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ABSTRACT

Avian remains are commonly found in Pleistocene cave sites. La Crouzade Cave (Gruissan, Aude, Southern France) is no exception, as it yielded thousands of bird bones recovered from the Middle and Upper Palaeolithic deposits. In Mousterian layers 8, 7 and 6 (MIS 3) the avifaunal spectrum is dominated by cliff-nesting taxa such as doves and corvids from the genus *Pyrrhocorax*. Some of these birds may have died naturally in situ but the presence of digestive damage on a great number of specimens indicates that most of the individuals were consumed by non-human predators (carnivorous mammals and raptors). Furthermore, the presence of a few cut-marked specimens suggests that Neanderthals took part in the accumulation. Striae located on wing bones such as ulna could be linked to feather removal. The bird assemblage from La Crouzade thus provides a new example of mixed accumulation in which Middle Palaeolithic human populations were involved.

1. Introduction

In addition to precise the regional palaeobiocenosis, the avifaunal spectrum of a site can provide valuable palaeoenvironmental and palaeoclimatic information (e.g. Mourer-Chauviré, 1975a; Vilette, 1983; Carrera et al., 2018b) since pleistocene species still exist nowadays and have specific ecological needs. As bird remains are also material of archaeozoological importance, a taphonomic analysis is needed in order to determine the origin of the bone accumulation (e.g. Denys, 1985; Denys et al., 1987; Andrews, 1990; Fernández-Jalvo and Andrews, 1992). The natural origin suggests a natural, in situ death of the birds (Vilette, 1983; Laroulandie, 2000; Roger, 2004), whereas the non-human predator origin implies the role of at least one Carnivoran or raptor in the accumulation. Accumulations produced by non-human predators can mix uneaten food remains and remains deriving from pellets or faeces. Humans can also take part in the accumulation, as the importance of small game in Palaeolithic economies has been increasingly highlighted over the years. By the end of the sixties, an important expansion of human diet was observed towards the end of the Palaeolithic (Binford, 1968; Flannery, 1969). This diversification, characterized by the adding of small preys to the diet, was termed "Broad Spectrum Revolution" (BSR) and linked to human demographic growth by Flannery (1969). The BSR hypothesis was later supported by several works which demonstrated that this increasing dietary breadth began long before the terminal Palaeolithic (Stiner et al., 2000; Stiner, 2001). While slow-moving, easy to catch preys (tortoises, shellfish) seemed to represent the major part of Middle Palaeolithic small game assemblages, agile preys (fast-running such as lagomorphs and quick-flying birds such as partridges) were mainly associated with Upper Palaeolithic contexts (Stiner and Munro, 2002). The increasing exploitation of birds (which quickly mature and whose populations can support higher hunting pressure than tortoises), was not only explained by Upper Palaeolithic human demographic growth and human related decrease in other resources but also by technological innovations that would make the collection of such fast moving preys easier (Stiner et al., 2000). However, during the last decades, several researchers have highlighted the use of birds by Neanderthals, who hunted them for food (e.g. Blasco et al., 2016; Fiore et al., 2016; Gómez-Olivencia et al., 2018; Lloveras et al., 2018c; Rufà and Laroulandie, 2021) or to obtain raw material such as feathers, tendons, long bones or unguals (e.g. Peresani et al., 2011; Finlayson et al., 2012; Morin and Laroulandie, 2012; Romandini et al., 2014; Radovčić et al., 2015; Fiore et al., 2016; Blasco et al., 2022). Qesem Cave (Israel) represents one of the earliest occurrences of human use of non-alimentary resources in birds, as cut marks and peeling found on a *Cygnus* carpometacarpus suggest feather procurement (Blasco et al., 2019). These studies showed that bird

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exploitation was far from being exclusive to Upper Palaeolithic modern humans and that earlier hominins were able to display similar symbolic behaviours. A mixed origin of the bird bone accumulation is often underlined (e.g. Laroulandie et al., 2016; Romero et al., 2017; Lloveras et al., 2018c; Rufà and Laroulandie, 2021), as several predators including humans were implicated. In order to determine bone accumulations origins, a methodology was set up, based on several criteria such as taxonomic composition and population structure, skeletal representation, breakage and bone surface modifications. The present work applies this methodology to the French Mediterranean cave site of La Crouzade, which provided hundreds of bird remains recovered from Mousterian (MIS 3) layers.

The aims of this study consist in completing the Mousterian avifaunal spectrum from La Crouzade, finding out the main agent(s) responsible for the accumulations and assessing the role Neanderthals played in the accumulations.

2. Archaeological context: La Crouzade cave

La Crouzade cave (Gruissan, Aude, Occitanie), situated about 3 km away from the current Mediterranean coastline, is a vast cavity dug into the Aptian limestones of the Massif de la Clape. Located at 55 m above sea level, it opens towards the west through two entrances, although only the lower one allows access to the cave (Fig. 1).

Following the discovery of the cave in 1866, several excavation seasons were conducted between 1906 and 1946 by Théophile and Philippe Héléna, who recovered many Upper and Middle Palaeolithic remains. Philippe Héléna established a first stratigraphic description of the site, identifying a basal Mousterian complex topped by Upper Palaeolithic layers (Héléna, 1928; Héléna and Héléna, 1930). A test pit was performed in 1995 near Héléna's 1930 excavations location in order to realise stratigraphic profiles and to sample for future sedimentologic studies (Perrenoud, 1995; Saos, 1996, 2003). Another sondage realised in 2015 allowed the finding of the Mousterian layers mentioned by Héléna, leading to programmed excavations conducted by Thibaud Saos (CERP Tautavel).

The Mousterian complex is subdivided into three layers. The oldest one, layer 8 (C8), is approximately 50 cm thick. Its top was reached during the 2018 excavation season; lithic artefacts, burnt bones and charcoals were recovered. Two radiocarbon-dated charcoals gave C8 ages of 42,200 ± 1000 BP and 43,400 ± 1400 BP (between 49,776 and 43,861 cal BP). A bone fragment provided a slightly younger age of 38,700 ± 900 BP (44,436–41,566 cal BP). On top of layer 8 is the 80-cm-thick layer 7 (C7) which mostly consists of dark brown silts. C7 provided a rich assemblage of lithic artefacts and faunal remains. The yellowish and sandy, 60-cm-thick layer 6 (C6) is the younger Mousterian layer (Saos et al., 2020, 2021). Referred to as the " bear

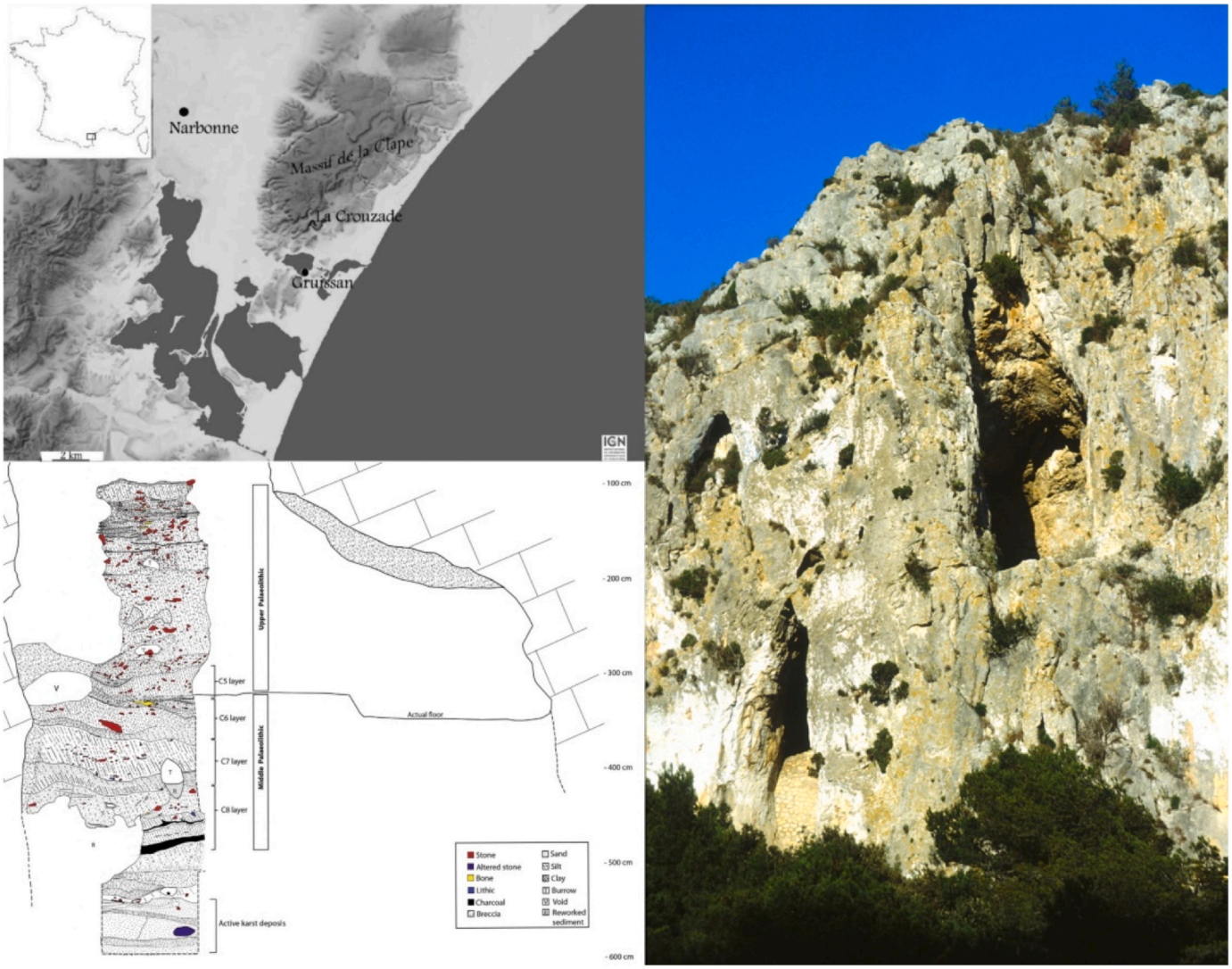

Fig. 1. Geographical location of La Crouzade cave (top left, modified from Saos et al., 2022), stratigraphic section (bottom left, modified from Saos et al., 2020) and view of the cave entrance (right).

layer ", C6 yielded a great number of cave bear (*Ursus spelaeus*) remains but few lithic material, suggesting that the cave was not inhabited permanently by humans, allowing bears to occupy it (Lumley-Woodyear, 1971). Two U/Th-ESR dated horse teeth recovered in C7 and C6 provided ages of 41 ± 2 (± 1σ) et 42 ± 3 ka (± 1σ) respectively (Saos et al., 2020).

