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Multi-taxa referential of a modern Eurasian Eagle-Owl (*Bubo bubo*) aerie

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Abstract

Small vertebrates on archaeological sites are generally the result of predation from different accumulator agents. Depending on their hunting habits, these agents can bias palaeobiodiversity representation; therefore, before undertaking any palaeoenvironmental analysis, it is essential to identify them. Multi-taxa analysis allows better identification of the main accumulator, but the lack of modern referentials is, for now, significantly limiting. The main goal of this study was to set up a comparative tool for small vertebrate taxa and to complete the existing referentials. We analyzed a Eurasian Eagle-Owl (*Bubo bubo*) accumulation – which provided the remains of thousands of rodents, lagomorphs, birds, amphibians, squamates and fishes – in order to study taxonomic composition, skeletal representation, digestion and fragmentation. We then compared these results with the available referentials for different taxa and discussed the use of different variables to better characterize such accumulations. We also present an original taphonomical method to study snakes vertebrae.

Keywords: Actualistic research; Eurasian Eagle-Owl (*Bubo bubo*); birds; small mammals, herpetofauna; South France

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1 Introduction

Small mammal fossil accumulations are generally the result of both coprocoenosis and post-depositional processes (Denys, 1985; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 1998; Desclaux et al., 2011; Fernández-Jalvo et al., 2016). Consequently, we can consider that the taphonomic analyses applied to small vertebrates has two main objectives: first, the identification of the accumulation modality (primary origin), and secondly, the characterization of post-depositional processes that may have affected the assemblages (Denys, 2011).

Distinguishing the main accumulator provides information on the representativity of the fossil accumulation, and possible biases between the fossil assemblage and the initial community. Moreover, some small mammal species may also have been exploited by humans for meat and fur. Detailed taphonomic analysis can enable the origin of small game within mixed accumulations to be determined and the respective role of human and non-human predators in the assemblages to be identified. Based on numerous modern referentials, several authors have participated in developing a specific methodology to determine the main small vertebrate accumulators and their impact on prey bones and the faunal spectrum (Denys, 1985; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Denys et al., 1996; Fernández-Jalvo et al., 1998, 2016; Bruderer and Denys, 1999; Desclaux et al., 2011; Denys et al., 2018). Despite the development of this accurate methodology, precise identification of the predator species at the origin of small vertebrate accumulations is still complex. Such difficulties can be linked to two main factors: first, post-depositional processes that can blur or hide the predator signal, and secondly, the partitioning of the referentials to a single taxon/group of prey (Denys, 2011). Indeed, there exist numerous referentials based only on one taxon/group, most often rodents (Denys, 1985; Andrews, 1990 ; Denys et al., 1996; Bruderer and Denys, 1999), lagomorphs (Hockett, 1995; Sanchis, 2000; Guennouni, 2001; Cochard, 2004a; Lloveras et al., 2008a, b; Lloveras et al., 2009), amphibians (Pinto Llona and Andrews, 1999) and birds (Bocheński et al., 1993; Bocheński and Tomek, 1994, 1997; Bocheński et al., 1997, 1998; Laroulandie, 2000, 2002; Bocheński and Tornberg, 2003; Alonso et al. 2019). To our knowledge, no pellet or feces referential has focused on small squamate remains (lizards, snakes). Nevertheless, all these small taxa can come from the same coprocoenosis and constitute a multi-taxa accumulation closest to the initial palaeocommunity (Denys, 2011). Understanding the establishment and potential modification of a small vertebrate

accumulation, therefore, constitutes a necessary precondition for palaeoecological reconstitutions (Andrews, 1990; Fernández-Jalvo et al., 1998, 2016; Demirel et al. 2011; Hanquet, 2011; Stoetzel et al. 2011; Denys et al., 2018). Here, we studied a Eurasian Eagle-Owl (*Bubo bubo*) accumulation created over a relatively long period (at least twenty years). Such an accumulation is close to what can be found in archaeological contexts (mixing of different seasons/years), with the additional effects of some pre-burial processes, such as weathering, trampling and wild fires. The choice of predator for this study was due to 1) its wide range of prey, allowing us to have relatively large samples for the different prey taxa, and 2) its habit of nesting in caves, which made it a significant accumulator in archaeological cave sites (Desclaux et al., 2011; Hanquet, 2011).

2 Material and methods

The material came from a Eurasian Eagle-Owl (*Bubo bubo*) aerie located in a small cavity (called Archiduc) which overhangs the Verdouble River and which is located in the vicinity of Tautavel (Pyrénées-Orientales) (fig. 1). The rock-climbing needed to reach it prevents the cave from disturbing visits. Eurasian Eagle-Owls have been observed on numerous occasions at this site during the last twenty years, and at least, one or more individuals could have successively occupied this site (personal observation by Christian Perrenoud). The material is composed of more than 13,000 remains collected in 2016 during four sessions. The collection was performed following the recommendations of the *Groupe Ornithologique du Roussillon* in order not to disturb the birds. For this study, two areas were distinguished: the 'inside area', which corresponds to the covered area of the cavity, and the 'outside area' which corresponds to the cavity porch. Limestone blocks in the outside area and the overhanging cliff above the cavity prevented strong erosion of the sediments. The first samples represent elements gathered through a simple sweeping of the ground surface. Others were made when some sediment was included to the findings. All the samples were water sieved using a 1.2 and 0.6 mesh.

The taxonomic identifications of rodents were based on Chaline (1972). Lagomorph identifications were realized using Callou (1997) and comparisons with osteological collections from the *Laboratoire départemental de Préhistoire du Lazaret* (Nice). The identification of birds was made using identification keys (e.g., Bocheński and Tomek 2009; Tomek and Bocheński, 2009) and the comparison collection from the Zoology Vertebrate

collections department with more specific visits to the Mammals and Birds section and Comparative anatomy unitin the *Muséum national d'Histoire naturelle* (Paris). For amphibians, identifications were mainly made using the osteological key of Bailon (1999); for squamate reptiles we followed the osteological criteria mentioned in Szyndlar 1984; Bailon 1991; Barahona and Barbadillo 1997 and the osteological comparison from "Anatomie Comparée" again in the *Muséum national d'Histoire naturelle* (Paris)..

Taphonomic analysis relied on the methodology and data provided by Denys (1985), Andrews (1990), Fernández-Jalvo and Andrews (1992), Pinto-Llona and Andrews (1999), Bocheński, 1997, Bocheński et al. (1998), Lloveras et al. (2008a, b), Fernández-Jalvo et al. (1998, 2016) and Denys et al. (2018).

Figure 1. Localization of the site, view of the vicinity of the Eurasian Eagle-Owl aerie (indicated by the orange circle) and view of the inside area with bone scatters.

The relative abundance of skeletal elements was defined following the formula of Dobson and Wexlar (1979), and Andrews (1990):

Ri = Ni/MNI x Ei

Ri: Relative abundance of element i; Ni: Number of elements i (replaced by the MNE in this study); MNI: Minimum Number of Individuals; Ei: Number of the element i in the skeleton of the prey.

Ei = theoretical frequency of the anatomic element i.

- for rodents: 2 hemimaxillae; 2 hemimandibles; 4 incisors; 12 molars; 2 humeri; 2 radii; 2 ulnae; 2 femorae; 2 tibiae; 2 scapulae; 2 pelves; 2 tali; 2 calcanei; 24 ribs; 54 vertebrae; 78 phalanxes and metapodia.
- for lagomorphs: 2 hemimaxillae; 2 hemimandibles; 2 superior incisors; 2 inferior incisors; 12 superior jugal teeth; 10 inferior jugal teeth; 2 humeri; 2 radii; 2 ulnae; 2 femora; 2 tibiae; 2 scapulae; 2 pelves; 2 tali; 2 calcanei; 24 ribs; 46 vertebrae; 72 phalanxes and metapodia.
- for birds: 1 maxilla; 2 hemimandibles; 1 furcula; 2 coracoids; 1 sternum; 2 humerii; 2 radii; 2 ulnae; 2 carpometacarpi; 2 ulnarae; 8 anterior phalanxes; 2 femora; 2 tibiotarsi; 2 tarsometatarsi; 2 scapulae; 28 vertebrae; 16 ribs and 28 posterior phalanxes [for the number of vertebra and posterior phalanx, which can be variable for birds, the mallard (*Anas platyrhynchos*) was taken as a referential for theoretical frequency with 28 vertebra, 16 ribs, 8 anterior phalanx and 28 posterior phalanxes as used by Desclaux (1992)].
- for amphibians: 46 bones 20 skull bones [2 premaxillae, 2 maxillae; 2 nasal; 2 frontoparietal (only 1 for Pelobates); 2 prootiques; 2 exoccipitals; 2 pterygoids; 2 squamosals; 1 sphenethmoïd; 1 parasphenoïd; 2 angulars]; 9 vertebrae; 1 urostyle; 2 scapulae; 2 coracoids; 2 claviculae; 2 ilia; 2 humerii; 2 radio-ulnae; 2 femora and 2 tibio-fibulae (in this work, the tarsal bones and phalanges are excluded).

To compare and visualize the data from the referential and the relative abundance of lagomorphs from this referential, we used Correspondence Analyses (CA) with R 3.1.2 (package FactomineR).

For a better estimation of taxonomic composition, age categories were established for lagomorphs and size categories for birds and small mammals. Indeed, numerous publications have already focused on age categories for lagomorphs from fossil or modern accumulations. Generally, the two parameters considered to determine these categories are the size and degree of ossification (Hale, 1949; Taylor, 1959; Rogers, 1982; Hocket, 1991; Guennouni, 2001; Cochard, 2004b; Jones, 2006; Pelletier et al., 2015). The age categories most commonly used are juveniles, sub-adults and adults, and are applied on long bones (humerus, radius, ulna, femur and tibia). Juvenile bones are characterized as being smaller than adult bones and by having uncoated epiphyses. Sub-adults present a similar size to adults, but the epiphyses are still uncoated. Epiphyses are fully coated in adults.

Size categories used on bird remains were defined following Laroulandie (2000):

- category 1: sparrow (*Passer* sp.), swallow (Hirundinidae), etc.
- category 2: thrush (*Turdus* sp.), starling (*Sturnus* sp.), etc.
- category 3: Common kestrel (*Falco tinnunculus*), pigeon (*Columba* sp.), mallard (*Anas platyrhynchos*), etc.
- category 4: Snowy owl (*Bubo scandiacus*), Eurasian Eagle-Owl *(Bubo bubo*), geese (*Anser* sp.), etc.
- category 5: vulture and eagle (Accipitridae), swan (*Cygnus* sp.), crane (Gruidae), etc.

A similar classification can also be applied to micromammals with two main size categories:

- category 1: less than 100 g, including voles (*Microtus* spp.), lemmings (*Dicrostonyx* spp.), field mice (*Apodemus* spp.), shrews (*Crocidura* spp.), etc.
- category 2: more than 100 g, including water voles (*Arvicola* spp.), rats (*Rattus* spp.), dormice (*Glis glis*, *Eliomys quercinus)*, Western European Hedgehog (*Erinaceus europaeus*), etc.

For the rodents, digestion was examined on incisors, molars and proximal femora. Following the frequency and intensity of the digestion, different categories were determined to discriminate groups of predators (Denys, 1985; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 1998, 2016). This methodology was previously applied on lagomorphs by Lloveras et al., (2008a, b). For birds, digestion was examined on the proximal and distal humerus and the femur, following previous works (Bocheński, 1997; Bocheński et al., 1998). In both cases, to make a correlation between other taxa possible, the same grades of digestion were used for lagomorphs' and rodents' post-cranial elements. Digestion on diaphyseal fractures was not taken into account because post-depositional fragmentation could have biased the percentage.

