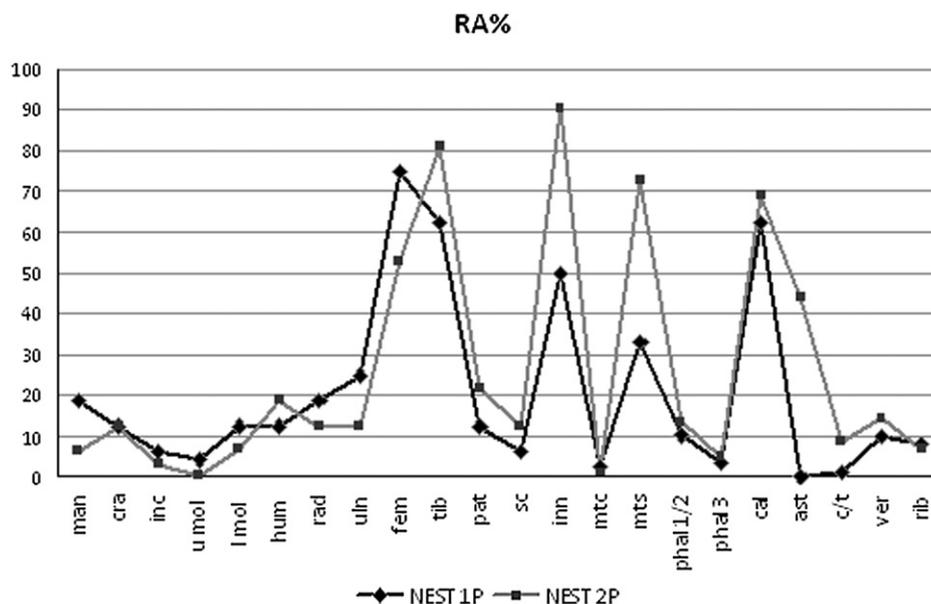


Fig. 3. Relative abundance of the different parts of the skeleton in the Portuguese samples 1P and 2P. Abbreviations; man: mandible, cra: cranium, inc: incisors, u mol: upper molars, l mol: lower molars, hum: humerus, rad: radius, uln: ulna, fem: femur, tib: tibia, pat: patella, sc: scapula, inn: innominate, 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.

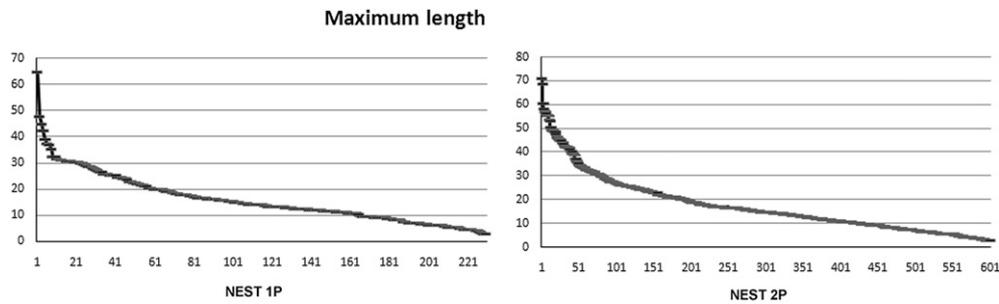


Fig. 4. Maximum length (in mm.) of the leporid remains recovered from Eagle Owl Nest 1P and Nest 2P (vertical axis). The horizontal axis shows the number of bones and teeth measured.

Breakage categories (Tables 3 and 4) show that:

- skulls never appear complete and in both nests they were identified by parts of neurocranium (NC) and zygomatic arch (ZA);
- mandibles are mostly represented by body fragments including the incisive part (MBI), body fragments (MB) and condylar process (PC);
- isolated teeth are complete in 81.8% and 66.7% of the cases and teeth placed “in situ” are always complete (100%);
- vertebrae are complete in 44% of cases in Nest 1P and in 41% in Nest 2P; vertebrae fragments are represented mainly by

- vertebral body (VB); ribs are almost always fragmented in both nests;
- fragments containing the acetabulum (AISIL, AIS, AIL) are the most common for the innominate and they were never recovered complete;
- scapulae are never complete and most fragments comprise the glenoid cavity and fossa;
- all breakage categories except complete are well represented for femur and tibia; humerus, radius and ulna appear more complete;
- metapodials are the best preserved, being complete in most cases (75% aprox.);