The Mousterian complex yielded a rich archaeological assemblage including lithic artefacts, faunal and human remains. The Héléna lithic collection was studied by Lumley-Woodyear (1971) and Lebègue (2004, 2012). Material from Saos collection shows similar trends in terms of raw material and technology. The Mousterian lithic assemblage is dominated by flint, followed by quartz and quartzite. Other scarcer raw materials found in Middle Palaeolithic layers include jasper, lydian, limestone, hornfels, sandstone, sandstone-quartzite, shale and rhyolite. Levallois is the predominant production method in all three layers. Several tool categories were identified, among which were scrapers (convergent, canted side, double side, triple, and endscrapers), points, notches, becs, burins or denticulates (Saos et al., 2020). Raw materials were mostly collected within a 20 km radius around the site (Grégoire, 2000).

Six human remains coming from Mousterian layers were attributed to Neanderthal. They were studied by Lumley-Woodyear (1973) and Bertrand (1999). Four anatomically modern humans (AMH) recovered in Upper Palaeolithic layers were studied by Gambier and Sacchi (1991). Maxilla La Crouzade VI was found in layer C5 (Aurignacian) and dated to 30,640 ± 640 BP (Henry-Gambier and Sacchi, 2008), then to 31,200 ± 400 BP (36,014–34,402 cal BP, Saos et al., 2020), making this specimen one of the oldest AMH fossils found in France.

The large mammal spectrum is diversified. *Ursus spelaeus* is the most represented Carnivoran. It is especially abundant in C6 and probably used the cave as a den. Other Carnivorans found within Mousterian layers include brown bear (*U. arctos*), lynx (*Lynx* sp.), leopard (*Panthera pardus*), cave lion (*P. spelaea*), cave hyaena (*Crocuta c. spelaea*), red fox (*Vulpes vulpes*), grey wolf (*Canis lupus*) and badger (*Meles meles*). Among herbivores, horse (*Equus ferus germanicus*), reindeer (*Rangifer tarandus*) and ibex (*Capra praepyrenaica*) are the most abundant taxa. They are found along with wild ass (*E. hydruntinus davidi*), steppe bison (*Bison priscus*), aurochs (*Bos primigenius*), chamois (*Rupicapra* sp.), saiga (*Saiga tatarica*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), giant deer (*Megaloceros giganteus*) and wild boar (*Sus scrofa*) (Gerber, 1973; Banès, 1996; Quiles, 2003; Testu, 2006; Boulbes in Saos et al., 2017). Mesofauna and microfauna (lagomorphs, chiropters, herpetofauna, ichthyofauna) are abundant as well. Large herbivores and leporids bear marks linked to carnivoran and human exploitation (Bachellerie, 2017; Morin et al., 2019).

Regarding birds, material from Héléna collection allowed the identification of sparrowhawk (*Accipiter nisus*), rock dove (*Columba livia*), yellow-billed chough (*Pyrrhocorax graculus*) and red-billed chough (*Pyrrhocorax pyrrhocorax*) in the Mousterian layers. The almost total absence of small-sized species was explained by the non-sieving of the sediments (Mourer-Chauviré, 1975b). A sample coming from recent excavation seasons (2016–2019) showed similar trends, as doves (*C. livia* and *C. livia/oenas*) and choughs (mostly *P. graculus*) are abundant throughout the whole stratigraphic sequence and account for approximately 50% of the bird remains in C7 and C6. The Middle Palaeolithic avifaunal spectrum is completed by Galliformes, Anseriformes, Charadriiformes, small Passeriformes and Strigiformes. Some individuals may have died naturally in situ but specimens with traces of digestion indicate that some individuals were eaten by predators (Garcia-Fermet, 2019, 2020).

3. Material and methods

The present work deals with bird remains recovered in the Mousterian layers (C8, C7 and C6) of La Crouzade cave during recent excavation seasons conducted by T. Saos (2016–2021). The sample includes 57 remains from C8, 1163 remains from C7 and 703 remains from C6, for a total Number of Identified Specimens (NISP) of 1923. Coordinated material (57 remains in C7, 9 in C6) accounts for 3.2% of the assemblage, whereas other bones come from dry and water sediment sieving (using sieve mesh sizes of 0.6 and 0.5 mm respectively, or 0.85 and 0.71 mm if diagonal mesh size is considered) and microfauna sorting.

Taxonomic determinations were made using identification manuals (Woelfle, 1967; Kraft, 1972; Tomek and Bochenski, 2000, 2009; Bochenski and Tomek, 2009; Kessler, 2017) and by consulting avian osteological reference collections from Muséum national d'Histoire naturelle de Paris and Centre Européen de Recherches Préhistoriques de Tautavel.

Remains that were not determined any further than Aves were classified by size: Aves small size (i.e. the size of a thrush bone or smaller), medium size (comparable in size to *Columba* or choughs) and large size (two remains that are comparable in size to *Corvus corax*). The NISP, Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated for each taxon in order to quantify the bird population. To calculate MNE and MNI, bone laterality and maturity were taken into account. Bones from immature individuals (i.e. whose age goes from hatchling to fledgling, Serjeantson, 2009) are not fully ossified and can be distinguished by their porous texture.

The taphonomic analysis was conducted in C7 and C6. Regarding C8, bone surface modifications were checked but skeletal representation and fragmentation were not investigated since the sample is too modest.

All taxonomically determined bird remains were classified into four size categories following Laroulandie (2000): size 1 (sparrow-sized birds), size 2 (e.g. common quail, boreal owl, turdids), size 3 (e.g. doves, choughs, partridges, Eurasian teal, mallard) and size 4 (eagle-owl). The different indexes were then calculated for the best represented size categories and taxa. The percentage of relative abundance (%RA) was computed according to a formula inspired by Dodson and Wexlar (1979): MNE Y/(MNI x FY) x 100, where Y corresponds to an anatomic element and FY corresponds to the frequency of this element in the skeleton. The wing-to-leg ratio was calculated by dividing the wing MNE by the sum of the wing and leg MNE: wing MNE/(wing MNE + leg MNE). Wing elements include humerus, ulna and carpometacarpus while leg elements include femur, tibiotarsus and tarsometatarsus (Ericson, 1987). The proximal-to-distal elements ratio was calculated by dividing the proximal MNE by the sum of the proximal and distal MNE: proximal NME/(proximal NME + distal NME). Proximal elements include scapula, coracoid, humerus, femur and tibiotarsus while distal elements include radius, ulna, carpometacarpus and tarsometatarsus (Bochenski and Nekrasov, 2001). The core-to-limb ratio was calculated by dividing the core NME by the sum of the core and limb elements: core MNE/(core MNE + limb MNE). Core elements include scapula, coracoid, sternum and pelvis while limb elements include humerus, radius, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus (Bochenski and Nekrasov, 2001). Results are expressed in percentages (formulae results multiplied by 100). A Z-test was calculated in order to assess the significance of the differences between observed and expected elements. The %RA and the different ratios were calculated on taxonomically determined remains only, for two reasons. First, undetermined remains generally complete taxonomically determined elements and do not have any influence on the MNE. Secondly, undetermined, fragmentary remains can be difficult to put within a size category or another since the taxon is not known. For example, house sparrows (size 1) have large beaks while Columbidae (size 3) have relatively thin beaks. An undetermined beak apex thus risks ending up in the wrong size category.

Breakage was analysed using fragmentation categories proposed by Bochenski et al. (1993) and used in later papers (Lloveras et al., 2018c; Wertz et al., 2021; Bochenski et al., 2022). Regarding coracoid, sternal part is considered proximal, scapular part is considered distal. A

carpometacarpus is considered complete as long as both articular parts are present (*os metacarpale minus* can thus be missing) (Bochenski et al., 1993). Small elements such as quadratum and carpal bones are classed as either complete/subcomplete or fragmented. For the furcula, three categories are considered: whole, sternal part or coracoideo-scapular part. The percentage of complete bones was calculated according to the following formula: whole bones NISP x 100 / total NISP. The proximal part-to-distal part ratio was calculated by dividing the proximal part NME by the sum of proximal and distal parts NME: proximal part NME/(proximal part NME + distal part NME). A complete bone accounts for one proximal part and one distal part (Bochenski, 2005). Results are expressed in percentages.