For amphibians, digestion was mostly observed on articular surfaces (humeral condyle, radio-ulna and ilium acetabular surface). According to the intensity of digestion, five classes were established (0= no alteration; 1= low appearance of the spongiosa–low thinning, 2= spongiosa well exposed and thinning with the start of bones loss; 3= loss of bone on the articular surfaces/extremities; 4= fracture zone with rounded edge) (Pinto-Llona and Andrews, 1999).

For lizards and snakes, the study mainly focused on the digestion of vertebrae, because they are the most abundant elements. To our knowledge, this is the first taphonomic study on snake vertebrae based on a modern owl accumulation. We identified five categories of digestion (0=non digested; 1= diapophysis and/or parapophysis affected; 2= prezygapophyseal processes was also affected; 3= condyle was also affected; 4= lamellar bone loss – it generally affects the following structures zygosphene, aliform processes of the neural arc, neural spine and/or vertebral body). Of course, the digestion process does not strictly follow this order of progression and is not realized symmetrically on the different structures. Numerous elements showed an intermediate alteration; consequently, other referentials will be needed to validate (or invalidate) our results. Post-depositional alterations were also present – mostly weathering for the outside area and burnt bones due to a wild fire – but these were not counted.

3 Results

Taxonomic composition

The assemblage showed a wide diversity of prey with at least 50 identified taxa (tab. 1).

For birds, 21 taxa were determined. Small passeriforms (size categories 1 and 2) were the most abundant (MNI=19 and 41, respectively), followed by *Perdix perdix* (MNI=10) and *Alectoris rufa* (MNI=5). Several raptors were also identified, such as *Athena noctua*, *Tyto alba*, *Otus scops* and *Falco tinnunculus*.

Table 1. Specific diversity of the Archiduc small vertebrate accumulation in MNI (Minimum Number of Individuals) and the MNE (Minimum Number of Elements) for the different groups.

Species	Inside area	Outside area	Total
Alectoris rufa (Red-legged Partridge)	3	2	5
Anas sp. (Duck)	1		1
Apus sp. (Swift)	3		3
*Athene noctua (*Little Owl)	2		2
Charadriiformes	1		1
Columba livia/oenas (Rock/Stock Dove)	2	1	3
Columba palumbus (Common Woodpigeon)	2	1	3
Corvus corax (Common Raven)	1		1
Coturnix coturnix (Common Quail)	3		3
Falco cf. *subbuteo* (Eurasian Hobby)		1	1
Falco tinnunculus (Common Kestrel)	2	1	3

Gallinula chloropus (Common Moorhen)	2		2
Gallus gallus (Chicken)	1		1
Hirundinidae (Swallows)	1		1
Lanius excubitor/meridionalis (Great grey shrike/Iberian Grey Shrike)	1		1
Merops apiaster (European Bee-eater)	1		1
Otus scops (Eurasian Scops-Owl)	1	1	2
Perdix perdix (Grey Partridge)	7	3	10
Pica pica (Eurasian Magpie)	1		1
Streptopelia turtur (European Turtle-dove)	3		3
Tachybaptus ruficollis (Little Grebe)		1	1
Tyto alba (Barn-owl)	1	1	2
Birds caterogy 1	8	11	19
Birds caterogy 2	21	20	41
Suncus etruscus (Pygmy White-toothed Shrew)		1	1
Crocidura russula (White-toothed Shrew)		1	1
Erinaceus europaeus (European Hedgehog)	1	2	3
Eliomys quercinus (Garden Dormouse)	3	2	5
Glis glis (Edible Dormouse)	1	1	2
Microtus nivalis (European Snow Vole)		2	2
Clethrionomys glareolus (Bank Vole)	1	2	3
Arvicola amphibius (European Water Vole)	2		2
Arvicola sapidus (Southern Water Vole)	10	3	13
Mus musculus (House Mouse)		1	1
Apodemus sp. (Field Mouse)	7	10	17
Rattus norvegicus (Brown Rat)	13	8	21
Oryctolagus cuniculus (European Rabbit)	46	30	76
Lepus europaeus (European Hare)	4	2	6
Mustela nivalis (Least Weasel)	2		2
Vulpes vulpes (Red Fox)	1	1	2
Felis catus (Cat)		1	1
Alytes obstetricans (Common Midwife Toad)	1	1	2
Discoglossus pictus (Painted Frog)	2	2	4
Pelobates cultripes (Western Spadefoot)	3	2	5
Pelophylax sp.	11	18	29
Lacertidae		1	1
cf. *Timon* sp.	1	1	2
Coronella girondica (Southern Smooth Snake)	1	1	2
Zamenis scalaris (Ladder Snake)	3	1	4
Natrix maura (Viperine Snake)	1	1	2
Cyprinidae	65	52	117
Anguillidae	7	1	8
Clupeidae		1	1
Total	**254**	**192**	**446**

MNE			
Aves	1127	988	2115
Lagomorphs	2073	1370	3443
Micromammals	3757	2307	6064
Carnivora	10	6	16
Herpetofauna	640	580	1220
Fishes	415	427	842
Total	**8022**	**5678**	**13700**

For small mammals, 14 taxa were identified. The most represented species were *Oryctolagus cuniculus* (MNI=82), *Rattus norvegicus* (MNI=21), *Apodemus* sp. (MNI=17) and *Arvicola sapidus* (MNI=13). The species showed a large size-range from *Suncus etruscus* to *Lepus europaeus,* though the larger ones dominated (*Oryctolagus cuniculus*, *Rattus norvegicus*, *Arvicola* sp.). The age profile of the lagomorphs showed a higher representation of adults. There were few differences between the young and sub-adult representations (tab. 2).

Table 2. Lagomorph age distribution (in MNI) for the different age categories.

	young	sub-adults	adults
Inside area	13	9	28
Outside area	4	9	19
Total	17	18	47

Amphibians were represented by four taxa: *Alytes obstetricans*, *Discoglossus pictus*, *Pelobates cultripes* and *Pelophylax* sp. (more probably *P. perezi* and/or *P.* kl. g*rafi*). The most abundant taxon was *Pelophylax* sp. (MNI=29), then *Pelobates cultripes* (MNI=5) and *Discoglossus pictus* (MNI=4).

Squamates were represented by at least four taxa: one lizard (cf. *Timon* sp.), and three snakes (*Coronella girondica, Zamenis scalaris, Natrix maura*). These were represented by one or two individuals in the assemblage (MNI determined with cranial elements). Snakes were mostly represented by numerous vertebrae with a vertebral body length of between 3 mm and 4 mm, corresponding to individuals with a total body length of between 50 cm and 70 cm (adult size for *C. girondica* and *N. maura*, juvenile or sub-adult size for *Z. scalaris*) and a body weight valued between 50 g and 80 g.

Three families comprised the fish community: Cyprinidae, Anguillidae and Clupeidae. The fish assemblage was subjected to a specific study, and more detailed results can be found in Guillaud et al. (2019).

Small carnivores were also found in the assemblage. Some remains were attributed to *Mustela nivalis*, juvenile *Vulpes vulpes* and juvenile *Felis catus*. No alterations of digestion were visible.

Skeletal composition, fragmentation and digestion

Birds

Skeletal composition

For the skeletal representation of birds, bones from *Apus* sp. were not considered due to their typical morphology, linked to their hyper-specialization to fly, which greatly increases the robustness of their wing bones.

In the inside area, birds from size category 1 showed a good percentage of representation (PR) for the humerus, tibiotarsus, tarsometatarsus and sternum (between 68% and 75%). The mean value of the skeletal representation was 29%. Concerning birds from size category 2, we observed a better representation of tarsometatarsus and humerus (100%) followed by femora, ulna, coracoid and sternum (between 70% and 83%). The mean PR was 49%. Birds from size category 3 showed a better representation of sternum (44%) followed by femur, tibiotarsus and metatarsus (between 31% and 35%). The mean value of the skeletal representation was 20%, which is low compared to the other size categories (fig. 2).

In the outside area, birds from size category 1 showed a better representation of humerus (72%), coracoids (72%) followed by tibiotarsus (54%) and ulna (50%). The mean PR was 3%. Size category 2 showed a better representation of ulna (97%) and coracoids (92%). Other elements such as the humerus, scapula, tibiotarsus, sternum and carpometacarpus also displayed a good preservation rate, between 60% and 75%. The mean PR was quite high (45%). Birds from size category 3 showed a better representation of sternum, femora and humerus (between 54% and 58%). The mean value of the skeletal representation was 32%; again, this is low compared to the other size categories (fig. 2).

If we consider the entire assemblage, category size 1 birds showed a better representation of humerus (73%) and sternum (63%). The mean percentage of representation was 28%. For category size 2 birds, coracoids (84%), humerus (84%) and ulna (80%) had a better representation. The mean percentage of representation was 47%, which is high compared to the other size categories. For birds from category size 3, there was a better presentation of sternum (48%), femora (45%) and humerus (37%). The mean value of the skeletal representation was 23%, which is low compared to the other size categories (fig. 2).