Table 3
Nest 1P: numbers and percentages of parts of the skeleton included in each breakage category. **Long bones, metacarpal and metatarsal** bones were classified as: complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal epiphysis (SDE) and distal epiphysis (DE). **Mandible** as: complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB) and condylary process (CP). **Cranium** as: complete (C), incisive bone (IB), incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). **Innominate** as: complete (C), acetabulum (A), acetabulum + ischium (AIS), acetabulum + ischium + ilium (AISIL), acetabulum + ilium (AIL), ischium (IS) and ilium (IL). **Scapula** as: complete (C), glenoid cavity (GC), glenoid cavity + neck (GCN), neck + fossa (NF) and fossa (F). **Vertebrae** as: complete (C), vertebral body (VB), vertebral 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).

Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
Humerus	2	66.7	0	0	0	0	0	0	0	0	1	33.3
Radius	2	66.7	0	0	0	0	0	0	1	33.3	0	0
Ulna	0	0	0	0	4	66.7	2	33.1	0	0	0	0
Femur	0	0	2	10	3	15	1	5	3	15	11	55
Tibia	0	0	4	16.7	5	20.8	4	16.7	10	41.7	1	4.2
Metacarpus	2	50	0	0	0	0	0	0	0	0	2	50
Metatarsus	21	75	0	0	1	3.6	0	0	0	0	6	21.4

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	0	0
MBI	2	40	IBM	0	0	AIS	7	41.2	GCN	1	100
MB	2	40	M	0	0	AISIL	0	0	NF	0	0
MBB	0	0	ZA	1	12.5	AIL	8	47.1	F	0	0
PC	1	20	NC	7	87.5	IS	1	5.9			
						IL	1	5.9			

Vertebrae	N	%	Phalanges 1/2	N	%	Phalanges 3	N	%
C	11	44	C	28	96.6	C	5	100
VB	10	40	P	1	3.4	P	0	0
VE	2	8	D	0	0	D	0	0
SP	2	8						

Patella	N	%	Car/tar	N	%	Cal	N	%	Ast	N	%	Ribs	N	%
C	2	100	C	2	100	C	10	90.9	C	0	0	C	3	11.1
F	0	0	F	0	0	F	1	9.1	F	0	0	F	24	88.9

Teeth	“In situ”						Isolated					
	Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	N	%	N	%	N	%	N	%	N	%
C	0	0	0	0	6	100	2	66.7	3	75	4	100
F	0	0	0	0	0	0	1	33.3	1	25	0	0

Table 4

Nest 2P: numbers and percentages of parts of the skeleton included in each breakage category. For abbreviations see caption on Table 3.

Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
Humerus	3	27.3	3	27.3	2	18.2	1	9.1	0	0	2	18.2
Radius	1	20	0	0	2	40	1	20	1	20	0	0
Ulna	2	40	0	0	2	40	0	0	0	0	1	20
Femur	4	6.1	5	7.6	16	24.2	10	15.2	17	25.8	14	21.2
Tibia	0	0	10	17.5	18	31.6	9	15.8	12	21.1	8	14
Metacarpus	2	100	0	0	0	0	0	0	0	0	0	0
Metatarsus	80	74.1	0	0	10	9.3	0	0	3	2.8	15	13.9

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	0	0
MBI	2	66.7	IBM	0	0	AIS	13	25.5	GCN	3	50
MB	0	0	M	0	0	AISIL	16	31.4	NF	1	16.7
MBB	0	0	ZA	2	25	AIL	13	25.5	F	2	33.3
PC	1	33.3	NC	6	75	IS	5	9.8			
						IL	4	7.8			

Vertebrae	N	%	Phalanges 1/2	N	%	Phalanges 3	N	%
C	32	41	C	65	86.7	C	14	100
VB	30	38.5	P	9	12	P	0	0
VE	7	8.9	D	1	1.3	D	0	0
SP	9	11.5						

Patella	N	%	Car/tar	N	%	Cal	N	%	Ast	N	%	Ribs	N	%
C	7	100	C	34	100	C	22	95.7	C	13	92.9	C	4	8
F	0	0	F	0	0	F	1	4.3	F	1	7.1	F	46	92

Teeth	"In situ"						Isolated					
	Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	N	%	N	%	N	%	N	%	N	%
C	1	100	0	0	8	100	1	50	0	0	3	100
F	0	0	0	0	0	0	1	50	1	100	0	0