All bone surfaces were macroscopically and microscopically observed in order to find alterations produced by the taphonomic agents responsible for the accumulations. Mechanical marks produced by non-human predators include pits and punctures, notches, scores, crenulated edges and gnawing marks on articular parts. Their localisation (proximal or distal part, shaft) and concentration (isolated, concentrated) were considered. Traces of digestion were classified in several categories according to the degree of damage (Lloveras et al., 2008a, 2008b, 2018c). Particular attention was paid to anthropogenic modifications (cut marks, peeling, crushing marks on distal humeri and proximal ulnae related to elbow disarticulation, burned bones, Laroulandie, 2000). Cut marks localisation, distribution (isolated, concentrated), orientation (oblique, longitudinal, transverse) and morphology (straight, curved) were taken into consideration.

4. Results

4.1. Taxonomic composition and population structure

Out of 1923 bird remains, 1058 could be taxonomically determined to different levels (order, family, genus or species). Unidentified Aves specimens mainly include vertebrae and posterior phalanges. The avifaunal spectrum is composed of at least 26 species and is dominated by *Columba livia/oenas* and *Pyrrhocorax graculus*. The 57 remains (3% of the assemblage) recovered in C8 allowed the identification of three species (*C. livia/oenas*, *P. pyrrhocorax* and *P. graculus*), for a MNI of 6 (3 doves, 2 red-billed choughs and 1 alpine chough). All of them are adults.

In C7 and C6, NISP, MNE and MNI were calculated for the " *Pyrrhocorax/C. monedula* " group, which includes all remains attributed to cave-nesting corvids *P. graculus*, *P. pyrrhocorax* and *Coloeus monedula* (cf. Bochenski et al., 2018), as well as undetermined Corvidae remains (Table 1). This choice is based on the assumption that most of the undetermined Corvidae remains belong to one of these three species. Indeed, almost all of the specifically determined Corvidae remains belong to *Pyrrhocorax* spp. or *C. monedula*. Moreover, undetermined Corvidae remains are similar in size and morphology to choughs and western jackdaw, and complete *P. graculus* skeletal representation well. The different indexes were also calculated for the *Pyrrhocorax/C. monedula* group.

Table 1
Avifaunal spectrum from the Mousterian layers of La Crouzade, expressed in NISP, MNE and MNI.

Taxon	C8				C7				C6			
	NISP	MNE	MNI	%MNI	NISP	MNE	MNI	%MNI	NISP	MNE	MNI	%MNI
Accipitridae indet. size 3					1	1	1	1.6				
Anas crecca									1	1	1	2.4
A. acuta/platyrhynchos					2	2	1	1.6	2	2	1	2.4
Spatula querquedula									2	2	1	2.4
Anatidae indet. size 3					4	4	1	1.6	4	4	_	
Charadrius morinellus					1	1	1	1.6	1	1	1	2.4
Cf. *Lymnocryptes minimus*					2	2	1	1.6				
Cf. *Scolopax rusticola*									1	1	1	2.4
Charadriiformes indet. size 2									1	1	_	
Charadriiformes indet. size 3									2	2	_	
Columba livia/oenas	12	12	3	50	302	226	19	30.6	192	153	13	31.7
Columbidae indet.	2	2	_		5	4	_					
Coturnix coturnix					3	3	1	1.6	9	9	2	4.9
Alectoris rufa					2	2	1	1.6				
Alectoris/Perdix					2	2	1	1.6				
Cf. *Lagopus*									1	1	1	2.4
Phasianidae indet. size 3					2	2	_		3	3	1	2.4
Crex crex					1	1	1	1.6				
Rallus aquaticus									1	1	1	2.4
Falco cf. *tinnunculus*					1	1	1	1.6				
Falco peregrinus					1	1	1	1.6				
Aegolius funereus					2	2	1	1.6				
Athene noctua					1	1	1	1.6	2	2	1	2.4
Bubo bubo					1	1	1	1.6				
Cf. Strigiformes size 2					1	1	_					
Pyrrhocorax/C. monedula	10	9	3	50	223	177	14	22.6	117	92	8	19.5
Corvus frugilegus					1	1	1	1.6				
Nucifraga/Pica					1	1	1	1.6				
Cf. *Garrulus glandarius*					2	2	1	1.6	1	1	1	2.4
Turdidae indet. size 2					16	15	3	4.8	3	3	1	2.4
Passeriformes indet. size 1					24	21	4	6.5	17	15	4	9.8
Passeriformes indet. size 2					42	36	5	8.1	31	25	3	7.3
Total identified	24	23	6	_	643	510	62	_	391	319	41	_
Aves small size			_	_	13	13	_	_	20	20	_	_
Aves medium size	33	31	_	_	506	484	_	_	291	277	_	_
Aves large size			_	_	1	1	_	_	1	1	_	_
Total	57	54	6	_	1163	1008	62	_	703	617	41	_

Layers C7 and C6 provided 1163 remains and 703 remains respectively (60% and 36.6% of the assemblage), among which 643 and 391 were taxonomically determined. At least 23 species are represented in C7 and 17 in C6. C7 and C6 yielded MNI values of 62 and 41 respectively. The avifaunal spectrum is quite similar in both layers, being dominated by *Columba livia/oenas* (C7: NISP = 302, MNI = 19 including 3 immature individuals; C6: NISP = 192, MNI = 13 including 2 immature individuals), which represents approximatively 30% of the total MNI in both layers. The *Pyrrhocorax/C. monedula* group accounts for around 20% of the total MNI in both layers (C7: NISP = 223, MNI = 14; C6: NISP, MNI = 8 including 1 immature). *P. graculus* is by far the most abundant corvid (C7: NISP = 121; C6: NISP = 79). Among smaller Passeriformes, the Turdidae family was identified. Other bird orders represented in both layers include Anseriformes, Galliformes, Charadriiformes, Gruiformes and Strigiformes. They are scarce and the different species never account for more than 5% of the total MNI, a value reached by common quail *Coturnix coturnix* in C6.

Diurnal birds of prey (Accipitriformes and Falconiformes) were identified in C7 only.

Considering size categories, size 3 (which includes medium-sized taxa such as doves and choughs) is by far the most represented (C7: MNI = 44 or 71% of the total MNI; C6: MNI = 29 or 70.7% of the total MNI). Size 1 accounts for 8.1% of the C7 MNI (MNI = 5) and 7.3% of the C6 MNI (MNI = 3). Size 2 includes 12 individuals (19.4%) in C7 and 9 individuals (22%) in C6. A distal ulna found in C7 and attributed to the Eurasian eagle-owl (*Bubo bubo*) is the only taxonomically determined size 4 specimen.

4.2. Skeletal representation

Almost all skeletal elements can be found within the C7 and C6 assemblages, though they are unequally represented. Vertebrae and posterior phalanges are the most abundant elements in all layers. Cranial (premaxilla, mandible and quadratum) and axial remains (furcula, sternum and synsacrum) are scarce.

The %RA calculation (Table 2) shows that in *C. livia/oenas*, the average percentage of survivorship of the different elements is comprised between 30% and 40%. Ulnae and ulnares get high, similar values in C7 (65.8% and 63.2% respectively) and C6 (61.5% for both). Coracoids, carpometacarpi and tarsometatarsi are well represented (at least 50% in both layers) whereas femora get relatively low values (C7: 34.2%; C6: 26.9%). Cranial and axial elements are underrepresented, especially in C6 (for example, pelvis gets 7.7% in C6). Regarding *Pyrrhocorax/C. monedula*, between 35% and 40% of the expected elements are represented. If long bones in C6 get relatively homogeneous values, it is not the case in C7: tibiotarsus and tarsometatarsus show values of 32.1% and 39.3% respectively whereas carpometacarpus and humerus get singularly high values of 75% and 82.1% respectively. Corvidae femora are better represented than those of *C. livia/oenas*, especially in C7 (64.3%).

Considering size 3 birds as a whole (which includes *C. livia/oenas*, *Pyrrhocorax/C. monedula* and the other medium-sized birds), %RA values are logically influenced by those got by *C. livia/oenas* and *Pyrrhocorax/C. monedula*, whereas other taxa such as Anatidae and Phasianidae have few influence on these percentages. Coracoids, ulnae, ulnares and carpometacarpi are the most represented elements. In C7, humerus gets a value close to the average (41.7%), which can be explained by its low representation in *C. livia/oenas* (34.2%) and marginal taxa but high representation in *Pyrrhocorax/C. monedula* (82.1%). In size 2 birds, %RA values are low and only the sternum in C6 exceeds 50% of survivorship. Carpometacarpus is the best preserved bone and gets values of 37.5% in C7 and 33.3% in C6. Size 1 birds are characterised by good coracoid (C7: %RA = 60; C6: %RA = 100) and sternum preservation (C7: 60%; C6: 66.7%). Humerus is well represented in C7 (70%) but no specimen was recovered in C6. However, the modesty of sizes 2 and 1 samples prevents us from investing too much significance in the results.

In layers C7 and C6, the wing-to-leg ratio shows a preponderance of wing elements in all groups except for size 1 (C7, size 1: 50%; size 2: 77.3%; size 3: 55.7%; *C. livia/oenas*: 51.4%; *Pyrrhocorax/C. monedula*: 59.6%; C6, size 1: 33.3%; size 2: 75%; size 3: 58.6%; *C. livia/oenas*: 57.9%; *Pyrrhocorax/C. monedula*: 57.8%). These values do not significantly differ from the expected ratios, except for C7 size 2 and C6 size 3.

Regarding the proximal-to-distal elements ratio (in C7: size 1: 77.4%; size 2: 55.9%; size 3: 51%; *C. livia/oenas*: 47.1%; *Pyrrhocorax/C. monedula*: 56.6%; in C6: size 1: 61.9%; size 2: 42.9%; size 3: 48.3%; *C. livia/oenas*: 50%; *Pyrrhocorax/C. monedula*: 44.1%), differences with expected values are not significant, except for C7 size 1 and for C7 *C. livia/oenas* in which differences are highly significant ($p < 0,01$). This means than in *C. livia/oenas*, proximal elements (scapulae, coracoids, humeri, femora and tibiotarsi) or at least some of them are underrepresented compared to distal ones.