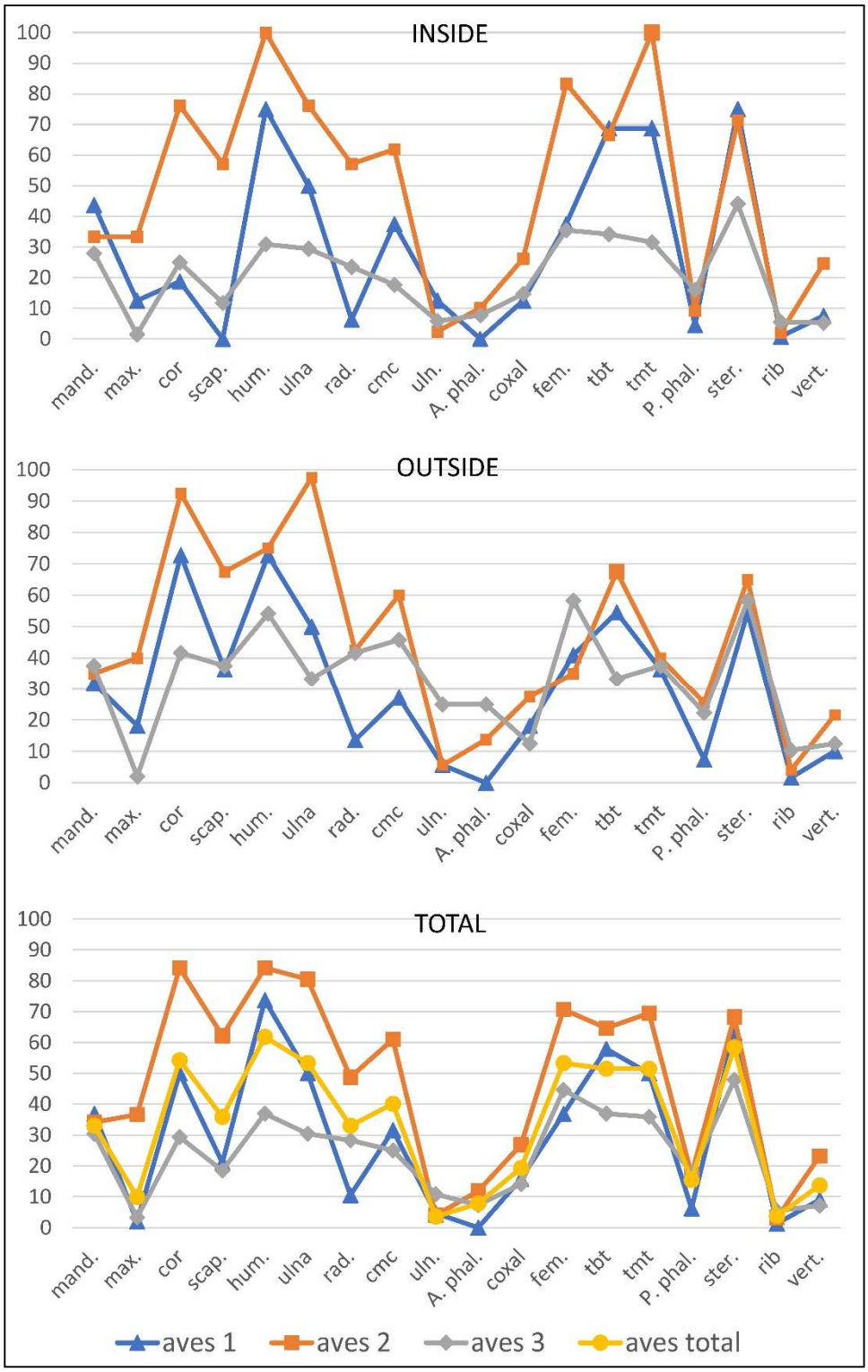


Figure 1. Relative abundance of the different skeletal elements of birds from size categories 1,2 and 3 presented on the inside zone, outside zone and in total (mand: mandible; max: maxillary; cor: coracoideum; scap: scapula; hum: humerus; rad: radius; cmc: carpometacarpus; uln : ulnar; A. phal. : anterior phalanxes; fem: femora; tbt: tibiotarsus; tmt: tarsometatarsus; P. phal: posteriors phalanxes; ster : sternum; vert: vertebra)

Fragmentation

The percentage of fragmentation (PF) for birds belonging to size category 1 was lower for the inside area (62%) than for the outside area (tab. 3). However, the small size of the sample makes interpretations difficult. For size category 2, the PF was similar between the inside area (81%) and the outside area (78%). Carpometacarpus evidenced the lowest PF (48% and 65%), while tibiotarsus had the highest (98% and 96%). Size category 3 displayed slightly lower fragmentation for the inside area than the outside area (87%). Tarsometatarsus showed a lower PF (55%) for the inside area, and carpometacarpus (61%) for the outside area. Tibiotarsus presented the highest PF for both areas (100%).

Table 3. Fragmentation rates (PF, %) of the different skeletal elements of birds from size categories 1, 2 and 3 for the inside zone and the outside zone.

	Aves 1		Aves 2		Aves 3	
	inside	outside	inside	outside	inside	outside
Humeri	43	68	84	84	81	96
Ulnae	56	88	77	78	73	80
Radii	100	75	67	80	77	95
Carpometacarpi	33	29	65	48	75	61
Coracoids	67	58	81	88	72	88
Femora	50	75	73	85	89	95
Tibiotarsi	100	79	96	98	100	100
Tarsometatarsi	67	91	71	67	55	71
Mean	**62**	**72**	**78**	**81**	**80**	**87**

Digestion

The mean digestion rate on the proximal femora was 34% for the inside area and 39% for the outside area (tab. 4). The intensity of the digestion was mostly light (fig. 3A-C). For the distal femora, the digestion rate reached 51% for the inside area and 41% for the outside area. The proximal humerus showed a digestion rate of 36% for the inside area and 31% for the outside area. The distal humerus had a digestion rate of 49% for the inside area and 33% for the outside area. It is difficult to compare the size categories due to the low number of remains; nevertheless, the digestion rate presents a high variability, according to the type of bones or extremities.

Table 4. Number and rate of digested bird femora and humerus extremities (0=none, 1=light, 2=moderate, 3= strong).

	femora

			0		1		2		3		% Total digested
			N	%	N	%	N	%	N	%	
Inside area	aves 1	prox	5	100	0	0	0	0	0	0	0
		dist	4	80	1	20	0	0	0	0	20
	aves 2	prox	28	72	11	28	0	0	0	0	28
		dist	10	48	9	43	2	10	0	0	52
	aves 3	prox	11	48	10	43	2	9	0	0	52
		dist	5	38	5	38	2	15	1	8	62
	total	**prox**	**44**	**66**	**21**	**31**	**2**	**3**	**0**	**0**	**34**
		dist	**19**	**49**	**15**	**38**	**4**	**10**	**1**	**3**	**51**
Outside area	aves 1	prox	6	86	1	14	0	0	0	0	14
		dist	5	83	1	17	0	0	0	0	17
	aves 2	prox	7	58	5	42	0	0	0	0	42
		dist	7	64	3	27	1	9	0	0	36
	aves 3	prox	4	44	5	56	0	0	0	0	56
		dist	5	42	5	42	2	17	0	0	58
	total	**prox**	**17**	**61**	**11**	**39**	**0**	**0**	**0**	**0**	**39**
		dist	**17**	**59**	**9**	**31**	**3**	**10**	**0**	**0**	**41**

			humerus								
			0		1		2		3		% Total digested
			N	%	N	%	N	%	N	%	
Inside area	aves 1	prox	7	88	1	13	0	0	0	0	13
		dist	7	70	2	20	1	10	0	0	30
	aves 2	prox	14	58	9	38	1	4	0	0	42
		dist	20	54	15	41	2	5	0	0	46
	aves 3	prox	11	61	5	28	2	11	0	0	39
		dist	9	39	11	48	3	13	0	0	61
	total	**prox**	**32**	**64**	**15**	**30**	**3**	**6**	**0**	**0**	**36**
		dist	**36**	**51**	**28**	**40**	**6**	**9**	**0**	**0**	**49**
Outside area	aves 1	prox	14	93	1	7	0	0	0	0	7
		dist	10	83	2	17	0	0	0	0	17
	aves 2	prox	18	64	9	32	1	4	0	0	36
		dist	18	72	6	24	1	4	0	0	28
	aves 3	prox	5	45	6	55	0	0	0	0	55
		dist	2	25	4	50	2	25	0	0	75
	total	**prox**	**37**	**69**	**16**	**30**	**1**	**2**	**0**	**0**	**31**
		dist	**30**	**67**	**12**	**27**	**3**	**7**	**0**	**0**	**33**