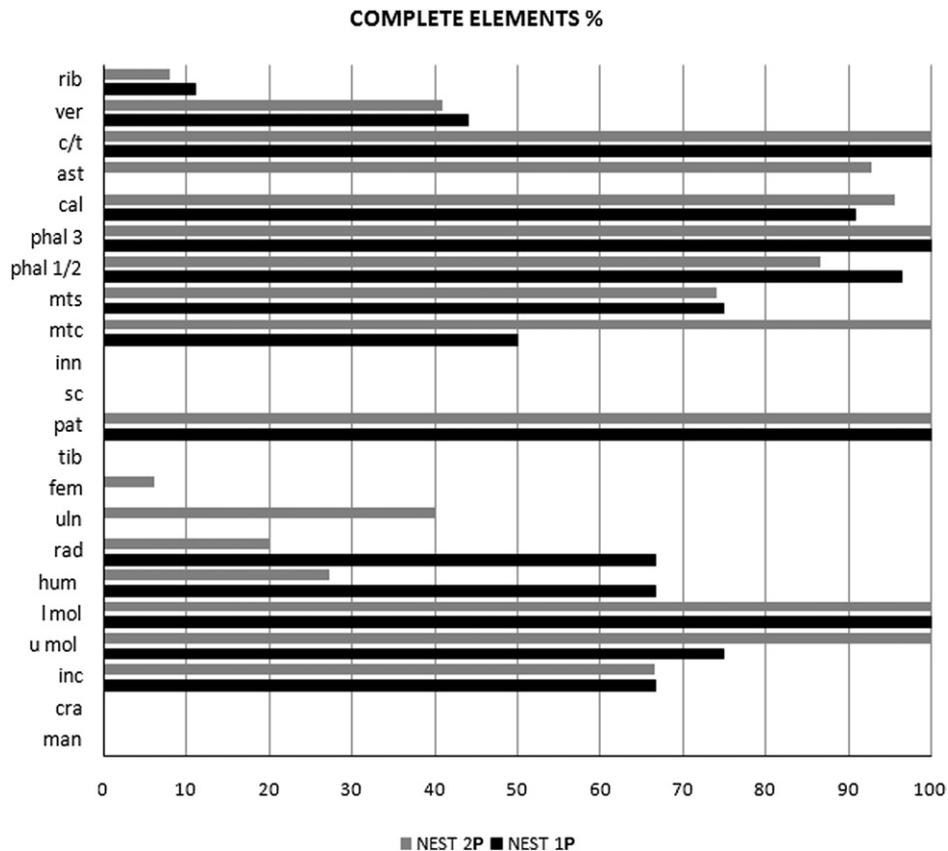


Fig. 5. Percentage of complete leporid remains from Nest 1P and Nest 2P. For abbreviations see caption of Fig. 3.

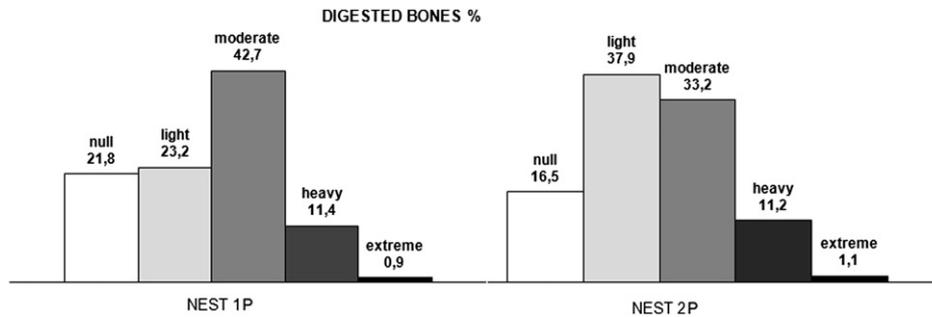


Fig. 6. Percentage of bone remains included in each digestion category.

- calcanea and astragali (the last only present in Nest 2P) are almost always complete;
- on the whole, 91.1% of phalanges appear complete.

Finally, the percentage of isolated teeth is 64.7% in Nest 1P and 40% in Nest 2P. Articulated elements are very scarce in both samples (Nest 1P = 0.85% and Nest 2P = 6.3%).

3.3. Digestion

Digestion damage was observed on the surface of 78.2% and 83.5% of bones from Nest 1P and Nest 2P, respectively. In both samples most bone remains show a light or moderate degree of digestion (Fig. 6 and Table 5), being slightly stronger in Nest 1P. However, multiple proportion test applied to number of bones included in each digestion category show no significant differences between these two samples ($\chi^2 = 2.6104$; $df = 4$; $p = 0.6249 > 0.05$).