The core-to-limb ratio shows values slightly lower than expected, except for sizes 1 and 2, whether we consider the C7 assemblage (size 1: 45.7%; size 2: 39.5%; size 3: 24.2%; *C. livia/oenas*: 25.7%; *Pyrrhocorax/C. monedula*: 21.5%) or the C6 one (size 1: 43.5%; size 2: 30.8%; size 3: 21.7%; *C. livia/oenas*: 22.5%; *Pyrrhocorax/C. monedula*: 18.8%). Differences with expected ratios are not significant except for C6 size 3.

4.3. Breakage

In layers C7 and C6, 725 out of 1866 elements are complete (38.9% of the assemblage). Most of them are vertebrae and posterior phalanges including unguals. The results for breakage categories (Bochenski et al., 1993) show similar trends between C7 and C6. No complete skull, mandible, sternum, pelvis, furcula or fibula was recovered. Cranial material, quadratum excluded, is limited to beak fragments (mainly premaxilla and dentary apexes). Sterna consist of small, anterior part fragments (less than 50% of the bone is preserved) and pelvis is mostly represented by synsacrum. Long bones are mostly represented by articular parts whereas shafts and complete specimens are scarce. Most of the small and robust elements are complete. This is the case for 100% of the carpal bones and 90.9% of the posterior phalanges (unguals excluded) recovered in C7 and C6.

Complete specimens account for 39% in C7 (453 specimens out of 1163) and 38.7% in C6 (272 out of 703). If only long bones are considered, complete specimens represent 8.8% of the C7 assemblage (49 specimens out of 554) and 10.4% of the C6 assemblage (34 out of 326, Table 3). Regarding size 3 birds only, 10.8% of long bones and scapulae are complete in C7 (45 out of 418) and 10.9% in C6 (26 out of 239). In C7, the highest values are obtained by coracoids (24.1%), carpometacarpi (17.2%) and tarsometatarsi (13.8%) whilst in C6 the most complete bones are carpometacarpi (27.3%), tarsometatarsi (13.8%) and femora (10.5%).

Material belonging to sizes 1 and 2 species is also very fragmented as only 12 long bones are complete (2 carpometacarpi, 1 humerus and 1 coracoid in C7; 3 carpometacarpi, 2 coracoids, 2 ulnae and 1 radius in C6).

Calculations of the proximal-to-distal part ratio show that both articular ends are generally well preserved, though in slightly unequal proportions. In some cases, the unbalance is more pronounced. The scapular (distal) part of the coracoid is always more represented than the sternal (proximal) one, whatever the layer or size category. The tibiotarsus shows the most unbalanced ratio: proximal parts only account for 28% in C7 and 37.9% in C6. Regarding C7 Corvidae humeri, which were particularly abundant (RA = 82.1%), proximal parts are underrepresented (32.4%).

It is interesting to notice that every single humerus distal part in C6 is separated from its shaft, being fractured just above the articulation. In C7, some distal specimens are still connected to the shaft.

Some specimens can be distinguished by their very small size, being limited to *caput humeri* or *condylus dorsalis* fragments.

Table 2
%RA of the different skeletal elements for the most represented size categories and taxa in C7 and C6. PMX, premaxilla; MAN, mandible; QUA, quadratum; STE, sternum; FUR, furcula; COR, coracoid; SCA, scapula; PEL, pelvis; HUM, humerus; RAD, radius; ULN, ulna; UCB, ulnar carpal bone; RCB, radial carpal bone; CMC, carpometacarpus; PH I DMA, phalanx I digitorum majoris alae; FEM, femur; TIT, tibiotarsus; TMT, tarsometatarsus; Pyrrho./C. monedula: Pyrrhocorax/C. monedula.

	Columba livia/oenas					Pyrrho./C. monedula					Size 3					Size 2				Size 1			
	C8	C7		C6		C8	C7		C6		C8	C7		C6		C7		C6		C7		C6	
	MNE	MNE	%RA	MNE	%RA	MNE	MNE	%RA	MNE	%RA	MNE	MNE	%RA	MNE	%RA	MNE	%RA	MNE	%RA	MNE	%RA	MNE	%RA
PMX		4	21.1	2	15.4		0	0	0	0		4	9.5	2	6.9	0	0	2	22.2	1	20	1	33.3
MAN		2	10.5	2	15.4		3	21.4	4	50		5	11.9	6	20.7	0	0	0	0	0	0	1	33.3
QUA		7	18.4	1	3.8	1	8	28.6	6	37.5	1	16	19	7	12.1	1	4.2	2	11.1	0	0	0	0
STE	1	7	36.8	2	15.4		2	14.3	3	37.5	1	9	21.4	6	20.7	2	16.7	5	55.6	3	60	2	66.7
FUR		6	31.6	1	7.7		5	35.7	2	25	1	13	31	4	13.8	1	8.3	0	0	0	0	0	0
COR	1	22	57.9	13	50		16	57.1	6	37.5	1	42	50	21	36.2	6	25	3	16.7	7	70	6	100
SCA		11	28.9	9	34.6		7	25	1	6.3		19	22.6	11	19	5	20.8	0	0	5	50	2	33.3
PEL		3	15.8	1	7.7		4	28.6	2	25	1	7	16.7	3	10.3	2	16.7	0	0	1	20	0	0
HUM	1	12	31.6	13	50		23	82.1	7	43.8	1	35	41.7	23	39.7	4	16.7	4	22.2	6	60	0	0
RAD	3	13	34.2	10	38.5		12	42.9	7	43.8	6	29	34.5	20	34.5	1	4.2	2	11.1	1	10	1	16.7
ULN	3	25	65.8	16	61.5	1	12	42.9	9	56.3	6	39	46.4	27	46.6	4	16.7	2	11.1	2	20	2	33.3
UCB	2	24	63.2	16	61.5		14	50	7	43.8	2	39	46.4	26	44.8	0	0	0	0	0	0	0	0
RCB		1	2.6	5	19.2		0	0	0	0		1	2.4	5	8.6	0	0	0	0	0	0	0	0
CMC	1	20	52.6	15	57.7		21	75	10	62.5	1	44	52.4	25	43.1	9	37.5	6	33.3	1	10	2	33.3
PH I *DMA*		15	39.5	15	57.7		12	42.9	9	56.3		28	33.3	24	41.4	6	25	0	0	0	0	0	0
FEM		13	34.2	7	26.9	5	18	64.3	7	43.8	6	32	38.1	14	24.1	1	4.2	2	11.1	1	10	2	33.3
TIT		16	42.1	12	46.2		9	32.1	5	31.3		26	31	18	31	3	12.5	0	0	5	50	3	50
TMT		25	65.8	13	50	2	11	39.3	7	43.8	3	36	42.9	21	36.2	1	4.2	2	11.1	3	30	3	50
Total	12	226	36.3	153	34.4	9	177	37.9	92	35.8	30	424	30.6	263	27.2	46	11.6	30	11.4	36	22.8	25	26.8

Table 3
Fragmentation of long bones in C7 and C6 (whole assemblage).

C7	Whole		Proximal		Distal		Shaft		Total	C6	Whole		Proximal		Distal		Shaft		Total
	NISP	%	NISP	%	NISP	%	NISP	%			NISP	%	NISP	%	NISP	%	NISP	%	
SCA	0	-	32	97	0	-	1	3	33	SCA	0	-	15	100	0	-	0	-	15
COR	14	20.3	19	27.5	36	52.2	0	-	69	COR	4	10.3	10	25.6	25	64.1	0	-	39
HUM	5	7.2	22	31.9	42	60.9	0	-	69	HUM	2	4.8	18	42.9	22	52.4	0	-	42
RAD	2	3.6	30	53.8	19	33.9	5	8.9	56	RAD	4	10	22	55	9	22.5	5	12.5	40
ULN	2	2.7	24	32.9	38	52.1	9	12.3	73	ULN	4	8.7	19	41.3	20	43.5	3	6.5	46
CMC	13	16.5	32	40.5	28	35.4	6	7.6	79	CMC	12	27.9	13	30.2	18	41.9	0	-	43
FEM	2	3.6	33	60	20	36.4	0	-	55	FEM	2	5.7	17	48.6	15	42.9	1	2.9	35
TIT	3	5.7	11	20.8	33	62.3	6	11.3	53	TIT	2	6.7	9	30	16	53.3	3	10	30
TMT	8	11.9	27	40.3	24	35.8	8	11.9	67	TMT	4	11.1	11	30.6	18	50	3	8.3	36
Total	49	8.8	230	41.5	240	43.3	35	6.3	554	Total	34	10.4	134	41.1	143	43.9	15	4.6	326

4.4. Bone surface modifications

4.4.1. Non-human predator activities

In C8, 25 remains (43.9%) show alterations related to non-human predators. Most of them are traces of digestion, which were observed on the 25 bones. For instance, the whole C8 femur sample (NISP = 8) is affected: the fragmentary remains can present pitting on the articular part (mainly on the *caput femoris*, *crista trochanteris* or on the distal *condyli*) and/or rounded and thinned fracture edges. Degree of corrosion is light on 64% of the remains, moderate on 24% and strong on 12%. Digested elements show that in C8, out of six bird individuals, at least five (the three choughs and two doves) were consumed by a predator. Among the 25 digested elements, two present mechanical alterations (a puncture on a proximal carpometacarpus and a notch on a proximal humerus).