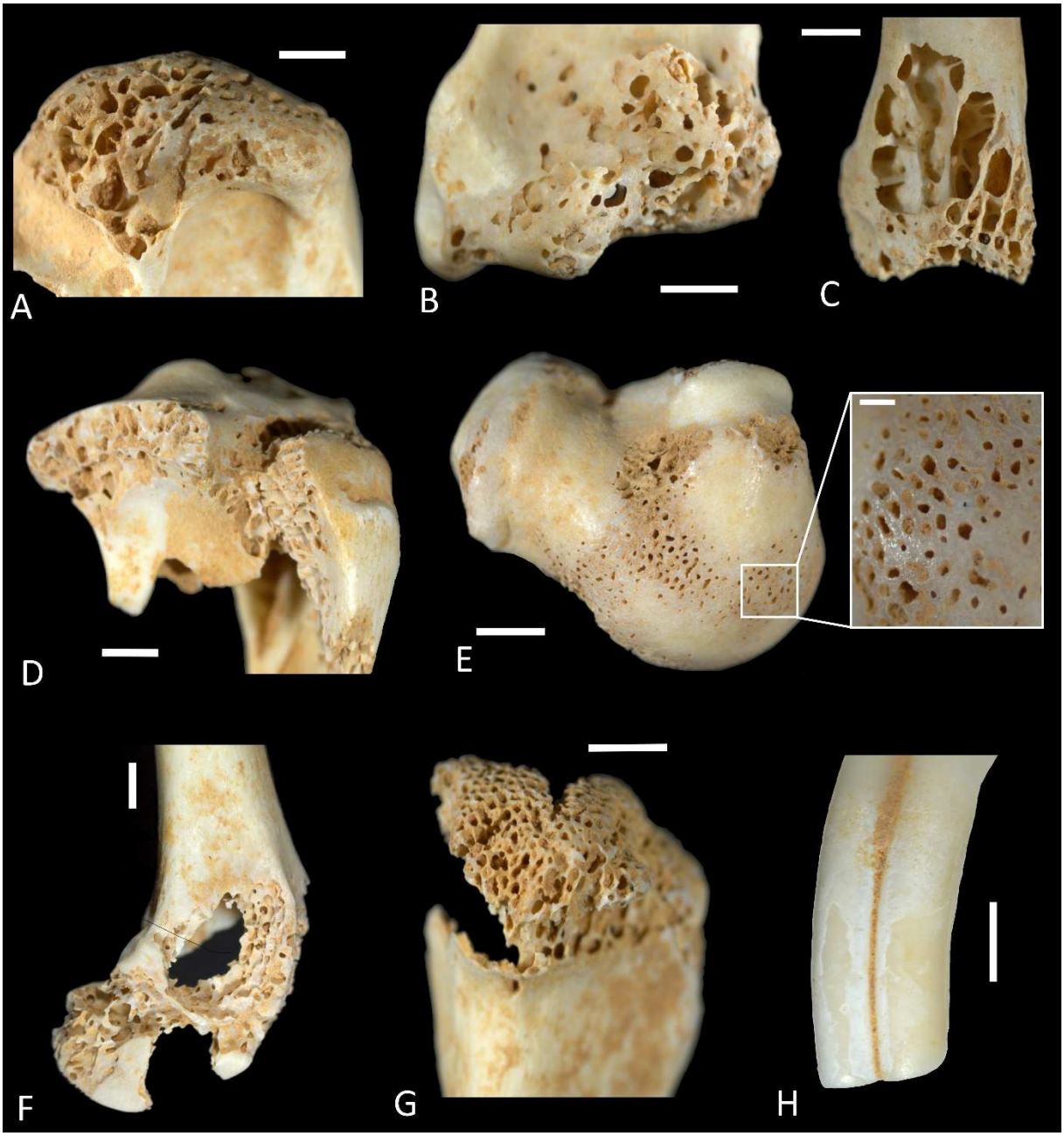


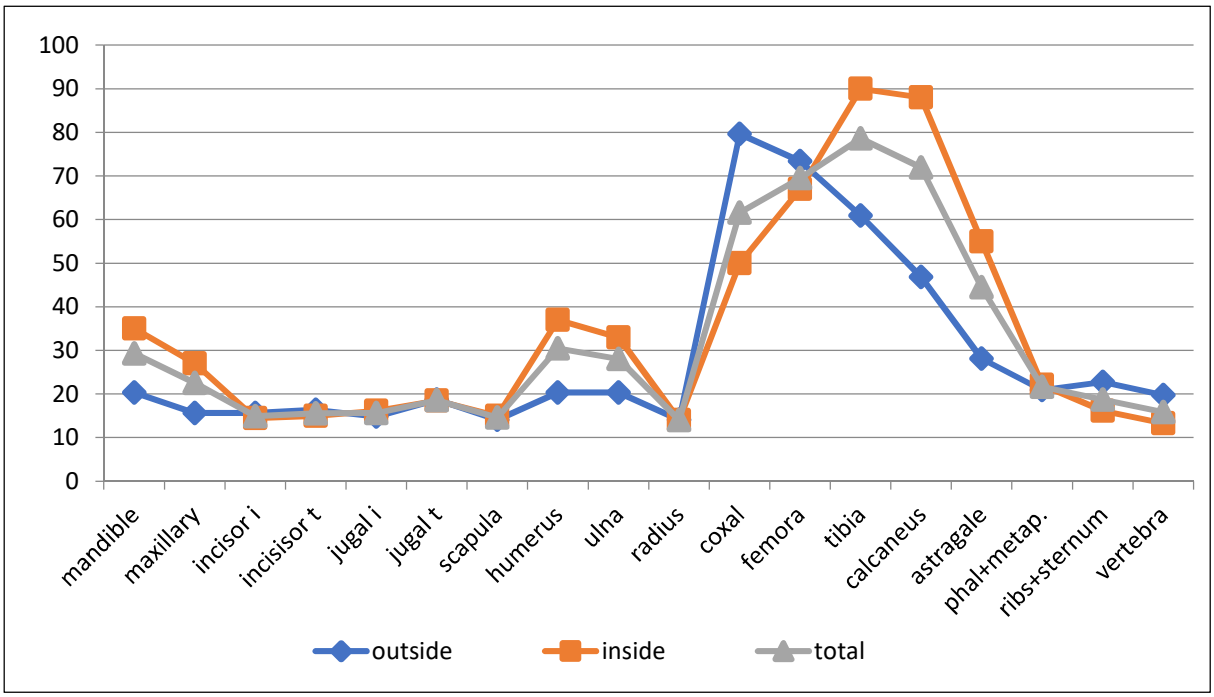
Figure 2. Different degrees of digestive damage to birds and lagomorphs remain, scale = 2mm. A: bird proximal humerus with light digestion; B: birds distal humerus with light digestion; C: bird distal tibiotarsus with moderate digestion; D: lagomorphs proximal tibia with light digestion; E: lagomorph proximal humerus with light digestion, closer view of the alteration (scale=0.5mm); F: lagomorphs distal femora with strong alteration; G: lagomorph proximal humerus with strong/heavy alteration; H: incisor with light digestion.

Lagomorpha

Skeletal composition

We observed numerous similarities between relative abundance curves from outside and inside areas, with an increased representation of hindlimbs (fig. 4), especially femora (67% and 72%), tibia (90% and 60%) and calcaneus (88% and 46%). Concerning forelimbs, the humerus displayed the best representation, even if it did not exceed 40%. Mandibles were the most represented cranial element. The mean PR value was 30% for the inside area and 37% for the outside area.

Figure 4. Relative abundance of lagomorph skeletal elements for the inside area, outside area and in total (incisor/jugal i = isolated incisor/jugal; incisor/jugal t = incisor/jugal total).



Fragmentation

Young and sub-adult lagomorphs showed a similar PF between the outside and the inside areas (77% and 81%) (tab. 5). Femora had the lowest fragmentation rate (74%). Ulnae were the most fragmented with a PF of 85% and 90%. But again, the small number of remains for some elements (such as the radius) makes further interpretation difficult. Fragmentation rates for adult were similar for outside and inside areas. Radii were the least fragmented (73% and 67%), but these elements were scarce. Femora were the most fragmented (99% and 100%).

Table 5. Fragmentation rates (PF, %) of the different skeletal elements of lagomorphs and micromammals from the inside and outside areas.

% fragmentation		Lagomorphs		Micromammals
		Young and sub-adults	Adults	
Humeri	ins.	71	93	46
	out.	86	90	50
Ulnae	ins.	85	71	58
	out.	90	100	67
Radii	ins.	100	73	33
	out.	50	67	67
Femora	ins.	74	99	43
	out.	74	100	39
Tibiae	ins.	79	100	49
	out.	88	98	63
total	**ins.**	**77**	**97**	**46**
	out.	**81**	**96**	**55**

Digestion

Only isolated teeth were considered due to the low number of *in situ* teeth. Digestion rates on incisors was 32% in the inside area (tab. 6). The alteration was mostly from moderate to strong (fig. 3D-L). For the outside area, 45% of the incisors were digested; nevertheless, this number must be considered carefully due to the low number of elements. The digestion rate of jugal teeth reached 14% in the inside area, mostly with a moderate intensity. For the outside area, digestion rate on jugal teeth was 31%, also with a primarily moderate intensity. The digestion rates on femoral heads was 35% for the inside area and 57% for the outside area, but again the number of elements was small.

Table 6. Number and rate of digested lagomorph teeth and femora proximal extremities (0=none, 1=light, 2=moderate, 3= strong, 4=heavy).

		0		1		2		3		4		% total digested
		N	%	N	%	N	%	N	%	N	%	
Inside area	incisor	19	67.9	0.0	0.0	6.0	21.4	3.0	10.7	0	0	32.1
	jugal	52	85.2	2.0	3.3	6.0	9.8	1.0	1.6	0	0	14.8
	femora	9	64.3	1.0	7.1	2.0	14.3	2.0	14.3	0	0	35.7
Outside area	incisor	6	54.5	1.0	9.1	2.0	18.2	2.0	18.2	0	0	45.5
	jugal	23	71.9	0.0	0.0	6.0	18.8	4.0	12.5	0	0	31.3
	femora	6	42.9	4.0	28.6	4.0	28.6	0.0	0.0	0	0	57.1

Micromammals

Skeletal composition

Relative abundance curves from the outside and inside areas showed a similar pattern. The femora and pelvis were well represented (between 86% and 92%). The tibiae were also well represented, even though the value for the outside area was lower than in the inside area. Despite this, the outside area showed a better representation, especially of cranial elements, particularly incisors. The mean PR value was 43% for the inside area and 49% for the outside area (fig. 5).

Fragmentation

Fragmentation rates were slightly lower in the inside area (46%) than in the outside area (55%). The lowest PF for the outside area was the radii (33%) and for the inside area the femora (39%). The ulna and radius presented the highest PF (67%) in the outside area. For the inside area, ulnae were the most fragmented elements (49%) (tab. 5).

Digestion

Digestion rates on incisors were 46% (39% isolated and 7% *in situ*) for the outside area and 41% (32% isolated and 9% *in situ*) for the inside area (tab. 7). For the outside area, 16% of incisors showed a light alteration, 20% a moderate alteration and 9% a strong alteration. For the inside area, light alteration was observed on 12% of the incisors, moderate alteration on 17% and strong alteration on 10%. Extreme alteration was observed on less than

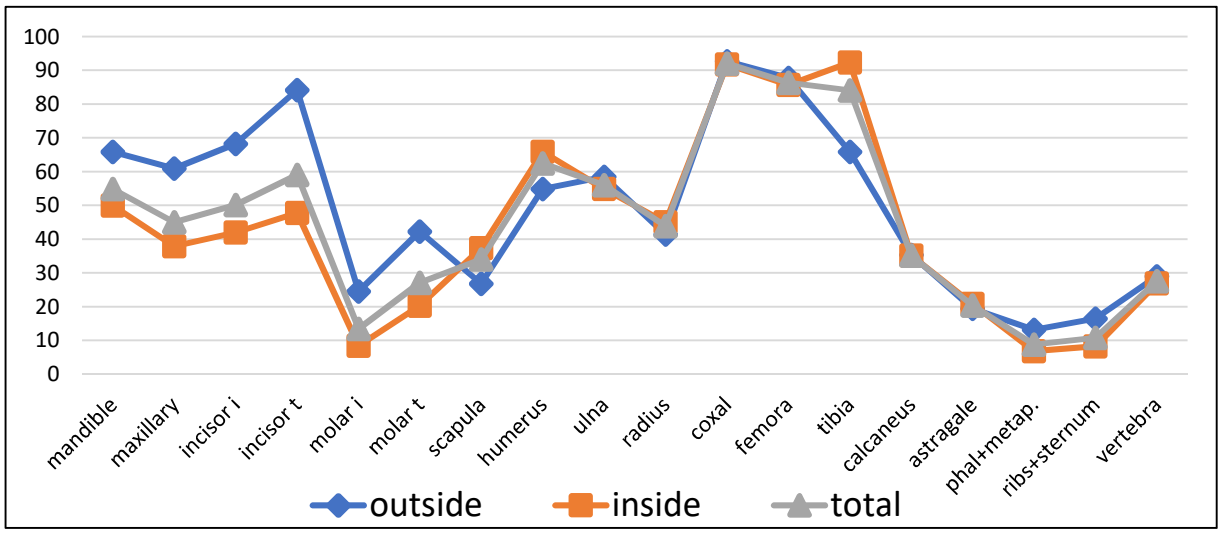


Figure 3. Relative abundance of micromammal skeletal elements for the inside area, outside area and in total (incisor/molar i = isolated incisor/molar; incisor/molar t = incisor/molar total).

1% of the incisors.

Table 7. Number and rate of digested micromammal teeth and femora proximal extremities (0=none, 1=light, 2=moderate, 3= strong, 4=heavy).