Different skeletal elements are altered in similar proportions although phalanges, metapodials and patellae appear to be slightly less affected. In general, the surface of bones is partially damaged by digestion corrosion. The articulation ends are the most altered areas.

Teeth are much less affected than bones (Fig. 7; Table 6), 47.1% and 93.3% of dental remains in Nests 1P and 2P, respectively, were not altered by the effects of digestion. Teeth from Nest 1P present

more digestion corrosion than those from Nest 2P. This is probably related to the fact that in Nest 1P isolated teeth outnumbered those still “in situ” which tend to be more protected and consequently less affected. No significant differences between incisors, upper and lower molars were observed.

3.4. Beak marks

Traces caused by the beak of Eagle Owls on bone surfaces were observed in four bones (1.7%) from Nest 1P and in nine bones (1.4%) from Nest 2P. Most of them occur on innominate (4) and mandible (4). The rest are located on tibia (2), femur (1), metatarsus (1) and vertebrae (1).

4. Discussion

Actualistic studies on the diet of Eagle Owls (Amo and González, 1998; Donázar, 1989; Hiraldo et al., 1975; Lourenço, 2006; Mikkola, 1983; Pérez Mellado, 1980; Serrano, 1998) show that diversity on prey species is influenced by seasonal, climatic and geographical factors, and also rabbit/hare numbers. When these taxa are abundant they usually constitute the most important prey. Also, Eagle Owls tend to prey on adult individuals because they select size categories of high profitability. However, when leporids density is low in an area, they switch to alternative prey (Penteriani et al., 2002) and their hunting strategy changes towards a selection of

Table 5
Numbers and percentage of rabbit bones included in each digestion category.

Digestion in bone remains	Nest 1P										Nest 2P									
	Null		Light		Moderate		Heavy		Extreme		Null		Light		Moderate		Heavy		Extreme	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Mandible	0	0	0	0	2	40	3	60	0	0	1	33.3	1	33.3	1	33.3	0	0	0	0
Cranium	2	25	4	50	1	12.5	1	12.5	0	0	2	25	4	50	2	25	0	0	0	0
Humerus	0	0	0	0	3	100	0	0	0	0	0	0	6	54.5	2	18.2	3	27.3	0	0
Radius	0	0	1	33.3	2	66.7	0	0	0	0	0	0	2	40	1	20	2	40	0	0
Ulna	1	16.7	0	0	4	66.7	1	16.7	0	0	0	0	1	20	3	60	1	20	0	0
Femur	2	10	3	15	12	60	3	15	0	0	4	6.1	18	27.3	25	37.9	16	24.2	3	4.5
Tibia	2	8.3	8	33.3	12	50	2	8.3	0	0	6	10.5	11	19.3	18	31.6	20	35.1	2	3.1
Patellae	2	100	0	0	0	0	0	0	0	1	14.3	2	28.6	4	57.1	0	0	0	0	0
Scapula	0	0	0	0	0	0	1	100	0	0	0	0	2	33.3	3	50	1	16.7	0	0
Innominate	0	0	2	11.8	11	64.7	4	23.5	0	0	0	0	20	39.2	28	54.9	3	5.9	0	0
Metacarpus	1	25	0	0	3	75	0	0	0	0	0	0	1	50	0	0	1	50	0	0
Metatarsus	16	57.1	9	32.1	3	10.7	0	0	0	0	21	19.4	43	39.8	39	36.1	5	4.6	0	0
Phalanges 1/2	9	31	5	17.2	14	48.3	1	3.4	0	0	33	44	33	44	7	9.3	2	2.7	0	0
Phalanges 3	4	75	1	25	0	0	0	0	0	0	9	64.3	5	35.7	0	0	0	0	0	0
Calcaneum	1	9.1	2	18.2	6	54.5	2	18.2	0	0	3	13	6	26.1	11	47.8	3	13	0	0
Astragalus	—	—	—	—	—	—	—	—	—	—	4	28.6	2	14.3	6	42.9	0	0	2	14.3
Carpal/tarsal	0	0	2	100	0	0	0	0	0	0	9	26.5	10	29.4	11	32.4	4	11.8	0	0
Vertebrae	5	20	8	32	8	32	2	8	2	8	4	5.1	36	46.2	31	39.7	7	9	0	0
Ribs	3	11.1	6	22.2	13	48.1	5	18.5	0	0	5	10	31	62	13	26	1	2	0	0