In C7 and C6, non-anthropogenic modifications were recorded on 232 (19.9%) and 243 remains (34.6%) respectively (Table 4, Fig. 2). Digestive damage was detected on 181 specimens in C7 (15.6%) and 186 in C6 (26.5%). In C7, the degree of corrosion is mostly light (54.7%, NISP = 99), though it can also be moderate (20.4%, NISP = 37) or strong (24.9%, NISP = 45). In C6, remains are affected by light (59.1%, NISP = 110), moderate (19.4%, NISP = 36) or strong digestion (21.5%, NISP = 40). Mechanical alterations affect 5.8% of the C7 and 10% of the C6 assemblages. Bone surface modifications are mainly found on the most represented taxa, i.e. doves and choughs which are size 3 birds. However, small Passeriformes, Charadriiformes, phasianids, anatids and small strigids also show predation marks.

Predation marks were mostly documented on long bones. In C7, the most affected long bones are femora (65.5%), ulnae (43.8%) and tibiotarsi (41.5%). In C6, femora (62.9%), humeri (61.9%) and tarsometatarsi (55.6%) are the most affected. In C7, MNI calculated from digested elements indicate that at least 7 doves (7 left distal ulnae) and 6 corvids (6 left proximal femora) were eaten, at least partly, by a predator. In C6, at least 8 doves (8 right distal humeri) and 4 corvids (3 left distal tarsometatarsi) were ingested.

Rodent gnawing was also evident on 7 specimens in C7 and 2 specimens in C6.

4.4.2. Anthropogenic activities

Layer C8 remains did not record any trace of anthropogenic activity.

In layer C7, modifications that could be related to Neanderthal activities were documented on 15 remains (1.3%). The alterations were recorded on *Pyrrhocorax/C. monedula* (66.7%, NISP = 10) and *C. livia/oenas* (33.3%, NISP = 5).

The most frequent alterations are cut marks or possible cut marks (Fig. 3), which were observed on 12 specimens (1%), more specifically on 8 corvid and 4 dove remains. The most affected bones are humeri and femora (NISP = 3). Cut marks and possible cut marks were also documented on tibiotarsi, coracoids, scapulae, sterna and ulnae. An ulna attributed to *P. pyrrhocorax* shows two parallel incisions located close to the fracture edge, on mid-shaft, near the *papillae remigales*. They are deep and oblique to the longitudinal axis of the bone. Moreover, this ulna seems pathologic, showing roughened texture. Some striae were attributed only dubiously to human activities due to their similitude with trampling marks. This is the case for a corvid femur (Fig. 3D) that shows a series of relatively superficial, transverse striae located at mid-shaft. These shallow marks may be the result of trampling. Moreover, the specimen displays a perforation on the shaft that was probably produced by a non-human predator. Thus, the anthropogenic origin of the striae remains uncertain. Alterations dubiously attributed to dismembering of the elbow by overextension of the forelimb were recorded on 3 remains (2 corvid distal humeri and 1 dove proximal ulna). One humerus shows a crushing mark, the second one presents peeling on *processus flexorius*. The ulna displays a notch fracture. The ventral fracture edge is smooth but the dorsal edge is slightly crenulated.

Table 4
NISP affected by non-anthropogenic bone surface alterations. PUN: puncture; NOC: notch; CRE/GNAW: crenulated edge/gnawing mark; DIG: digestion; DIG + MD: Digestion and mechanical damage; Charadriif.: Charadriiformes; Pyrrho./C.mon.: Pyrrhocorax/C. monedula.

		C7						C6								
		PIT	PUN	NOC	CRE/GNAW	DIG	DIG + MD	Total	PIT	PUN	NOC	CRE/GNAW	SCO	DIG	DIG + MD	Total
Size 1	Passeriformes indet.		2				1	3		1				6		7
Size 2	Passeriformes indet.	1	1			4		6						3		3
	C. coturnix							0				1		2		3
Size 3	*S. querquedula*							0						1		1
	Anatidae indét.							0						2		2
	Cf. *S. rusticola*							0				1				1
	Charadriif. indet.							0						2		2
	C. livia/oenas	2	8	2	11	77	8	108	2	5	1	11	3	69	6	97
	Columbidae indet.					1	1	2								
	Cf. *Lagopus*							0							1	1
	Phasianidae indet.					2		2						2	1	3
	A. noctua							0	1							1
	A. funereus					1		1								
	Pyrrho./C. mon.	5	3	3	7	42	6	66	3	3	1	6		38	4	55
Aves indet. small size						2		2								0
Aves indet. medium size		1	2		3	35	1	42	1	5		12		48	1	67
Total		9	16	5	21	164	17	232	7	14	2	31	3	173	13	243
%		0.8	1.4	0.4	1.8	14.1	1.5	19.9	1	2	0.3	4.4	0.4	24.6	1.8	34.6

In layer C6, 3 specimens show possible anthropogenic damage. A *C. livia/oenas* humerus and proximal scapula present probable cut marks; the scapula is burned on its whole surface and shows a dark brown and black colouration. An anatid sternum shows what looks like peeling as well as striae, but their anthropogenic origin is dubious as they may be related to post-depositional processes such as trampling instead.

It cannot be ruled out that some of the recorded tooth marks have an anthropogenic origin. But since we were not able to prove it, they were considered among non-human modifications.

4.4.3. Post-depositional modifications

Manganese oxides deposits were observed on 14.1% of the C7 specimens and 26.6% of the C6 ones, in the form of more or less large, sometimes anastomosed, dark spots on the bone surface. Longitudinal fissures related to weathering affected 10.7% of the C7 assemblage and 3.6% of the C6 one. Bones covered with concretionned sediment represent 2.7% of the assemblage in C7 and 1% in C6. Some specimens display a shiny, polished aspect (C7: 4.5%; C6: 0.4%). This modification was also observed on some C7 rabbit remains and linked to water-rolling (Lebreton in Saos et al., 2016). Striae that could be related to trampling were recorded on 1.5% of the C7 assemblage and 1.4% of the C6 one.

5. Discussion

Recent excavation seasons conducted in La Crouzade cave yielded a great number of bird remains coming from Palaeolithic layers. Palaeontological results evidenced the presence of a diversified avifaunal spectrum, though clearly dominated by two groups: *Columba livia/oenas* and *Pyrrhocorax/C. monedula*. Both *C. livia* and *C. oenas* are frequently found in prehistoric cave sites (Clot and Mourer-Chauviré, 1986). At La Crouzade, the rock dove was identified from Helena and Saos collections material (Mourer-Chauviré, 1975b; Garcia-Fermet, 2020). Both *Pyrrhocorax* species, which are known to nest in rocky cliffs, are also very frequently met in cave sites (Finlayson, 2019). Their presence at La Crouzade is thus not surprising and could a priori suggest a natural, in situ death. La Crouzade avifaunal spectrum is completed by Galliformes, Anseriformes, Charadriiformes, Gruiformes, Falconiformes, Accipitriformes and Strigiformes. Most of the birds are medium-sized species, corresponding to size category 3 (Laroulandie, 2000). The presence of species that are not used to inhabit caves (partridges…) implies the role of a predator (raptor, Carnivoran or human) in the accumulation. Among Strigiformes, only the largest species such as *Bubo bubo* and *B. scandiacus* frequently feed on medium-sized birds. The eagle-owl is a very eclectic predator that takes on species of all sizes with a preference for medium-sized species such as doves, whilst small Passeriformes are consumed occasionally. On the other hand, smaller predators such as *Tyto alba*, *Strix aluco*, *Asio otus* and *Asio flammeus* mainly prey on birds ranging in size from tits and sparrows to thrushes (Watson, 1957; Blondel and Badan, 1976; Williams and Franck, 1979; Cramp and Simmons, 1980; Cramp, 1985; Bayle et al., 1987; Gross, 1944). The prey spectrum of La Crouzade thus makes *Bubo* spp. a more likely accumulator agent than all other listed Strigiformes.

In layers C7 and C6, most of the anatomical elements are present. Posterior phalanges and vertebrae are very abundant (Table A1). Cranial material is very scarce, as it is the case in *B. bubo* and *Falco rusticolus* accumulations (Bochenski et al., 1993, 1998), since both species are known to behead their prey prior to the ingestion, sometimes outside of the nest area (Hagen, 1952; Bengston, 1971; Glutz von Blotzheim and Bauer, 1980). On the contrary, actualistic referentials show that cranial remains are well represented in *B. scandiacus*, *A. otus*, *S. aluco*, *Aquila heliaca* and *Aquila fasciata* pellets (Bochenski, 1997; Bochenski and Tomek, 1994; Bochenski et al., 1993, 1997; Lloveras et al., 2014b) as they are in some carnivoran accumulations (e.g. *Lynx pardinus*, Rodríguez-Hidalgo et al., 2016). Differential conservation could also explain the scarcity of the cranial material, which is very thin and fragile in birds. Indeed, the