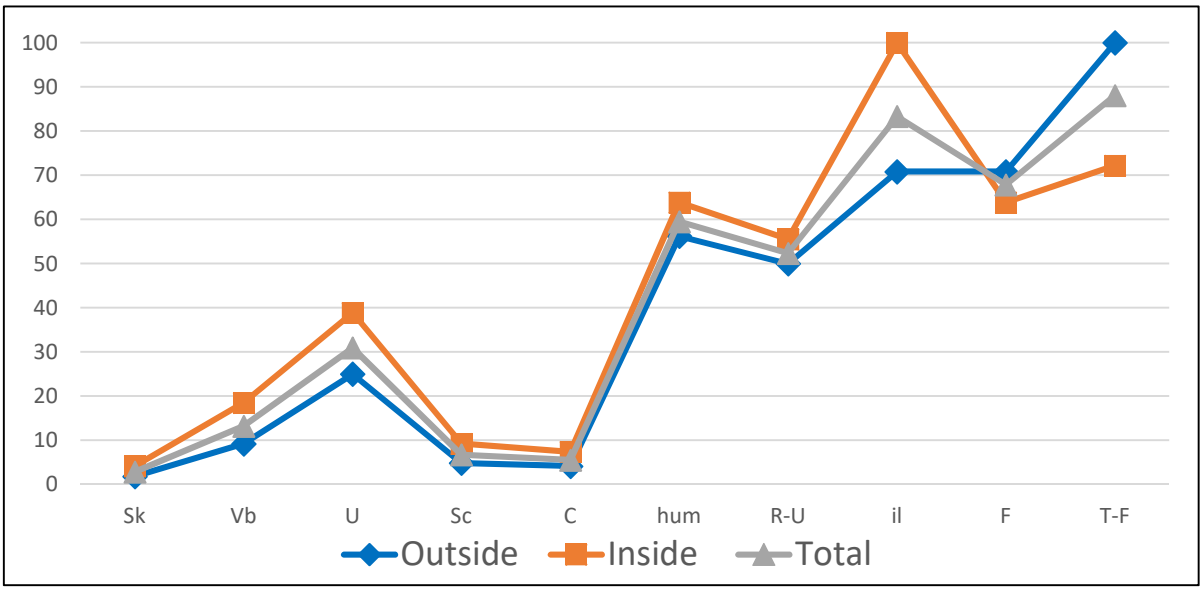
			0		1		2		3		4		% total digested
			N	%	N	%	N	%	N	%	N	%	
Outside area	incisor	*ex situ*	32	43.8	10	13.7	12	16.4	7	9.6	0	0	**46.6**
		in situ	7	9.6	2	2.7	3	4.1	0	0.0	0	0	
		total	**39**	**53.4**	**12**	**16.4**	**15**	**20.5**	**7**	**9.6**	**0**	**0**	
	Arvicolinae molar	*ex situ*	32	55.2	4	6.9	3	5.2	5	8.6	0	0	**20.7**
		in situ	14	24.1	0	0.0	0	0.0	0	0.0	0	0	
		total	**46**	**79.3**	**4**	**6.9**	**3**	**5.2**	**5**	**8.6**	**0**	**0**	
	Murinae molar	*ex situ*	15	15.5	7	7.2	3	3.1	7	7.2	0	0	**26.8**
		in situ	56	57.7	4	4.1	3	3.1	2	2.1	0	0	
		total	**71**	**73.2**	**11**	**11.3**	**6**	**6.2**	**9**	**9.3**	**0**	**0**	
	femora		11	52.4	4	19.0	4	19.0	2	9.5	0	0	**47.6**
Inside area	incisor	*ex situ*	76	54.7	13	9.4	20	14.4	11	7.9	1	0.7	**41.0**
		in situ	6	4.3	4	2.9	4	2.9	4	2.9	0	0	
		total	**82**	**59.0**	**17**	**12.2**	**24**	**17.3**	**15**	**10.8**	**1**	**0.7**	
	Arvicolinae molar	*ex situ*	46	67.6	10	14.7	4	5.9	5	7.4	0	0	**27.9**
		in situ	3	4.4	0	0.0	0	0.0	0	0.0	0	0	
		total	**49**	**72.1**	**10**	**14.7**	**4**	**5.9**	**5**	**7.4**	**0**	**0**	
	Murinae molar	*ex situ*	8	6.5	1	0.8	2	1.6	1	0.8	0	0	**13.7**
		in situ	99	79.8	5	4.0	6	4.8	2	1.6	0	0	
		total	**107**	**86.3**	**6**	**4.8**	**8**	**6.5**	**3**	**2.4**	**0**	**0**	
	femora		64	81.0	8	10.1	6	7.6	1	1.3	0	0	**19.0**
Total	incisor	*ex situ*	108	50.9	23	10.8	32	15.1	18	8.5	1	0.5	**42.9**
		in situ	13	6.1	6	2.8	7	3.3	4	1.9	0	0	
		total	**121**	**57.1**	**29**	**13.7**	**39**	**18.4**	**22**	**10.4**	**1**	**0.5**	
	Arvicolinae molar	*ex situ*	78	61.9	14	11.1	7	5.6	10	7.9	0	0	**24.6**
		in situ	17	13.5	0	0.0	0	0.0	0	0.0	0	0	
		total	**95**	**75.4**	**14**	**11.1**	**7**	**5.6**	**10**	**7.9**	**0**	**0**	
	Murinae molar	*ex situ*	23	10.4	8	3.6	5	2.3	8	3.6	0	0	**19.5**
		in situ	155	70.1	9	4.1	9	4.1	4	1.8	0	0	
		total	**178**	**80.5**	**17**	**7.7**	**14**	**6.3**	**12**	**5.4**	**0**	**0**	
	femora		75	75.0	12	12.0	10	10.0	3	3.0	0	0	**25.0**

Digestion rates on Arvicolinae molars were around 20% (all isolated) for the outside area and 28% for the inside area. For the outside area, 7% of the molars showed a light alteration, 5% a moderate alteration and 8% a strong alteration. For the inside area, 14% of the molars showed a light alteration, 6% a moderate alteration and 7% a strong alteration.

Digestion rates on Murinae molars were around 26% (17% isolated and 9% *in situ*) for the outside area and 13% (3% isolated and 10% *in situ*) for the inside area. For the outside area, 11% of the molars showed a light alteration, 6% a moderate alteration and 9% a strong alteration. For the inside area, 5% of the molars showed a light alteration, 6% a moderate alteration and 2% a strong alteration.

Digestion rates on femoral heads were 47% in the outside area and 19% in the inside area. For the outside area, 19% of the femora showed a light alteration, 19% a moderate alteration and 9% a strong alteration. For the inside area, 10% of the femora showed a light alteration, 8% a moderate alteration and 1% a strong alteration.

Amphibians



Skeletal composition

Relative abundance curves from the outside and inside areas showed a similar pattern,

Figure 4. Relative abundance of amphibian skeletal elements for the inside area, outside area and in total.

even if percentages from the outside area were slightly higher. For both areas, hindlimbs were the best represented parts, followed by forelimbs and ilia (fig. 6).

Fragmentation

The fragmentation rate on long bones was around 61% for the outside area and 54% for the inside area (fragmentation category 3 in Pinto-Llona and Andrews, 1999). The

fragmentation of the forelimbs (shorter and more robust) was lower than for the hindlimbs and the ilium (longer and fragile) (tab. 8).

Table 8. Fragmentation rates (PF, %) of the different skeletal elements of amphibians from the inside and outside areas.

% fragmentation	Inside	Outside
Humeri	25	32
Radio-ulnae	23	50
Ilium	100	56
Tibio-fibulae	48	69
Total	**54**	**61**

Digestion

There was a slight difference between the digestion rates of the outside area (42%) and the inside area (56%) (tab. 9).

Table 9. Digestion of amphibian long bones, and number and percentage of digested elements depending on intensity (0=none, 1=light, 2=moderate, 3= strong, 4=heavy).

		0		1		2		3		4		**Total digested**
		N	%	N	%	N	%	N	%	N	%	
Inside	Humeri	3	19	4	25	7	44	1	6.5	1	6.5	**81**
	Radio-ulnae	4	31	7	54	2	15	0	0	0	0	**69**
	Ilium	4	25	6	38	3	19	1	6	2	12	**75**
	Femora	16	76	3	14	0	0	2	10	0	0	**24**
	Tibio-fibulae	12	52	5	23	1	4	1	4	4	17	**48**
Outside	Humeri	10	53	5	26	2	10.5	2	10.5	0	0	**47**
	Radio-ulnae	5	36	6	43	3	21	0	0	0	0	**64**
	Ilium	2	15	5	38	3	23	3	23	0	0	**65**
	Femora	22	73	3	10	2	7	0	0	3	10	**27**
	Tibio-fibulae	28	72	3	8	0	0	6	16	2	4	**28**

On the acetabular cavities, the digestion was mainly light (category 1) with a low appearance of spongiosa; between 40% and 60% of the radio-ulna and ilium were digested. On the humeral condyle we observed that the appearance of spongiosa was more pronounced (category 2), especially on the inside area (44% of digested bones) (fig. 7A-F). Category 3 was less represented (maximum of 23%) for the ilium on the outside area. About 20% of femora and tibio-fibulae show thinning and loss of bone, while the appearance of rounded surfaces on fracture zones is low (less than 20%). Other elements (skull bones, vertebrae, urostyle and scapula) were digested (fig. 7D, H-L). Following Pinto-Llona and Andrews

(1999) this sample was attributed to category 3 (around 50%), which differs from their own study where the Eurasian Eagle-Owl was placed in category 5 (with the majority of bones presenting a strong alteration) predator.

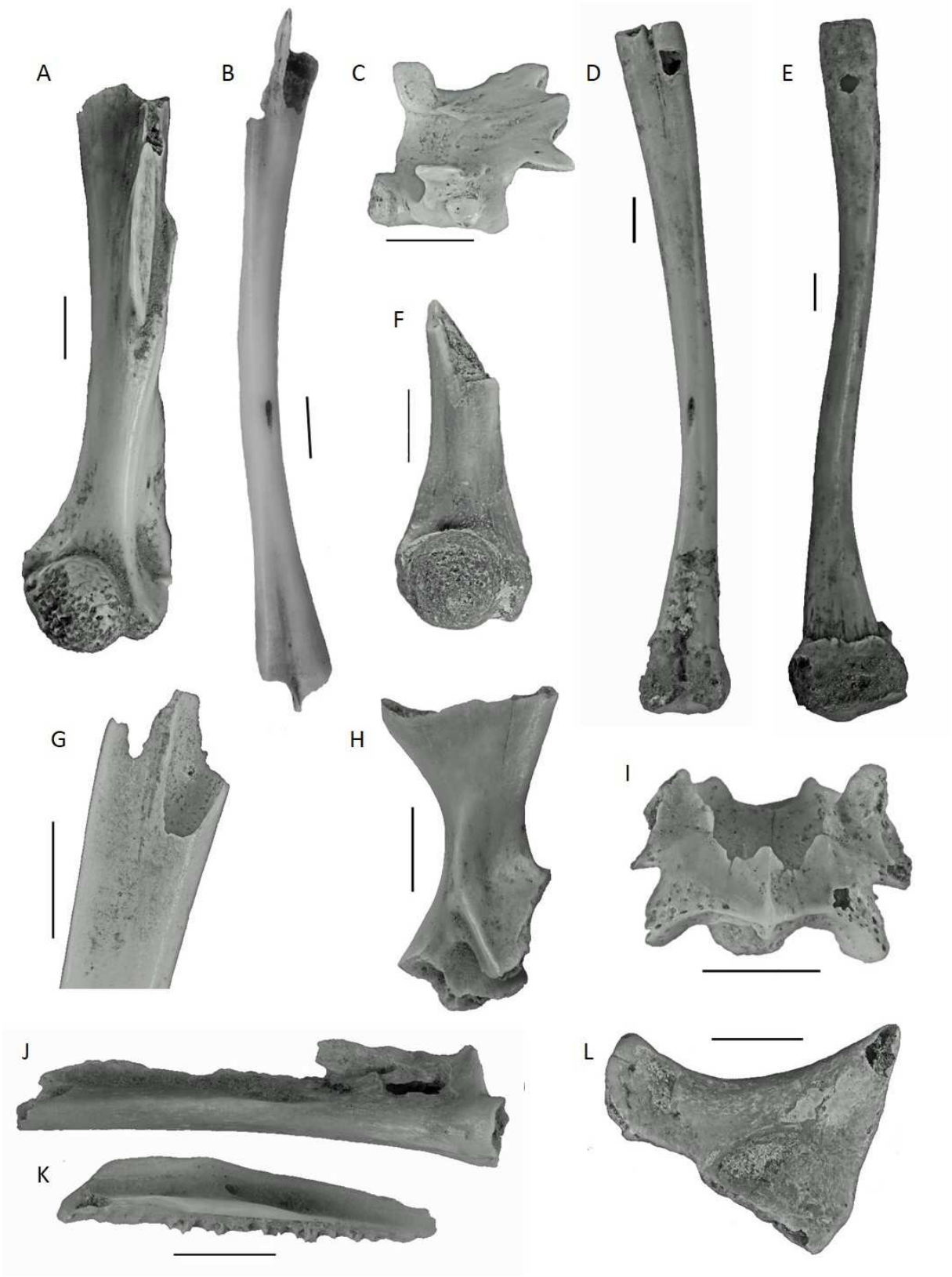


Figure 7. Amphibian anurans digested bones, scale= 2 mm. *Discoglossus pictus* [A: humerus with category 2 digestion; B: tibio-fibulae, category 3 digestion; C: vertebra, category 2]; *Pelobates cultripes* [F: humerus, category 2; *Pelophylax* sp.; D: tibio-fibulae, category 0; E: femur, category 0; G: tibio-fibulae, proximal extremity, category 3; H: scapula, category 1; I: vertebra, category 2; J: urostyle, category 3; K: maxilla, category 4] and *Pelobates cultripes*, L: cranial fragment, category 4.

Squamates

Remarks about anatomical representation

Only one lizard was found in each area. And as the estimation of the MNI for snakes is difficult (and always under evaluated), due to the high number of vertebrae in each individual, it was deemed unfeasible to study the anatomical representation for squamates.