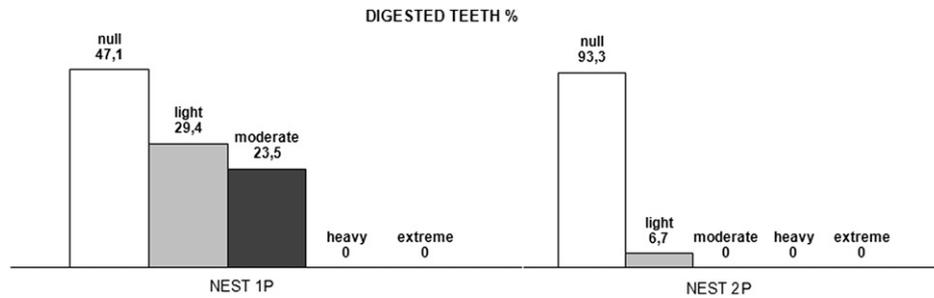


Fig. 7. Percentage of dental remains included in each digestion category.

Table 6

Numbers and percentage of rabbit teeth included in each digestion category.

Digestion in dental remains	Nest 1P										Nest 2P										
	Null		Light		Moderate		Heavy		Extreme		Null		Light		Moderate		Heavy		Extreme		
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
Incisors	1	33.3	2	66.7	0	0	0	0	0	0	3	100	0	0	0	0	0	0	0	0	0
Upper molars	1	25	2	50	1	25	0	0	0	0	0	0	1	100	0	0	0	0	0	0	0
Lower molars	6	60	1	10	3	30	0	0	0	0	11	100	0	0	0	0	0	0	0	0	0

young leporid individuals in order to maximize the existing resources (Donazar and Ceballos, 1989). Such behavioural patterns would result in prey nest accumulations as those described here – low contribution of leporid remains in relation to other prey (i.e., small birds, fish, rodents, molluscs) and very high frequency of immature individuals (95.2% in Nest 1P and 86% in Nest 2P).

Following the same methodological approach we have recently studied two other leporid accumulations from Eagle Owls nests located in North-east Spain (Lloveras et al., 2009). There, rabbits are the dominant prey and immature specimens represent 50% in both

samples. Given the differences in the percentage of adult and immature individuals between both sets of samples, comparisons between Portuguese and Spanish assemblages will help us to assess the intra-specific variability, and specifically the deviations that ‘age of prey’ may produce in the different taphonomical features that identify Eagle Owls as a leporid predator. A summary of the results obtained in the present study as well as in the previous taphonomical analysis of Spanish Eagle Owl nests accumulations is presented in Table 7. Portuguese samples are similar enough to be treated as one homogeneous data set and the same happens with

Table 7

Anatomical representation, breakage, digestion and beak mark comparisons on rabbit remains from Eagle Owl nest accumulations. Results obtained in the present study are summarized in Nest 1P and Nest 2P columns, these results have been joined in column 1P + 2P. Results obtained by Lloveras et al. (2009) are summarized in Nest 1S and Nest 2S columns, these results have been joined in column 1S + 2S. Results obtained by Cochard (2004a, 2004b) are summarized in Carry-le-Rouet column. X: Digestion categories where authors place most of the rabbit remains analysed. *Value estimated from a graphic.

Eagle Owl (<i>Bubo bubo</i>) nest assemblages comparisons	Present study		Present study	Lloveras et al. (2009)		Lloveras et al. (2009)	Cochard (2004b)
	Nest 1P	Nest 2P	Nest 1P + 2P	Nest 1S	Nest 2S	Nest 1S + 2S	Carry-le-Rouet (France)
N	237	638	875	1808	1932	3740	1467
Immature individuals %	95.2	86	88.4	50	50	50	100
RA > values	tib-inn-mts-cal	fem-tib-cal-inn	inn-tib-cal-mts	pat-cal-inn-fem	cal-inn-tib-mts	cal-pat-inn-fem	tib-inn-fem-mts
RA < values	ast-c/t-mtc	mtc-mol s	mtc-mol s-inc-phal 3	mtc-c/t	rad-c/t-mtc	sc-c/t-mtc	ver-phal
PCRLB/CR	+pc	+pc	+pc	+pc	+pc	+pc	+pc
P/D	+proximal	+proximal	+proximal	+proximal	+proximal	+proximal	+proximal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb
Complete elements %							
Mean value long bones	7.1	6.9	7	14.6	10.8	13.8	35*
Mean value total	43.5	47	46	53.9	45.9	49.8	86
Length							
Maximum	64.7	71.1	71.1	86.30	90.0	90	–
Minimum	2.7	2.9	2.7	2.3	2.5	2.3	–
Average	15.9	17.7	17.16	14.07	14.78	14.45	–
% < 10	28.3	28.9	28.6	49	40	43.7	–
Digestion							
% Digested remains	76.4	81.7	80.2	68.8	65.6	65.9	85
% Digested long bones	91.1	93.1	92.5	88.9	83.9	85.1	–
<i>Degree (of bones)</i>							
Null	21.8	16.5	17.9	31.2X	34.4X	32.1X	–
Light	23.2X	37.9X	34.1X	40.2X	40.2X	40.6X	–
Moderate	42.7X	33.2X	35.7X	19.8	19.8	20.2	–
Heavy	11.4	11.2	11.2	8.0	5.3	6.7	–
Extreme	0.9	1.1	1.1	0.7	0.15	0.5	–
Beak marks %	1.7	1.4	1.5	2	1.34	1.6	1.7