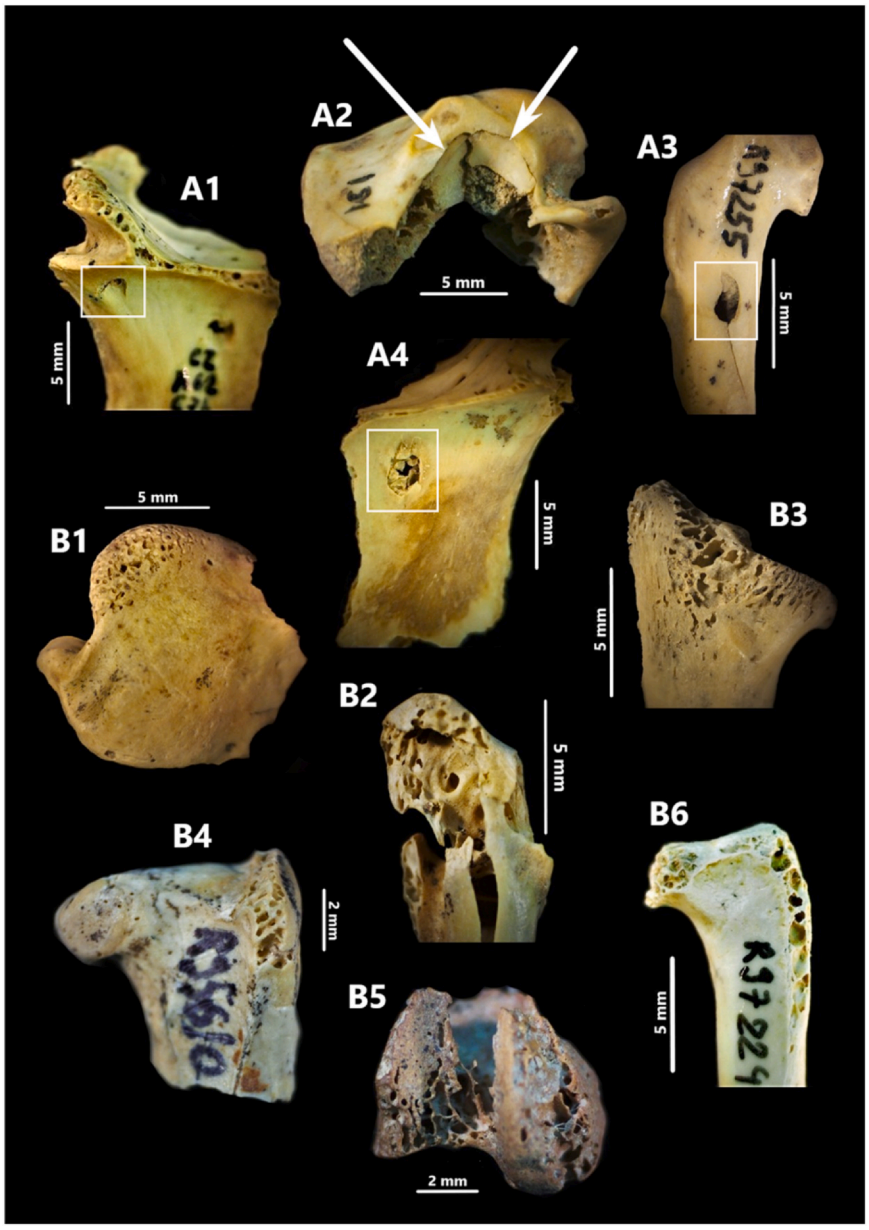

Fig. 2. Examples of non-human alterations observed on La Crouzade layers 7 and 6 remains. Mechanical modifications (A) and digestive damage (B). Sternum of *C. livia/oenas* from layer 7 (same specimen, A1 and A4), proximal humerus of *C. livia/oenas* from layer 7 (adhering flakes indicated by white arrows, A2), scapular coracoid of *C. livia/oenas* from layer 6 (A3), proximal humerus of *C. livia/oenas* from layer 6 (B1), scapular coracoid of *C. livia/oenas* from layer 6 (B2), proximal ulna of *C. livia/oenas* from layer 6 (B3), proximal femur of *C. livia/oenas* from layer 6 (B4), distal femur of *P. graculus* from layer 6 (B5), proximal femur of *P. graculus* from layer 7 (B6).

presence of quadrate bones and beak apexes implies that at least some skulls were deposited inside the cave but were not preserved or were reduced to small, undetermined fragments.

Long bones are relatively abundant and carpometacarpus is frequently among the most represented. Carpometacarpus dominance along with tarsometatarsus is associated with raptor predation (Mourer-Chauviré, 1983a). The relative robustness of this bone could also explain its good preservation. Other well represented bones in terms of MNE include coracoid, humerus and ulna. These elements are often among the most numerous in raptor accumulations (pellets and uneaten remains, Bochenski et al., 1993, 1997, 1999; Bochenski and Tomek, 1994; Bochenski and Nekrasov, 2001; Laroulandie, 2002; Alonso et al., 2020; Lebreton et al., 2020). However, coracoid and humerus can be well represented in accumulations in which humans took part (Mourer-Chauviré, 1983a; Blasco et al., 2016).

In size 3, ulnar carpals are also among the best represented bones. Small size and morphology make ulnare one of the most robust elements in bird skeleton, despite some variability among the different orders. Absence of ulnares in sizes 1 and 2 could be explained by a sieving or sorting bias.

Wing bones are slightly more numerous than leg bones, which corresponds to a natural accumulation according to Ericson (1987). However, Ericson's theory is a dichotomy that only opposes natural accumulation and anthropogenic accumulation, without taking non-human predators into consideration. Moreover, wing bones can predominate or be found in equal proportion as leg bones in accumulations deriving from raptors pellets (Bochenski et al., 1993; Bochenski and Nekrasov, 2001; Laroulandie, 2000, 2002) and uneaten food remains (Bramwell et al., 1987; Bochenski et al., 1999; Bochenski and Tornberg, 2003; Lloveras et al., 2014b). Wing elements can also prevail in anthropogenic accumulations (Gourichon, 1994; Laroulandie, 1998; Laroulandie and Lefèvre, 2014). Carnivoran accumulations are dominated by either wing or leg elements (Mallye et al., 2008; Monchot and Gendron, 2011; Rodríguez-Hidalgo et al., 2016). At La Crouzade, the wing-to-leg ratios obtained on size 3 birds (51–60%) fall into the " *B. bubo* or *S. aluco* pellets " group (Bochenski and Nekrasov, 2001).

Proximal elements account for approximately 50% of the long bones assemblage and are thus slightly underrepresented compared to distal elements. In uneaten food remains of diurnal raptors such as *Aquila chrysaetos* and *Accipiter gentilis*, proximal elements strongly dominate

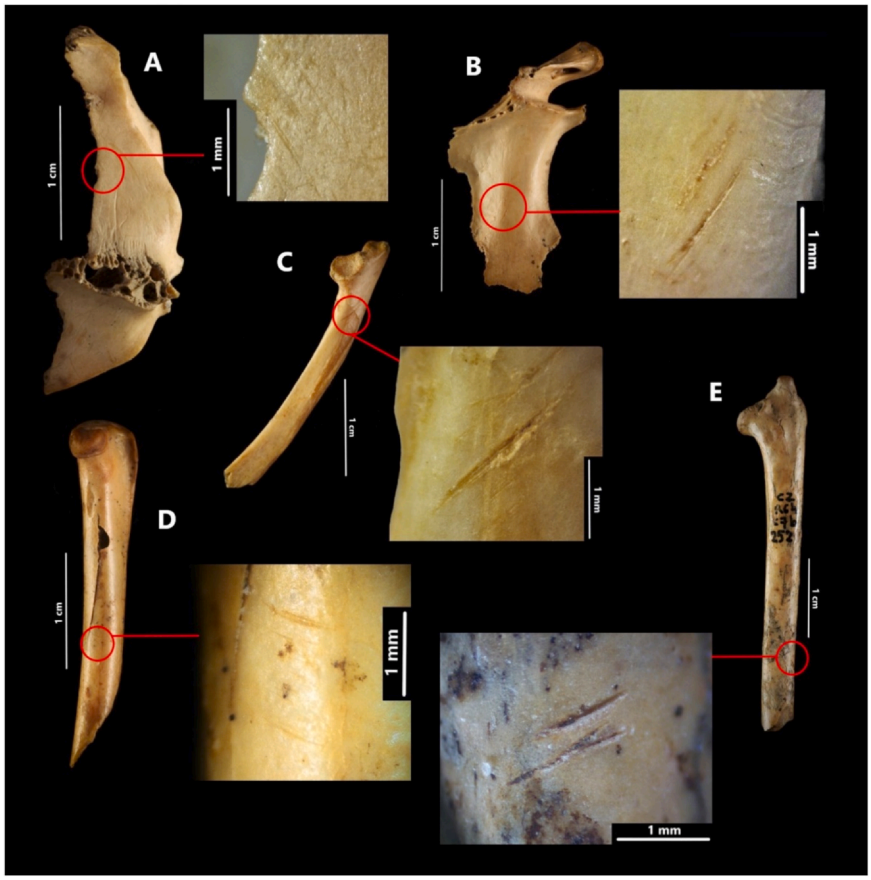

Fig. 3. Examples of La Crouzade bones displaying cut marks (B, C, E) or possible cut marks (A, D). Anatid sternum from C6 (A), *C. livia/oenas* sternum from C7 (B), *P. graculus/C. monedula* scapula from C7 (C), *P. graculus* femur from C7 (D), *P. pyrrhocorax* ulna from C7 (E).

(Lloveras et al., 2018b; Wertz et al., 2021), which is not the case here. Results correspond more to the " gyrfalcon and imperial eagle pellets " category (Bochenski and Nekrasov, 2001). This is the case in C7 *C. livia/oenas*, for which the difference between the observed (47.1%) and expected (55.55%) ratios is highly significant.

Core-to-limb ratios (approximately 20–25% in size 3 birds) are close to those obtained on *Lynx pardinus* uneaten food remains (Rodríguez-Hidalgo et al., 2016) and raptor pellets (Bochenski et al., 1993, 1997, 1998; Bochenski and Tomek, 1994). However, in the lynx accumulation, sternum and synsacrum show relatively high %RA, which is not the case in La Crouzade. Besides, the proportion of core elements (especially sternum) is much more important in raptor uneaten food remains (Bochenski et al., 1997, 1999; Bochenski and Tornberg, 2003; Lloveras et al., 2014b; Wertz et al., 2021).