Fragmentation

For snakes, the PF of vertebrae is low, particularly in the inside area (only 1%). It is higher in the outside area (15%), more likely as a result of post-depositional processes. In general, snake vertebrae are compact and strong, and generally the most broken parts are the apophyses/processes that protrude from the vertebral body.

Digestion

In snakes, the percentage of digested vertebrae is high (greater than 75%) (tab. 10, fig. 8). For *Zamenis scalaris* and *Natrix maura*, all the digestion categories are represented and show similar values (between 10 and 36%) (fig. 8 and 9).

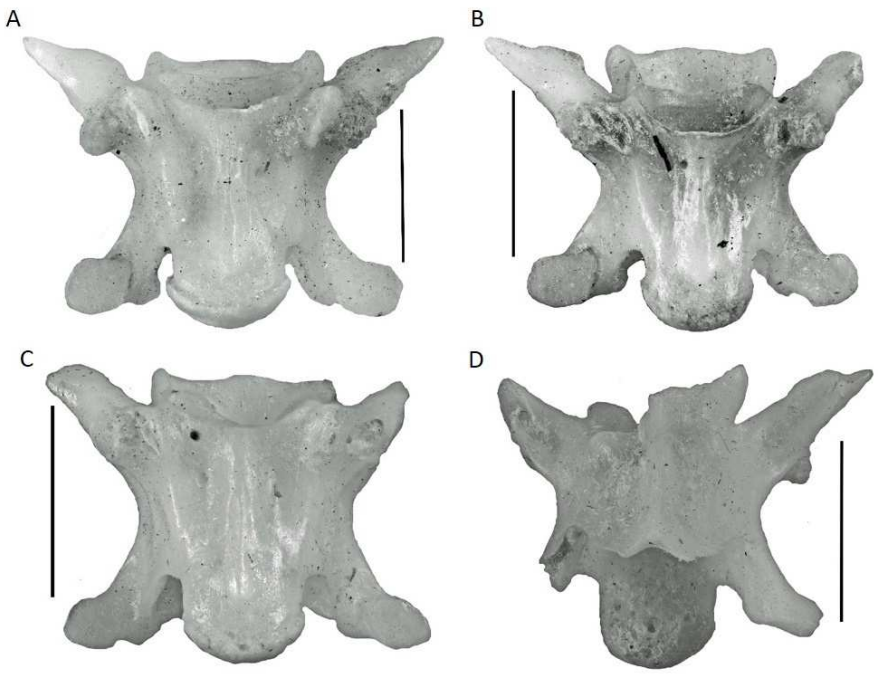
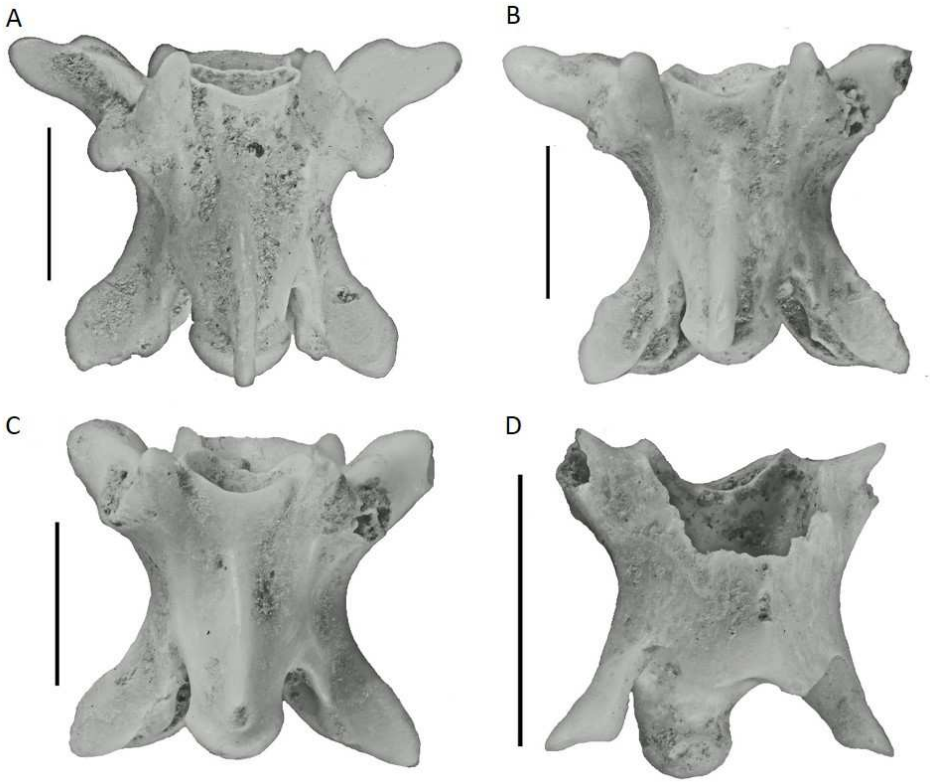


Figure 5. *Zamenis scalaris* (P), vertebrae with different digestion categories, A: category 0; B: category 2; C: category 3, D: category 4. Scale= 2 mm.

This is clearly observable on the individual of *Zamenis scalaris* from a single fresh pellet (one of the few intact pellets) from the inside area, where 87% of the vertebrae are digested (36% for category 1; 15% for category 2; 10% for category 3 and 26% for category 4). The vertebrae of *Coronella girondica* evidenced a different pattern with a lower intensity of digestion (mostly categories 1 and 2). This can be linked to their low number and that,



although they are a similar size, their mineralization is higher than in other species (because they are adult individuals).

Figure 9. *Natrix maura*, vertebrae with different digestion categories, A: category 0; B: category 2; C: category 3, D: category 4. Scale= 2mm.

Table 10. Digestion of snake vertebrae, and number and percentage of digested elements depending on intensity (0=none, 1=light, 2=moderate, 3= strong, 4=heavy). *Zamenis scalaris* (P) correspond to an only individual in an intact pellet.

		0		1		2		3		4		**Total digested**
		N	%	N	%	N	%	N	%	N	%	
Inside	*Coronella girondica*	4	80	1	20	0	0	0	0	0	0	**20**
	Zamenis scalaris	41	26	29	18	37	23	28	18	23	14	**74**
	Zamenis scalaris (P)	24	13	65	36	27	15	17	10	46	26	**87**
	Natrix maura	13	17	9	12	18	37	13	17	13	17	**83**
Outside	*Coronella*	6	25	15	63	1	4	0	0	2	8	**75**

	girondica											
	Zamenis scalaris	30	25	14	12	25	21	16	13	34	29	**75**
	Natrix maura	27	16	35	20	21	12	19	11	71	41	**84**
Total		**121**	**32**	**103**	**24**	**102**	**16**	**76**	**10**	**143**	**18**	**69**

4 Discussion

The proximity of the Verdouble River explains the presence of some species characteristic of humid areas and water ponds: *Arvicola* sp., *Gallinula chloropus*, *Podiceps rufficolis*, *Anas* sp., and the noteworthy proportion of amphibians and fishes. Commensal species can be linked to the vicinity of the village of Tautavel: *Mus musculus, Rattus norvegicus*, *Columba livia/oenas*. Other species link to the surrounding scrubland.

We can conclude, therefore, that this accumulation is a good representation of the local environment.

The sizeable prey diversity highlighted in this study corresponds well to previous referentials for the Eurasian Eagle-Owl and we observed the recurrence of some prey species. For birds, Columbidae, *Alectoris rufa* and *Gallinula chloropus* were often represented (Lourenço, 2006; Bayle and Schauls, 2011). Raptors were also common, especially *Asio otus*. Raptor consumption is often observed for *Bubo bubo* (Mikkola, 1976), and this predation over another potential accumulator is one argument for other raptors playing no role (or a very small one) in this accumulation.

For small mammals (except lagomorphs), larger species such as *Erinaceus* sp., *Rattus* sp., and *Arvicola* sp., were the most frequent as evidenced elsewhere by Lack, 1946; Papageorgiou et al., 1993; Serano, 2000; Lourenço, 2006; Sándor and Ionescu, 2009; Bayle and Schauls, 2011; Lloveras et al., 2012.

The age categories of lagomorphs were dominated by adults, although this number can easily be susceptible to seasonal changes and prey availability (Donázar and Ceballos, 1989; Cochard, 2004a; Lloveras *et al*., 2012); nevertheless, the presence of deciduous teeth in this accumulation is interesting. Some authors consider their presence as antagonistic of an accumulation made by a nocturnal raptor because very young individuals are usually only found in warrens. The presence of deciduous teeth may thus indicate an *in situ* death or predation by a mammalian carnivore inside the warren (Arriaza et al., 2015; Pelletier et al., 2015, 2017). However, it is known that young rabbits can leave the warren after only two or three weeks (Biadi and Le Gall, 1993) and the last deciduous teeth fall out after thirty days (Horowitz et al., 1973). Consequently, there is a time period of around one week when young

individuals (with deciduous teeth) can venture outside the warren and potentially be hunted by owls. We can postulate, therefore, that these inexperienced individuals represent easy prey for raptors. The snakes consumed were small (around 50 cm) which corresponds to sub-adult individuals for *Zamenis scalaris* and *Natrix maura* and to adult individuals for *Coronella girondica*.

Fragmentation

The fragmentation rate was higher in this accumulation than what has previously been determined from other raptor referentials, except for the pellets of *Aquila heliaca* (tab. 11). We also observed a lower fragmentation rate for small birds, as previously described by Bocheński et al. (1993). This is due to the fact that small birds are swallowed whole, while bigger prey are generally dismembered before ingestion. The fragmentation rates showed numerous variations depending on the size of the prey and the post-depositional processes. In our case, there seems to be no specific predator signature on the fragmentation rate of the bird bones.

Table 11. Fragmentation rates (PF, %) of bird elements from other referentials. Bocheński et al. (1993) [1]; Bocheński and Tornberg (2003) [2]; Bocheński and Tomek (1994) [3]; Laroulandie (2000) [4]; Bocheński et al. (1999) [5].

	Bubo bubo[1]	*Strix aluco*[1]	*Falco rusticolus* (lagopus)[2]	*Falco rusticolus* (other)[2]	*Falco rusticolus* (total)[2]
Humeri	72	45	22	11	18
Ulnae	58	42	30	12	22
Radii	53	42	52	19	37
Carpometacarpi	24	23	3	1	2
Coracoids	76	79	30	12	24
Femora	67	48	55	26	43
Tibiotarsi	83	76	68	44	55
Tarsometatarsi	26	40	8	7	7
Total	**57**	**49**	**34**	**17**	**26**
	Asio otus[3]	*Bubo bubo* (*Columba* sp.)[4]	*Aquila heliaca* (pellets)[5]	*Aquila heliaca* (not ingested)[5]	*Aquila heliaca* (total)[5]
Humeri	13	98	84	20	36
Ulnae	12	71	90	14	52
Radii	22	83	73	36	46
Carpometacarpi	9	43	79	6	43
Coracoids	78	88	78	14	47
Femora	47	93	87	12	65
Tibiotarsi	90	90	97	73	85
Tarsometatarsi	39	13	83	21	62
Total	**39**	**72**	**84**	**25**	**55**

This was confirmed by the fragmentation rate for lagomorphs, which was higher than that observed in other referentials (Maltier, 1997; Sanchis, 2000; Guennouni, 2001; Cochard, 2004a, b). For micromammals, fragmentation rates were also slightly higher than what has previously been described for the Eurasian Eagle-Owl (tab. 12). Indeed, they are closer to those observed for *Strix aluco* or *Athene noctua* (Andrews, 1990). However, the values observed in our study still remain below the fragmentation rates of diurnal raptors and small carnivores. These low fragmentation rates, in comparison to the other groups (birds and lagomorphs), can be explained by the fact that micromammals are swallowed whole. And although small birds (category 1 and 2) can also be swallowed whole, their bones may have a better resistance to post-depositional processes.