the Spanish samples. Thus, in order to facilitate their comparison results have been joined (columns 3 and 5, respectively in Table 7).

Regarding anatomical representation no great differences are found (Fig. 8). Relative abundance (RA) shows that bones of the hindlimb (innominate, femur, tibia, calcaneum and metatarsals), with the exception of patella and astragalus, are always the skeletal elements best represented. In both nests' assemblages there are higher values of postcranial elements (PCRLB/CR), an important loss of distal (specifically phalanges and carpals/tarsals) vs proximal limb elements (P/D) and higher values of hindlimb than forelimb elements (AN/PO).

Cochard (2004b) notes that the taphonomical pattern of leporid remains accumulated in Eagle Owl nests from France varies as a consequence of the age of prey, mainly as regards anatomical representation. This author suggests that assemblages dominated by young individuals are characterized by a major presence of cranial remains and limb bones. Results from the present work do not agree with that information. Our data shows that anatomical representation maintains a similar tendency in Portuguese and Spanish samples, in fact the representation of cranial remains is slightly lower in the immature individuals assemblage. Therefore, this variable does not seem to be affected by the age of prey. It should be taken into account that Cochard did not really work with an assemblage originally constituted only by immature individuals. He divided his original sample into two groups of study, one constituted only by juveniles and another by adult + sub-adults. The results commented above refer only to the sample that comprised 100% young and very young individuals, which is different from the present study. There may lay the disagreement of the results.

In relation to the frequency of complete elements two situations were assessed: (1) the percentage of complete long bones and (2) the percentage of complete elements in the total sample. No discrepancy occurs on the latter observation as both assemblages present values close to 50% (Table 7). As far as the mean value of whole long bones is concerned, results from the Portuguese nests (1P and 2P) appear to differ from the Spanish ones (1S and 2S) – they present lower values of complete long

bones (7% and 13.8%, Table 7). This may be explained by the major fragility of long bones from young individuals, which could break up more easily as a result of the trampling action of the chicks and adult owls. However, multiple proportion test applied to number of complete long bones show no significant differences between the two Iberian samples ($\chi^2 = 2.7929$; $df = 4$; $p = 0.5930 > 0.05$). That means that despite the differences in numbers of complete long bones, both samples are homogeneous with respect to numbers of complete bones for each skeletal element. Once again, this result diverges with that registered by Cochard (2004b). The average value of complete elements in his sample is 35% (Table 7). The most plausible explanation for this higher value lies on the different methodology used – Cochard pools together complete and “almost complete” elements.

Another aspect to take into account is the size of the leporid remains. Minimum length values are approximately the same for the four Iberian nests; however, maximum length is smaller for the Portuguese samples (Table 7). Such can be accounted for by the fact that long bones are usually the longest elements recovered and they are shorter in young rabbits. Curiously the average length value is higher and the percentage of remains smaller than 10 mm is lower in these samples, too (Table 7). Statistical T-Student test applied to the maximum length of the determined remains in both set of data shows significant differences for the size of the recovered fragments in both collections ($\bar{x}_1 = 17.1659$; $SD_1 = 11.21$; $\bar{x}_2 = 14.4504$; $SD_2 = 11.21$; $p = 0.000$). That may indicate that the Portuguese sample is less fragmented than the Spanish one. Since other variables analysed (like percentage of complete elements) are not consistent with this assumption the most likely reason is a greater shortfall of small elements such as phalanges, carpals/tarsals, isolated teeth or patellae in the Portuguese samples. In fact these skeletal parts are less abundant in Nest 1P and Nest 2P (Fig. 8, see also Table 1 and Lloveras et al., 2009) and proportion indices (AUT/ZE) also indicate major loss of distal elements (19.5 and 48.4 in Nest 1P and Nest 2 respectively vs 63.5 and 60.4 in Nest 1S and Nest 2S; see Table 2 and Lloveras et al., 2009). A similar situation (greater loss of small elements in