Skeletal representation results should be treated with caution as a great number of bird remains whose stratigraphic context is unknown were not included in the present work. The context of a mixed accumulation and the uncomplete knowledge of predator signature variability also make the results more difficult to interpret. Furthermore, new material recovered during future excavation seasons is likely to modify skeletal profiles.

The degree of breakage (whole C7 and C6 assemblage: around 61%; long bones and scapulae only: around 91%) is much higher than in raptor uneaten food remains and *A. otus* pellets (Bochenski, 2005; Wertz et al., 2021). In a fox den, 48% of the specimens were complete or subcomplete (Monchot and Gendron, 2011), though all long bone fragments were relatively large in size (more than 1/3 of the total bone length), which is not the case in La Crouzade cave. A lynx accumulation yielded 85% of complete specimens (Rodríguez-Hidalgo et al., 2016). Strigiformes accumulations can show degrees of breakage similar to that of La Crouzade (Alonso et al., 2020). However, in this example of eagle-owl accumulation, long bone and phalanx fragmentation is more homogeneous than in La Crouzade assemblage, where only 9% of the long bones are complete whilst more than 90% of the posterior phalanges are. This could imply a strong impact of post-depositional processes resulting in differential preservation according to the bones relative robustness.

Predominance of scapular coracoids over sternal parts was also observed in pellet-deriving accumulations (Bochenski et al., 1993). Besides, coracoid is one of the least fragmented long bones alongside carpometacarpus and tarsometatarsus, especially in C7. This is the case in *F. rusticolus* pellets (Bochenski et al., 1998) whereas coracoid shows relatively high fragmentation percentages in Strigiformes accumulations (Bochenski et al., 1993; Bochenski and Tomek, 1994; Bochenski, 1997). Distal tibiotarsi are much more abundant than proximal parts, as it was documented in *B. bubo* pellets (Bochenski et al., 1993). On the contrary, proximal parts are more numerous in *S. aluco* pellets and largely prevail in *F. rusticolus* pellets (Bochenski et al., 1993, 1998). Contradictory results provided by coracoid and tibiotarsus fragmentation suggest that several predators took part in the accumulations.

From a qualitative point of view, fragmentation of some La Crouzade humeri matches fragmentation observed in *B. bubo* pellets (cf. Laroulandie, 2000, 2002, De Cupere et al., 2009, Bochenski and Tomek, 2020). The eagle-owl often breaks the proximal part just below the articulation (De Cupere et al., 2009). This pattern is found on columbid (C7 and C6), corvid (C7) and anatid (C6) specimens. Some of them show a notch-shaped fracture edge that probably results from an old perforation. Besides, some very fragmentary specimens less than 1 cm long (fragments of *caput humeri* or *condylus dorsalis*…) are consistent with food remains found in carnivoran faeces (Laroulandie, 2000).

Bone surface modifications were documented on a large spectrum going from small Passeriformes to size 3 taxa (the most affected) and

including small raptor species. In C8, the high proportion of digested bones (around 44%) indicates the important role of a predator, probably a raptor, in the accumulation. In C7 and C6, traces of digestion are the most numerous alterations (15% in C7, 26% in C6) whereas mechanical modifications are scarcer (5.8% in C7, 10.1% in C6). This is inconsistent with carnivoran accumulations in which the proportion of mechanically modified bones is relatively high whilst traces of digestion are rare or even totally absent (Mallye et al., 2008; Monchot and Gendron, 2011). At Grotte des Barasses II (Ardèche), where Carnivorans such as *V. vulpes* are thought to be the main accumulator agents, mechanically modified specimens represent more than 20% of the assemblage (Rufà et al., 2018). Still, some La Crouzade specimens show crenulated fracture edges, sometimes flanked with pits or punctures, which is consistent with damage caused by Carnivorans (Laroulandie, 2000; Mallye, 2007; Mallye et al., 2008; Monchot and Gendron, 2011; Rufà and Laroulandie, 2020), indicating that mammals played a role in the accumulation. These marks have no equivalent in raptor accumulations (Laroulandie, 2000). By their morphology, size and localization, some punctures recorded on size 3 birds are consistent with damage produced by raptor beaks or claws (cf. Laroulandie, 2000, 2002; Bochenski et al., 2009; Rufà and Laroulandie, 2019). Digestive damage is mostly light, as it is the case in Strigiformes pellets (e.g. Royer et al., 2019; Rufà and Laroulandie, 2019; Alonso et al., 2020; Lebreton et al., 2020). Traces recorded on some specimens evoke those produced by *B. bubo* on ingested bones (cf. De Cupere et al., 2009; Bochenski et al., 2018; Bochenski and Tomek, 2020; Rufà and Laroulandie, 2019; Lebreton et al., 2020). The presence of moderately or strongly digested bones reinforces the hypothesis of a mixed accumulation; some elements show a longitudinal, digested gap (see Fig. 3), as observed in *F. rusticolus* pellets (cf. Bochenski et al., 1998). The high proportion of digested specimens indicates that most of the assemblage derivates from pellets and/or faeces rather than uneaten food remains.

The hypothesis that several predators played a role in the avian remains accumulation is consistent with studies conducted on La Crouzade amphibian and squamate remains. Indeed, traces of digestion were documented on more than 90% of the herpetofaunal assemblage. These small vertebrates were likely accumulated by a strigid (*A. flammeus* or *B. bubo*) and/or a medium-size Carnivoran such as *Meles meles* (Bailon and Bochaton in Saos et al., 2021). Mechanical traces (0.4%) and digestive damage (13.3%) were also recorded on C7 leporid remains (Morin et al., 2019).

Thus, several facts hint the role of the eagle-owl in the accumulation. Indeed, the largest Eurasian strigid is used to nest in caves and feeds on every kind of available prey including leporids, amphibians, lizards and snakes, fish and of course birds. Regarding avian preys, the eagle-owl has a preference for medium-sized species such as doves whilst small birds such as thrushes are taken occasionally. Other raptor species can be consumed. Within the assemblage, the presence of gnawed bones and strongly digested small fragments imply that Carnivorans and perhaps diurnal birds of prey also took part in the accumulation. Predation marks on an immature *Pyrrhocorax* tarsometatarsus suggest predator occupation of the cave in spring or summer, since in Alpine choughs fledging starts between late June and early September, after one month spent inside the nest (Delestrade and Stoyanov, 1995).

Besides non-human predators, anthropogenic bone surface modifications indicate that Neanderthals also took part in the C7 and C6 accumulations, although not as the main agents. Cut marks documented in C6 evidence the exploitation of at least one *C. livia/oenas* and one anatid individual. The anatid sternum shows what might be peeling, in the form of parallel grooves on a roughened surface (White, 1992). Although some raptors like *A. chrysaetos* can occasionally produce peeling on sterna and pelvises (Laroulandie, 2005a), this alteration is traditionally associated with human activities (Laroulandie, 2000). However, erosion and other post-depositional processes could have also caused such damage on the sternum, due to the bone's particular morphology. Moreover, the rounded and shiny border of the bone suggests it was subject to trampling. The superficial striae it displays are dubious and could also be related to trampling rather than anthropogenic activities. It is thus difficult to demonstrate that this anatid was exploited by humans. Striae on a *C. livia/oenas* scapula would indicate defleshing activities (Fiore et al., 2016). This specimen is the only burned remain in the assemblage. Combustion marks located on proximal scapulae indicate cooking of carcasses whose wings were removed (Laroulandie, 2005b). However, it is impossible to know whether the burning damage was localised on the articular end or not, due to fragmentation. Anthropogenic, voluntary roasting of this element is thus difficult to prove.

In C7, anthropogenic modifications only affect cliff-dwelling species (*C. livia/oenas* and *Pyrrhocorax/C. monedula*). They mostly consist of cut marks located on long bones. Most of them, located on fleshy elements (e.g. *C. livia/oenas* sternum) are referable to defleshing activities (Finlayson et al., 2012; Blasco et al., 2016), thus indicating exploitation for food. Dove consumption by Neanderthals was evidenced in other Mediterranean sites (Roger, 2004; Blasco and Fernández Peris, 2012a; Blasco et al., 2013, 2014, 2016; Romero et al., 2017; Lloveras et al., 2018c). Perhaps one of the most intriguing specimens is a corvid ulna which shows two parallel incisions located near *papillae remigales*. Like doves, corvids were frequently hunted by humans for food, but also for the recovery of raw materials such as feathers or bones (e.g. Peresani et al., 2011; Finlayson et al., 2012; Blasco et al., 2016; Fiore et al., 2016; Laroulandie et al., 2016; Romero et al., 2017; Gómez-Olivencia et al., 2018; Lloveras et al., 2018c). Experimental data indicate that the removal of secondary remiges is likely to produce oblique marks on the ulna shaft (Pedergnana and Blasco, 2016; Romandini et al., 2016; Blasco et al., 2019; Martin, 2020; Rufà et al., 2023). At Fumane cave and Gibraltar, the overrepresentation of corvid wing bones associated with the presence of cut marks concentrated on these elements was interpreted as the collection and use of feathers by humans (Peresani et al., 2011; Finlayson et al., 2012; Fiore et al., 2016). At Gorham's cave, cut marks on corvid ulnae sharing the same distribution, localization and orientation as in the La Crouzade specimen were consistently associated with feather removal activities (Blasco et al., 2016). In flapping birds, humeri and ulnae are covered with a relatively high proportion of meat (Blasco et al., 2016). Feather removal on the La Crouzade ulna could thus be related to meat procurement rather than feather use. Cut marks found on several *Pyrrhocorax* femora supports the hypothesis that corvids were not hunted for raw material procurement only.

A red-billed chough proximal humerus shows several groups of striae located on the cranial face, referable to wing detachment (cf. Fiore et al., 2016).