Table 12. Fragmentation rates (PF, %) of micromammal remains observed by Andrews (1990).

	Asio otus	*Asio flammeus*	*Bubo bubo*	*Strix aluco*	*Athene noctua*	*Falco tinnunculus*	*Circus cyaneus*	*Martes martes*	*Vulpes vulpes*
Humeri	4	12	18	47	65	56	78	100	100
Ulnae	5	8	3	31	0	68	40	75	100
Femora	4	7	17	48	88	79	80	100	100
Tibiae	7	13	14	15	66	68	77	100	100

The fragmentation rate for small vertebrate is higher in this accumulation than the in previous referential. This rate could be linked to trampling by the Eurasian Eagle-Owl itself, and/or other post-depositional processes, such as weathering, considering that the pellets remained on the ground for a long time (~20 years) before being collected. Comay and Dayan (2018) highlight postcranial breakage as a reliable variable to determine the main accumulator. If this is true for fresh pellets, it is debatable for long-term accumulation, as with this referential and accumulations on archeological sites where post-depositional processes have a high impact on the fragmentation rate, as in the case of the Arago cave (Lebreton et al., 2016).

Skeletal representation

For birds, the skeletal representation of long bones (including coracoids) did not show a particular pattern with regards the differential representation of wing or leg bones, and was variable between areas (inside and outside) and between size category. This was not dependent on fragmentation, as the bone with the best representation was not the least fragmented. For birds in size category 3, variation in inside and outside fragmentation rates correspond to the presence of morphologically different taxa; however, for birds in size categories 1 and 2, which regroup mostly Passeriformes, that is not the case.

For lagomorphs, numerous referentials were established for different predators (tab. 13). To compare and visualize the data from the referential and the relative abundance of

lagomorphs from this referential, we used Correspondence Analyses (CA). Graphic projection of the CA allowed us to distinguish two groups (fig. 10).

Table 13. Relative abundance (%) of lagomorph skeletal elements observed in different accumulations and for different predators. (Desclaux, 1992 a)[1]; (Maltier, 1997)[2] ; (Sanchis, 2000)[4] ; (Guennouni, 2001)[5]; (Lloveras *et al*., 2009)[6] ; (Cochard, 2004 b)[7] ; (Hockett, 1995)[8]; (Hockett, 1993, 1995)[9]; (Hockett, 1991)[10]; (Lloveras *et al*., 2008a)[11]; (Lloveras *et al*., 2008b)[12].

	Bubo bubo							
	Allauch[1]	Alzon[2]	P.Zafra[3]	A.Busot I[4]	Tabià[4]	Niu A-7[4]	A. Busot II[4]	Alpes[5]
Mandibles	92.0	0.0	23.0	54.0	40.0	35.0	13.0	52.0
Maxillae	40.0	6.0	15.0	64.0	20.0	0.0	12.0	41.0
Scapulae	29.0	25.0	10.0	59.0	30.0	19.0	14.0	28.0
Humeri	72.0	31.0	33.0	100.0	100.0	23.0	26.0	38.0
Ulnae	67.0	31.0	28.0	91.0	50.0	23.0	19.0	22.0
Radii	34.0	19.0	10.0	77.0	70.0	23.0	9.0	10.0
Pelves	42.0	87.0	95.0	41.0	50.0	100.0	91.0	95.0
Femora	74.0	81.0	100.0	58.0	80.0	58.0	100.0	78.0
Tibiae	65.0	69.0	74.0	57.0	60.0	65.0	43.0	100.0
Calcanei	24.0	37.0	18.0	18.0	20.0	65.0	43.0	40.0
Tali	26.0	56.0	5.0	16.0	0.0	35.0	34.0	0.0
Pr mean	**51.4**	**40.2**	**37.4**	**57.7**	**47.3**	**40.5**	**36.7**	**45.8**

	Bubo bubo			*Bubo virginianus*	*Tyto alba*		*Aquila adalberti*	*Lynx pardinus*
	nest 1[6]	nest 2[6]	Carry-le Rouet[7]	Dondero shelter[8]	T.L. Chamber[9]	Two Ledges[10]	Pellets[11]	Scats[12]
Mandibles	23.7	42.3	38.0	55.0	83.0	86.0	34.4	82.1
Maxillae	47.3	30.7	25.0	41.0	66.0	15.0	43.8	64.3
Scapulae	15.8	11.5	32.0	59.0	57.0	83.0	15.7	53.6
Humeri	34.2	23.1	35.0	66.0	100.0	100.0	15.6	57.1
Ulnae	23.7	23.1	34.0	73.0	88.0	81	25	60.7
Radii	31.6	9.6	32.0	100.0	43.0	51.0	3.1	42.8
Pelves	89.5	63.4	75.0	82.0	46.0	38.0	6.3	60.7
Femora	89.5	53.8	55.0	50.0	56.0	47.0	3.1	64.3
Tibiae	68.4	63.4	65.0	48.0	51.0	51.0	50.0	42.8
Calcanei	92.1	92.3	38.0	52.0	92.0	51.0	40.6	39.3
Tali	7.0	55.7	20.0	27.0	40.0	49.0	18.8	25.0
Pr mean	**47.5**	**42.6**	**40.8**	**59.4**	**65.6**	**59.3**	**23.3**	**53.9**

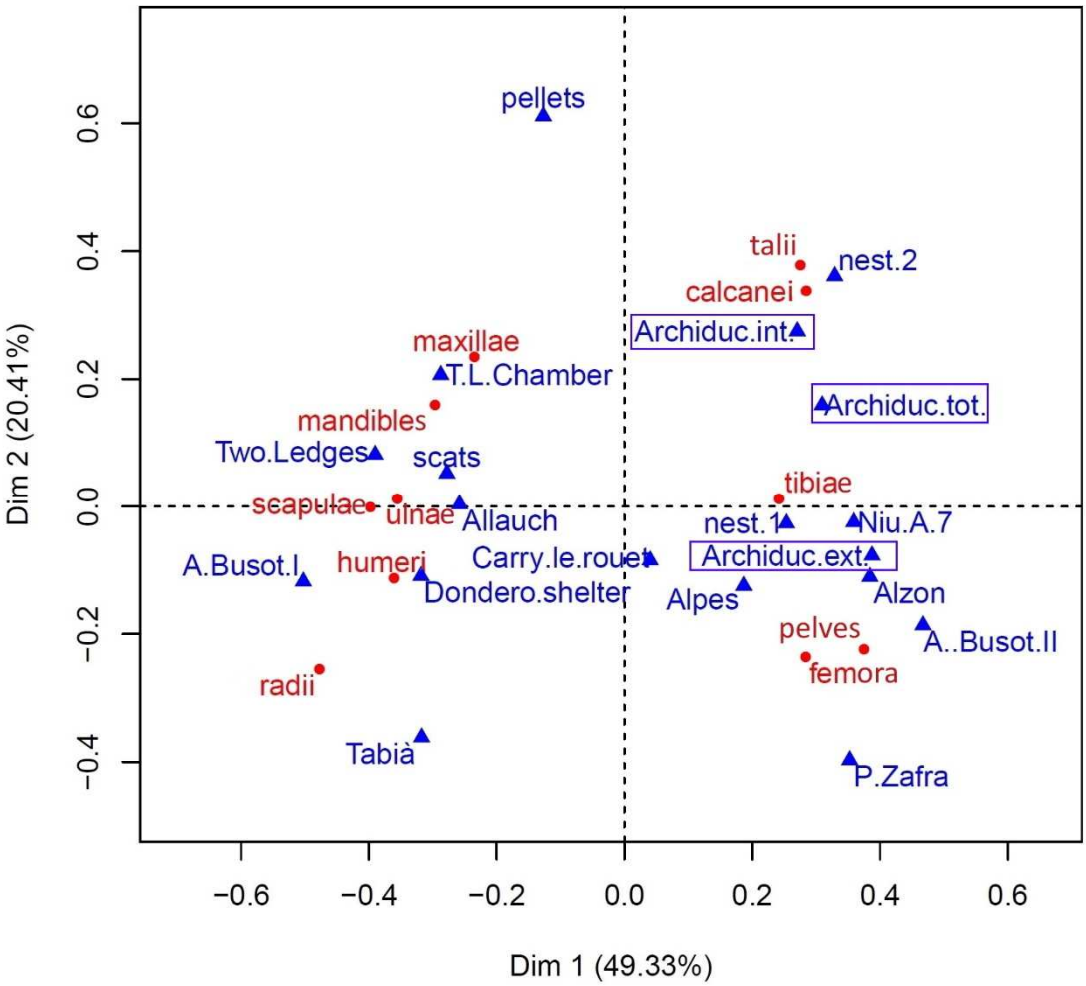


Figure 10. Correspondence Analysis (CA) on lagomorph relative abundance from the Archiduc locality (this study) and other referentials (tab.13). Axis 1 represents 49% of the inertia and axis 2, 20%.

The first group was constituted by accumulations with a high proportion of forelimbs, mandibles and maxillae, and included pellet accumulations from *Aquila heliaca* (pellets) (Lloveras et al., 2008a) and Tabia aerie (*Bubo bubo*). The second group was composed of accumulations with a high representation of hindlimbs. The dichotomy between these accumulations has previously been observed by several authors (Hockett, 1991, 1995; Sanchis, 2000; Cochard, 2004a, b). One hypothesis to explain these differences in the relative abundance of bones is the nature of the site (pellets/aerie) (Hockett, 1991, 1995; Hockett and Haws, 2002); nevertheless, this hypothesis has been questioned (Cochard, 2004a). Indeed, in our CA (fig. 10), raptor aeries and pellets were located in the group with the best representation of cranial elements and forelimbs. According to Cochard (2004a, b), such differences between accumulations may be linked to several factors; for example, the dietary behaviour of the Eurasian Eagle-Owl can vary geographically, seasonally and due to the amount of available prey –abundance can favour selection towards the fleshiest part

(hindlimbs). Conversely, the age of the prey and predator size plays a role during ingestion and contributes to skewing the results. Lloveras et al. (2012), however, highlighted that the age of the prey produces less variability in the assemblages than has previously been suggested by other authors (Cochard, 2004a). In any case, the age of the prey does not seem to have played a role in our CA (fig. 10). If we observe the relative abundance mean rate, we notice that sites with a good representation of forelimbs and cranial elements have a mean rate higher than 50%. The only exception came from the Tabia aerie (47.3%) and pellet accumulations from *Aquila heliaca* (pellets) (23.3%), but these two assemblages are based on small samples and remain on the periphery of the group. All the accumulations with a dominance of hindlimbs displayed a mean relative abundance lower than 50%. This is linked to the fact that hindlimbs are more robust (Hockett, 1995); therefore, an assemblage which has been subject to damage (due to predation or post-depositional processes) will present a low representation of forelimbs and cranial elements compared to hindlimbs.