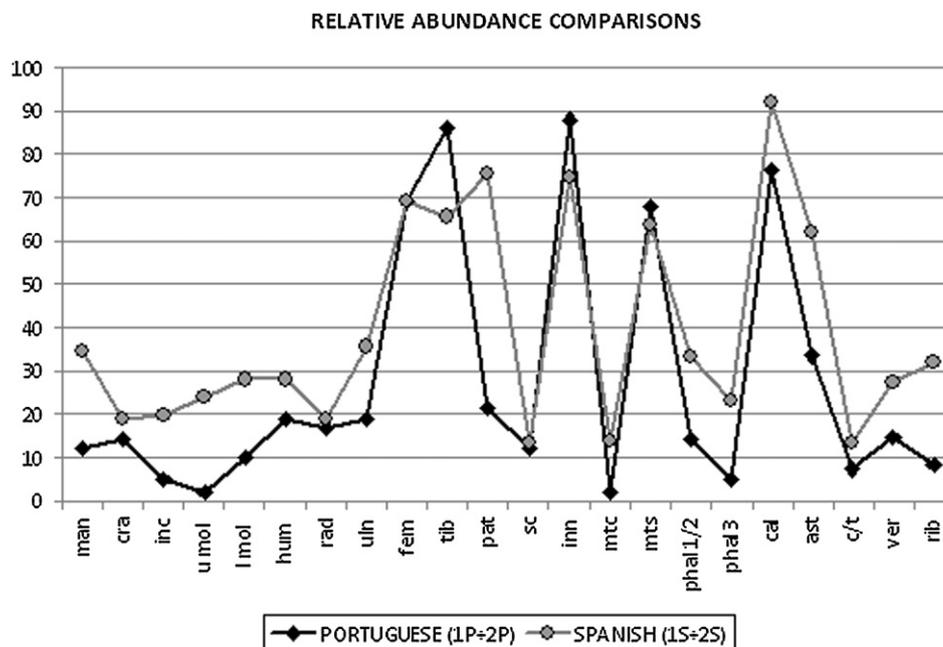


Fig. 8. Relative abundance (RA) of skeletal elements in the Portuguese (1P + 2P) and the Spanish (1S + 2S) samples. For abbreviations see caption of Fig. 3.

juvenile leporid remains from Eagle Owl nests) was also registered by Cochard (2004a, 2004b). However, it should be noted that there might have been other factors playing a part. For example, the location of the nest might have promoted the loss of remains. The two Portuguese nests were located on protected shelters difficult to reach.

As far as digestion damage is concerned, the percentage of digested remains is higher in Portuguese than in Spanish samples (80.2 vs 65.9, Table 7). The same trend is observed in percentages of digested long bones (92.5 vs 85.1, Table 7). Moreover, when digestion degrees are examined a bias towards stronger damage is observed for Portuguese leporid remains. Multiple proportion test applied to number of digested bones included in each digestion damage category show significant differences between both samples ($\chi^2 = 67.897$; $df = 4$; $p = 0.0000 > 0.05$). In the Spanish assemblages most remains presented a null-light degree of digestion corrosion whilst for Portuguese samples it is a light-moderate degree. This bias to stronger damage is to be expected in samples with very high percentage of young individuals since their bones are more fragile and vulnerable to digestion.

Finally, puncture marks caused by the beak of the Eagle Owl are relatively abundant in all the cases (Table 7) with a percentage always superior to 1% and no differences are observed between the two sets of samples.

In short, comparisons made between nests dominated either by immature or adult leporid remains can be summarised as follows (Table 7):

- Anatomical representation is not much affected by the age of prey, only a slightly lower number of cranial remains and a higher loss of small skeletal elements (phalanges, carpal/tarsal bones, ribs) has been noted in the Portuguese nests (Fig. 8). This bias may be related to other factors such as

worse conservation or simply the tendency to fall out of the nest.