Some striae would require further examination with the support of a SEM to confirm their anthropogenic origin. Comparisons with marks displayed by leporid or large mammal bones are also needed.

Probable crushing marks (*enfoncements*) and peeling traces on *Pyrrhocorax* distal humeri would correspond to disarticulation of the elbow on a fresh carcass by overextension of the forelimb. The process can generate a light squashing of the *fossa olecrani*, a hole or a notch. Ulnae can display notch fractures and peeling (Gourichon, 1994; Laroulandie, 2000; 2005a; 2005b; Laroulandie et al., 2008). However, it has been proved that small Carnivorans such as *V. vulpes* can also produce peeling on bones (Arilla et al., 2019), encouraging to consider the damage carefully before interpreting. On La Crouzade specimens, the anthropogenic origin of some marks located on distal humeri is difficult to demonstrate due to the few number of specimens affected, the lack of standardisation in the alterations and the fact that they are not perfectly consistent with modifications produced by modern humans in Upper Palaeolithic contexts such as La Vache (cf. Laroulandie, 2005a). Holes are not exactly located on the *fossa olecrani*, their diameter and morphology show some variability. In some cases, modifications are limited to damage on *condyli dorsalis* and *ventralis* and/or

processus supracondylaris dorsalis (*PSD*) as well as peeling on *processus flexorius*, evoking alterations observed on Fumane and Arbreda specimens and also linked to anthropogenic disarticulation (cf. Fiore et al., 2016; Lloveras et al., 2018c). It is likely that both performed gestures and olecranon interspecific morphological variability have an influence on the mark resulting from the action. Thus, new experimentations conducted on various taxa such as corvids and columbids may be needed in order to better appreciate the variability in elbow disarticulation marks and to explain damage on the *condyli* and *PSD*. This could be applied to other articulation points such as wrist or knee joints.

Humans could be responsible for some tooth marks observed on bones (e.g. on the *crista deltopectoralis* of the corvid humeri). Human tooth marks are difficult to distinguish from carnivoran ones (cf. Lloveras et al., 2009; Morin et al., 2019) and further criteria are needed to identify them.

Some individuals belonging to cliff-nesting taxa such as *P. graculus* could also die naturally in situ. However, if the excavation zone was used as a nesting area, one would expect to find a great proportion of immature individuals, since Alpine chough chicks have a high mortality rate (Delestrade and Stoyanov, 1995). In Vaufrey, the corvid (*P. graculus*) accumulation is thought to be mostly natural and is characterised by the absence of major bias in skeletal representation, the high proportion of immature individuals and the absence of predator-related surface modifications (Laroulandie, 2000; Rufà and Laroulandie, 2021). In La Crouzade, the low proportion of immature bones (0.3%) associated with high percentages of fragmentation and predator marks suggests that most of the birds did not die naturally. Post-depositional processes may also be responsible for the disappearance of immature bones (Laroulandie, 2010).

The La Crouzade assemblage thus shows similar trends to those observed in other Mousterian cave sites. The avifaunal spectrum is predominated by cliff-nesting taxa such as *Columba* and *Pyrrhocorax* as it is the case in numerous Mediterranean sites including the Gibraltar sites, Pié Lombard, Cova Negra or Arbreda cave (Blasco et al., 2016; Martínez Valle et al., 2016; Romero et al., 2017; Lloveras et al., 2018c). Non-human predators are responsible for most of the accumulation, as in Les Fieux (Lot), Pié Lombard (Alpes-Maritimes), Payre, Abri des Pêcheurs and Barasses II (Ardèche), Vaufrey (Dordogne) (Laroulandie et al., 2016; Romero et al., 2017; Rufà et al., 2016b, 2018; Rufà and Laroulandie, 2020), or in Teixoneres and Arbreda (Catalogne), (Rufà et al., 2016a; Lloveras et al., 2018c). Neanderthals mainly took advantage of the presence of gregarious, ground-feeding birds that probably shared the same shelters, as reported by several authors (Blasco et al., 2016; Martínez Valle et al., 2016; Lloveras et al., 2018, Blanco et al., 2021). Food procurement seems to be the main motivation, as it is the case in a large part of Mediterranean Europe including French coasts, Iberian and Italian peninsulas (cf. Blasco et al., 2022). The use of birds (especially raptors) as raw material sources, reported in several parts of Europe (e.g. Morin and Laroulandie, 2012; Radovčić et al., 2015; Laroulandie et al., 2016), was not evidenced in La Crouzade.

The bird assemblage from La Crouzade Cave thus provides further support of frequent small, quick-flying game exploitation in the Mediterranean area prior to the Upper Palaeolithic. It shows that Neanderthal prey spectrum at La Crouzade was broad, as humans exploited not only large mammals (Bachellerie, 2016, 2017) and rabbits (Morin et al., 2019) but also doves and choughs. However, the low frequency of anthropogenic damage on bones could suggest that birds were economically less important to Neanderthals than large herbivores such as reindeer and bovids. Most of the human-induced modifications on bird bones come from C7. In this layer, the presence of tools that were re-sharpened and recycled until exhaustion suggests that Neanderthals were limited in mobility, perhaps due to harsh climate (Saos et al., 2020, 2022). In this case, rocky birds that nested in the surrounding area may have provided useful food supply to Neanderthals. Moreover, the many non-anthropogenic alterations found on birds indicate frequent raptor and carnivore occupations at La Crouzade, in all Mousterian layers. Since it's unlikely that these predators inhabited the cave at the same time as humans, we can conclude that Neanderthal occupations were discontinuous. This corroborates previous studies conducted on bovid and reindeer remains which evidenced late summer-early autumn and winter human occupations (Bachellerie, 2016, 2017; Saos et al., 2020).

All sites did not yield evidence of Neanderthal use of birds (e.g. Rufà et al., 2016a). Thus, it would be interesting to apply the methodology mobilized for the present study to other cave sites from the area of La Crouzade, such as Portel-Ouest (Ariège), L'Hortus (Hérault), Bize-Tournal (Aude) or the older Les Ramandils (Aude) in order to determine in which localities they did exploit them and to better apprehend the reasons that caused Neanderthals to include these small preys to their diet.

6. Conclusions

The Mousterian La Crouzade avifaunal spectrum is dominated by medium-sized birds, most of them being rocky taxa (*Columba livia/oenas*, *Pyrrhocorax* spp.).

The taphonomic analysis conducted on avian bone remains evidences the mixed origins of the assemblage in layers C7 and C6: raptors, Carnivorans and Neanderthals all took part in the accumulations.

Non-human predators are the main accumulator agents. They brought most of the columbids, corvids, anatids, phasianids, Charadriiformes and small strigids to the cave. High percentages of fragmentation and digestive damage indicate that most of the assemblage derivates from pellets and/or faeces rather than uningested food remains. Several clues (in-cave context, prey size and skeletal representation, qualitative fragmentation of some specimens, degree of digestion) suggest that the Eurasian eagle-owl (*Bubo bubo*) played an important role in the accumulations. Besides, the eagle-owl presence is attested by a distal ulna fragment in C7. Medium-sized Carnivoran intervention is attested by gnawed articular parts and crenulated edges. The C8 sample is modest but the high proportion of digested remains implies the important role of a predator (probably a raptor) in the accumulation.

Human-induced modifications were documented in C7 and C6, though they are much scarcer than non-anthropogenic ones. Still, Neanderthals exploited some corvids and columbids. Cut marks located on fleshy elements and related to defleshing indicate that food procurement was the primary motivation. Striae located on ulna could be linked to feather removal, although it is difficult to say if secondary remiges were used after their extraction. Possible crushing marks and peeling on distal humeri would indicate elbow disarticulation by overextension of the forelimb.

Some bird individuals could have died naturally in situ. The very high proportion of gregarious, rocky taxa in the assemblage suggests that entire colonies of *Columba* and *Pyrrhocorax* nested in cliff cavities surrounding La Crouzade cave.

The present data show that La Crouzade cave was frequently inhabited by raptors or Carnivorans, thus implying that Neanderthal occupations were not continuous.

Among the assemblage, several specimens show damage whose origin is dubious. Regarding striae, stereomicroscopic observation did not always permit the confirmation of their anthropogenic nature. Further examination with the support of a SEM is needed, as well as comparisons with marks observed on rabbit and large mammal bones. Regarding the possible crushing marks, new experimentations would allow a better appreciation of elbow disarticulation-induced marks variability and the establishment of new criteria.

La Crouzade cave still represent a new occurrence of Neanderthal bird exploitation, as it is the case in other Western and Mediterranean Europe sites.

CRediT authorship contribution statement

Thomas Garcia-Fermet: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization. **Anne-Marie Moigne**: Conceptualization, Writing – review & editing, Resources. **Agnès Testu**: Conceptualization, Writing – review & editing, Resources, Supervision. **Thibaud Saos**: Writing – review & editing, Resources. **Sophie Grégoire**: Conceptualization, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Table A1
Skeletal elements not included in %RA calculations, expressed in MNE. VER: vertebra; Ant. PH: anterior phalanx (excluding phalanx I *DMA*); FIB: fibula; Post. PH: posterior phalanx (excluding talon); TAL: talon. LSZ: large size; MSZ: medium size; SSZ: small size.

	C8			C7			C6		
	Aves LSZ	Aves MSZ	Aves SSZ	Aves LSZ	Aves MSZ	Aves SSZ	Aves LSZ	Aves MSZ	Aves SSZ
VER		7		1	141	7		88	15
Ant. PH		1			30			12	
FIB					4			5	
Post. PH		8			147	1	1	92	1
TAL		8			111	1		49	1
Total		24		1	433	9	1	246	17

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at 10.1016/j.qeh.2023.100001.

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