For small mammals, CA was used to compare the relative abundance of our accumulation with referentials made by Andrews (1990) (tab. 14, fig. 11). Graphical projection of this CA regroups fragile elements, on the left side, alongside predators displaying a higher relative abundance mean rate. On the right side, we observed robust elements, alongside predators showing lower relative abundance rates. The Archiduc accumulation is located between the two groups. As for lagomorphs, relative abundance was a tributary of the element robustness; nevertheless, no dichotomy between forelimbs and hindlimbs was observed.

Table 14. Relative abundance (%) of micromammal skeletal elements observed in other predator accumulations (after Andrews, 1990). (*T.a=Tyto alba; B. s=Bubo scandiacus; A.o=Asio otus; A.f=Asio flammeus B.b=Bubo bubo; S.a=Strix aluco; A.n=Athene noctua; F.t=Falco tinnunculus; C.c=Circus cyaneus; H.f=Hieraatus fasciatus; G.g=Genetta genetta; V.v=Vulpes vulpes; A.l=Alopex lagopus; M.m=Martes martes*)

	T. a	*B. s*	*A. o*	*A. f*	*B. b*	*S. a*	*A. n*	*F. t*	*C.c*	*H.f*	*G.g*	*V. v*	*A. l*	*M.m*
Mandibles	66.8	71.4	96	93.6	92.2	95.4	68.7	96.7	97.8	80.8	99.4	50	100	66.7
Maxillae	58.6	57.1	84.8	52.5	40	74.2	18.7	66.2	95.6	82.4	45.9	25	83.3	50
Incisors t	6.3	14.3	7.6	27.7	55	34.1	50	60.3	69.5	32.7	55.9	68.8	0	75
Molars t	11.2	10.7	4.2	15.8	31.2	5.4	26	32.8	27.5	23.1	11.3	31.3	33.3	41.6
Scapulae	54.1	67.9	51	26.9	27.8	18.9	25	28.8	6.5	80.8	3.4	12.5	0	33.3
Humeri	65.9	82.1	86.3	89.7	71.1	58.3	68.7	70.3	50	98.1	48.2	75	50	100
Ulnae	66.5	64.3	76.3	64.1	65.5	52.3	43.7	52.3	19.6	90.4	16	37.5	16.6	66.7
Radii	61	71.4	69.3	61.5	33.3	49.2	12.5	41.4	21.7	88.5	12	25	16.6	16.6
Pelves	65.5	92.9	87.6	51.2	40	52.3	18.7	33.1	8.7	86.6	22.4	25	0	16.6
Femora	68.8	89.3	95.4	73.1	73.3	81.1	75	61.2	21.7	94.2	59.7	100	16.6	33.3
Tibiae	75.6	96.4	94	71.8	62.2	79.5	87.5	53.2	19.6	67.3	36.7	62.5	33.3	16.6
Calcanei	34.4	60.7	19	24.3	23.3	8.3	18.7	14.5	4.3	69.2	8	25	0	0

Tali	34.7	46.4	7.9	24.3	25.5	0.8	6.2	19.5	2.2	98.1	4	12.5	33.3	0
Phal+metap.	18.1	49.7	11	15.8	10.5	4.1	8.8	8.8	5.1	39.6	1	22.8	30.3	18
Ribs+sternum	45.7	83.3	35.5	35.5	6.6	7.8	7.2	6.9	6.3	18.4	0.4	8.3	7.5	7.5
Vertebrae	39.3	41.5	27.6	20.8	24.6	5	8.9	12.3	1.6	72	11.2	23.4	27.1	23.9
Pr mean	48.3	62.5	53.3	46.8	42.6	39.2	34.0	41.1	28.6	70.1	27.2	37.8	28.0	35.4

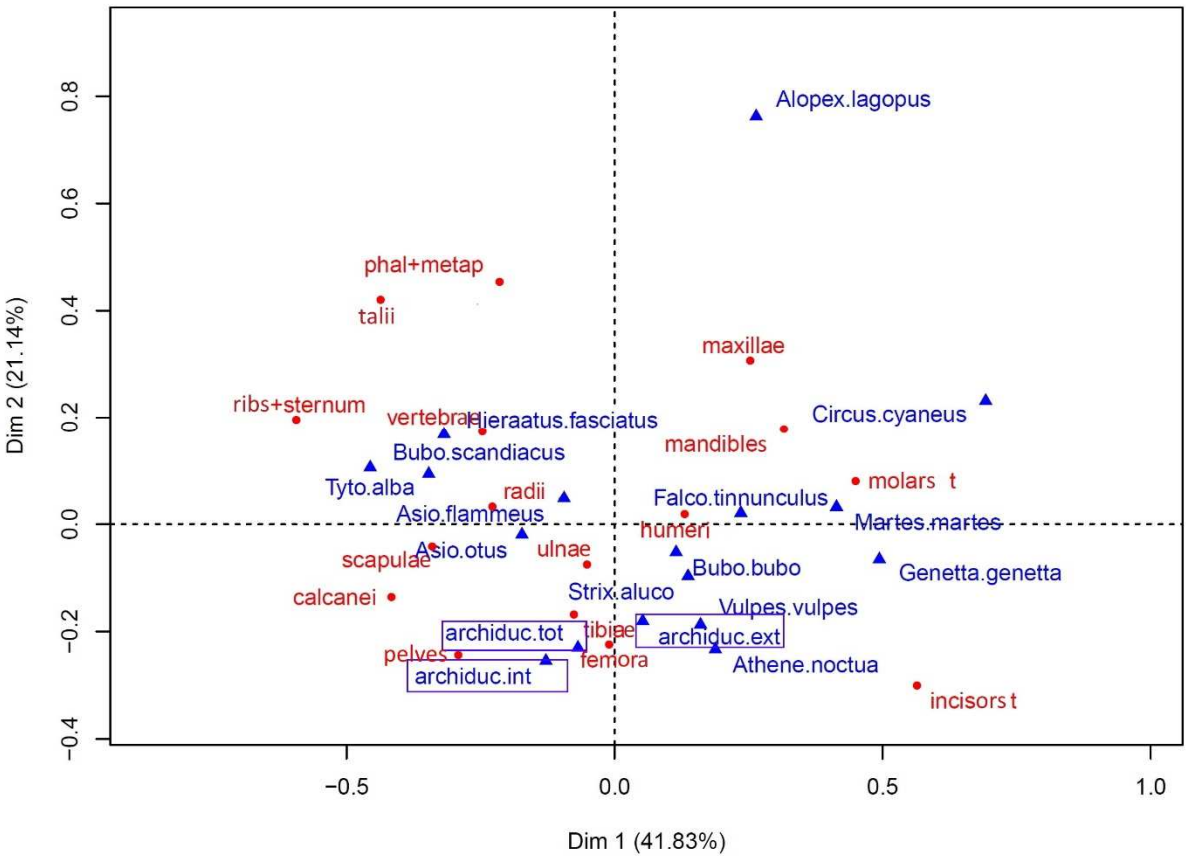


Figure 11. Correspondence Analysis (CA) on micromammal relative abundance from the Archiduc locality (this study) and other referentials (tab.14). Axis 1 represents 41% of the inertia and axis 2, 21%.

Surface alteration

The digestion frequencies observed in the bird remains from the Archiduc accumulation fall within the variability observed by Laroulandie (2000, 2002) for the *Columba* sp. remains from Saint-Vincent pellets (*Bubo bubo*). This frequency is below that observed by Bocheński and Tomek (1997) for Eurasian Eagle-Owl pellets. However, for these referentials, as for our accumulation, the number of elements is low, which explains the variability. Observations from *Tyto alba* pellets (Denys et al., 2018) show a digestion rate of 30%, all elements included, with mostly low and moderate digestion grades. These observations are close to our results; but, according to Bocheński et al. (1998), *Tyto alba* belongs to category 1 and *Bubo bubo* to category 2. This variability is easily explained by the

type of bones, extremities (proximal/distal) and size, that can impact the frequency and intensity of digestion (Laroulandie, 2000, 2002).

The digestion rates observed on the teeth and long bone proximal extremities of lagomorphs fell within the variability of those observed by Lloveras et al. (2009) in *Bubo bubo* pellets; however, in the Archiduc assemblage we observed a higher proportion of moderate digestion grades. Digestion by *Bubo bubo* can easily be distinguished from other predators, notably diurnal raptors like *Aquila adalberti* and carnivores like *Lynx pardinus,* which display a stronger digestion (Lloveras, 2008a, b).

For micromammals, the digestion rates corresponded to expectations for a category 3 predator (Andrews, 1990; Fernández-Jalvo et al., 2016), with digestion intensity on molars being slightly lower than for other referentials (between categories 2 and 3). This difference could be due to intra-predator variability or because the molars come from relatively large prey species, such as *Arvicola* sp. or *Rattus norvegicus*, whose teeth have a thicker enamel which is more prone to resist digestion. Unfortunately, the absence of smaller species (Arvicolinae and Murinae) did not allow comparisons to be made. The digestion rates on the femora were also slightly lower than those observed by Andrews (1990) for *Bubo bubo,* but were still higher than for smaller nocturnal raptors.

For this same accumulation, Guillaud et al., (2018), also observed alteration due to digestion on fish remains which corresponds to an intermediate category.

Crossing the digestion data from different prey taxa is the most reliable way to identify the predator at the origin of the accumulation. In their multi-taxa referential from *Tyto alba* pellets, Denys et al. (2018) discussed the value of the humerus and femora for inter-taxa comparisons. Indeed, if we want to compare the digestion rates between mammals, birds and herpetofauna, using a post-cranial bone as a referential element is the only option. Greater variability, however, can be observed between post-cranial elements and from one species to another, especially for birds. The mixing of an accumulation is also common in a fossil assemblage. The presence of dead individuals *in situ* can affect the digestion rate if they are taken into account in the same way as hunted prey. In this case, a study centred on the intensity rather than the frequency could be more reliable, although the fossilization rate of strongly altered elements can also be subject to bias.

The referential of a *Bubo bubo* accumulation is particularly important for archaeological studies because it is often a main accumulator on archaeological site (Denys, 1997). This is certainly the case for the Stratigraphic Unit (SU) P and Q-R at Arago cave (Lebreton et al., 2016), a Middle Pleistocene accumulation which shares significant

similarities with the Archiduc accumulation. The taxonomic composition from both shows a broad diversity (lagomorphs, rodents, shrews, birds, amphibians, reptiles and fish) and a wide range of prey (from lagomorphs to rodents and shrews). Furthermore, the pattern of digestion for these SU's correspond to a category 2–3 predator, which coincides with our observation at the Archiduc.

5 Conclusion

This referential allows a multi-taxa taphonomic approach to a small vertebrate assemblage from a *Bubo bubo* aerie. Among the different variables used to describe this accumulation, not all are directly dependent on the predator. This is notably the case for the relative abundance of skeletal elements which can be impacted by the robustness of the elements, especially during depositional and pre-burying phases. With that said, it is impossible to observe a specific signal from the predator. On the other hand, digestion and taxonomic composition allow a reliable characterization of the predator. *Bubo bubo* is characterized by high diversity of prey, the presence of middle-sized birds (size category 3) and relatively large small mammals such as lagomorphs. This allows us to distinguish it from the small- and medium-sized nocturnal owls. Other lagomorph accumulators are large diurnal raptors and mammalian carnivores, but they display higher rates and grades of digestion (category 4 and 5) than those observed for *Bubo bubo* (category 2-3). This referential will also help to determine the accumulator in possible mixed accumulations (human/animals) of small vertebrates, specially birds and lagomorphs. The small vertebrate must be taken in consideration as a whole in order to improve the strength of palaeoenvironmental studies on archaeological sites.

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