- More immature individuals result in a slightly lower percentage of complete long bones, although average values stay always over 7%.
- Equally, the value of maximum length decreases, but it stays over 64 mm. On the other hand, the average length value increases slightly. This is probably a consequence of the major loss of the smallest skeletal elements.
- There is a small increase in the percentage of digested remains and a slight bias to stronger digestion (light-moderate).

The variations observed in the present study are not as large as it was originally expected. In fact, as Table 8 shows the pattern previously established for Eagle Owl leporid nest accumulations (Lloveras et al., 2009) does not change significantly. This means that the most important differences established in relation to other predators hold up (Table 8):

- High values for relative abundance of posterior skeletal elements, more hindlimbs than forelimb bones, and more postcranial than cranial elements. Although these are features that cannot be considered as truly diagnostic of Eagle Owls.
- A moderate breakage pattern. The size of leporid remains and the frequency of complete elements appear to be higher in comparison with other predators such as the Spanish Iberian Eagle (Lloveras et al., 2008a), the Iberian lynx (Lloveras et al., 2008b) or the fox (Lloveras et al., 2011). Diurnal raptors and terrestrial carnivores tend to break the bones of their prey more than Eagle Owls, even when the sample is mostly constituted of immature individuals.
- A light degree of digestion corrosion. Digestion produced on leporid bones is much lighter than that observed on diurnal

Table 8

Anatomical representation, breakage, digestion and beak/teeth mark comparisons on rabbit remains accumulated by Eagle Owl, diurnal raptors and terrestrial carnivores. X: Digestion categories where authors place most of the rabbit remains analysed.

Leporid predator comparisons	Nocturnal raptors		Diurnal raptors	Terrestrial carnivores		
	Eagle Owl <i>Bubo bubo</i>		Spanish Imperial Eagle <i>Aquila adalberti</i>	Iberian Lynx <i>Lynx pardinus</i>	Fox <i>Vulpes vulpes</i>	
Reference	Present study	Lloveras et al. (2009)	Lloveras et al. (2008a)	Lloveras et al. (2008b)	Lloveras et al. (2011)	
Origin	Nest (1P + 2P)	Nest (1S + 2S)	Pellet	Scat	Scat	Non-ingested
N	875	3740	824	1522	265	639
RA > values	inn-tib-cal-mts	cal-pat-inn-fem	phal 3-u mol-tib	man-teeth-cra	long bones-sc-cra	mts-cal-ast-tib
RA < values	mtc-mol s-inc-phal 3	sc-c/t-mtc	rib-fem-rad-ver	c/t-ver-ribs	mtc-c/t-inn	cra-sc-rib-inn-ver
PCRT/CR	+pc	+pc	+cranial	+cranial	=	+postcranial
P/D	+proximal	+proximal	+distal	+proximal	+proximal	+distal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+forelimb	=	+hindlimb
Complete elements %						
Mean value long bones	7	13.8	0	2.5	0	5.4
Mean value total	46	49.8	27	43	12	89.4
Length (in mm)						
Maximum	71.1	90	36.1	30.1	26.8	86.2
Minimum	2.7	2.3	1.8	1.1	3	4.0
Average	17.16	14.45	8.36	7.1	9.1	19.3
% < 10 mm	28.6	43.7	73	80	61	28
Digestion						
% Digested remains	80.2	65.9	98	97.2	99.5	–
% Digested long bones	92.5	85.1	100	100	100	–
Degree						
Null	17.9	32.1X	2.0	2.8	0	–
Light	34.1X	40.6X	18.2	12.0	6	–
Moderate	35.7X	20.2	46.8X	22.0X	26X	–
Heavy	11.2	6.7	27.4X	43.8X	43X	–
Extreme	1.1	0.5	5.6	19.3X	25X	–
Beak/teeth marks %	1.5	1.6	0.5	0.26	3	9.5
Age – % of adults	11.6	56.8	–	21.4	87	–

raptors and terrestrial carnivores scats accumulations (Lloveras et al., 2008a, 2011; Hockett, 1996; Schmitt, 1995; Schmitt and Juell, 1994).

5. Conclusions

The age at death of leporids accumulated in Eagle Owl nests is a characteristic that introduces some variability in the taphonomical signature of this nocturnal raptor and therefore taphonomists need to be aware of it. However, this study has demonstrated that the variability is less than originally thought. It is recommended that other variables as predator age and size, number of chicks, or the season of capture are further investigated. Similarly, it has been shown that different methodological approaches produce slightly divergent results. A matter that needs to be explored and certainly solved if taphonomical models are going to be applied to archaeological leporid remains assemblages.

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