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## Article

# Unravelling the Taphonomic Stories of Bird Bones from the Middle Pleistocene Layer VIII of Grotte Vaufrey, France

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**Abstract:** In recent years, several studies have significantly changed our knowledge concerning the use of birds by Neanderthals. However, what remains to be clarified is the geographical and chronological variability of this human behaviour. The present case study provides new information on this topic/debate. The Grotte Vaufrey was discovered during the 1930s and was excavated during different periods. Work carried out by J.-P. Rigaud during the 1980s motivated many multidisciplinary studies in the cave, but accurate studies were not focused on avian remains. In this work, we provide new data on the bird remains from layer VIII (MIS 7), which is the richest among all the sequences and which has an important Mousterian component. Corvids are predominant in the assemblage and are associated with medium-sized birds and small Passeriformes, among others. Most of the remains present modern fractures, which hinder taphonomic interpretation. However, some alterations associated with raptor or mammalian carnivore activities, together with the anatomical representation and age profile, suggest a non-human accumulation of the majority of the bird remains, especially in the case of corvids that naturally died in the cave. However, at least some bones show evidence of anthropic activity, suggesting the occasional use of large- and medium-sized birds by human populations.

**Keywords:** birds; zooarchaeology; taphonomy; natural origin; carnivores; cut marks; Neanderthal; Middle Paleolithic



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## 1. Introduction

The use of birds by past human communities has been a widely discussed subject during the last two decades, which has contributed to our knowledge of the evolution of past human behaviour. The discoveries published about birds processed by humans in the pre-Upper Palaeolithic period have prompted the development of zooarchaeological research on avian remains. Until the 1990s, faunal analyses mainly focused on large herbivores, which are considered more nutritionally profitable than small prey [1]. Thus, birds, as other small animal remains, had commonly passed unnoticed from accurate taphonomic studies under the general assumption that they were introduced to the archaeological record by non-anthropogenic inputs. Nevertheless, the use of fast-running (e.g., rabbits and hares) or quick-flying prey (birds) by human groups could not only be linked to dietary purposes [2] but also to the non-edible products they can offer—including feathers, furs, tendons, or bones [3–12]. This fact makes birds attractive to humans as they can provide elements to protect, raw materials to produce tools, or other aesthetic or symbolic components related to human culture. Thus, there is increasing awareness of the necessity of identifying accumulator agents of small prey remains in archaeological sites.

Determining the origin of an accumulation is challenging, as different actors could have occupied archaeological sites, mixing the waste of their activities with those performed by humans. Such palimpsests are difficult to tackle as it is not always possible to

differentiate events during the excavation process. Many neo-taphonomic studies have been conducted to create a referential corpus that could help distinguish small prey accumulators in archaeological sites, such as those produced by mammalian carnivores or diurnal and nocturnal raptors. In the case of small fast-running prey, the referential framework has been widely developed in southwestern Europe, where these animals are abundant [13–19]. Studies on quick-flying animals have mostly focused on predators such as diurnal and nocturnal birds of prey [20–43]. The modifications that mammalian carnivores can produce on bird accumulations are still barely explored [31,34,38,42,44].

Additionally, it must be taken into account that some accumulations could be partially or totally the consequence of natural accumulations where any predator—neither human nor non-human—intervened. Caves and shelters are places of nesting and roosting for many bird species that could die inside. In a hypothetical scenario in which natural death takes place, complete skeletons are expected to be found in articulation, as they are not modified by predators. Nevertheless, this situation is ideal, as only carcasses from individuals that are quickly covered by sediment can maintain their original position after death [45]. Prior to and during burial, carcasses are exposed to predators who can scavenge on them [46–48], as well as to other natural processes that could alter bone surfaces [24,49–52]. Even after being buried, many postdepositional alterations could modify the original position of the remains, hindering possible interpretations when recovering and studying them [53,54].

To distinguish these natural accumulations from those of predatory origin, different studies were conducted. In 1987, Ericson proposed that the proportion of wing and leg elements could be a guide for identifying the possible anthropogenic origin of an assemblage. He argues that anthropogenic bird accumulations tend to have wing elements underrepresented, while in natural accumulations, the proportion is similar or wings tend to be overrepresented [55]. In line with this argument, some work has already been published suggesting the anthropogenic origin of avian accumulations in the base of anatomical representation [56,57]. However, Ericson's model was criticized and some authors suggested that factors like functional anatomy or the mode of locomotion should be taken into account when assessing an assemblage, as they could influence on bone density and, as a consequence, lead to differential preservation of bones [58–60]. The bone density hypothesis is nowadays only partially accepted; it has been proven that anthropogenic accumulations can present an equal or higher proportion of wing elements. Besides, other cultural factors could influence skeletal part representation [61–63]. Therefore, anatomical representation is no longer used as a unique criterion to determine bone accumulations' origin, and data should be contrasted with other evidence. The presence of taphonomic traits related to predatory activities is currently the most effective way to diagnose a predator's intervention on avian remains. The presence of chewing and gnawing marks, digestive damage, cut marks, or burning are indicators of these actions [64,65]. However, human activities involving birds are not always easy to interpret, as these animals can also be processed without using tools. In order to detect possible anthropogenic activities, some work has been performed to distinguish other distinctive traits that could be attributed to humans, such as the presence of human teeth marks [66], peeling resulting from bone bending [42,67,68] or wrenches and holes related to the disarticulation of the elbow joint [69].

The capacity of prehistoric humans to capture and use bird products is conceived of as an important acquired ability because it proves that they are versatile enough to adapt to different conditions and maximize the resources present in their environment for different purposes [3,70–73]. This is part of what is called “complex behaviour.” Thus, there is growing interest in exploring when and why this complex behaviour appeared. Currently, we know that the evidence of bird use by pre-modern human populations has its highest expression during the Late Middle Palaeolithic (MIS 5–3) [3–6,8–10,74–76]. However, the first current data existing on anthropic bird processing goes back to the Early Pleistocene. The most ancient evidence was documented at the 1.2 Ma level TE9a

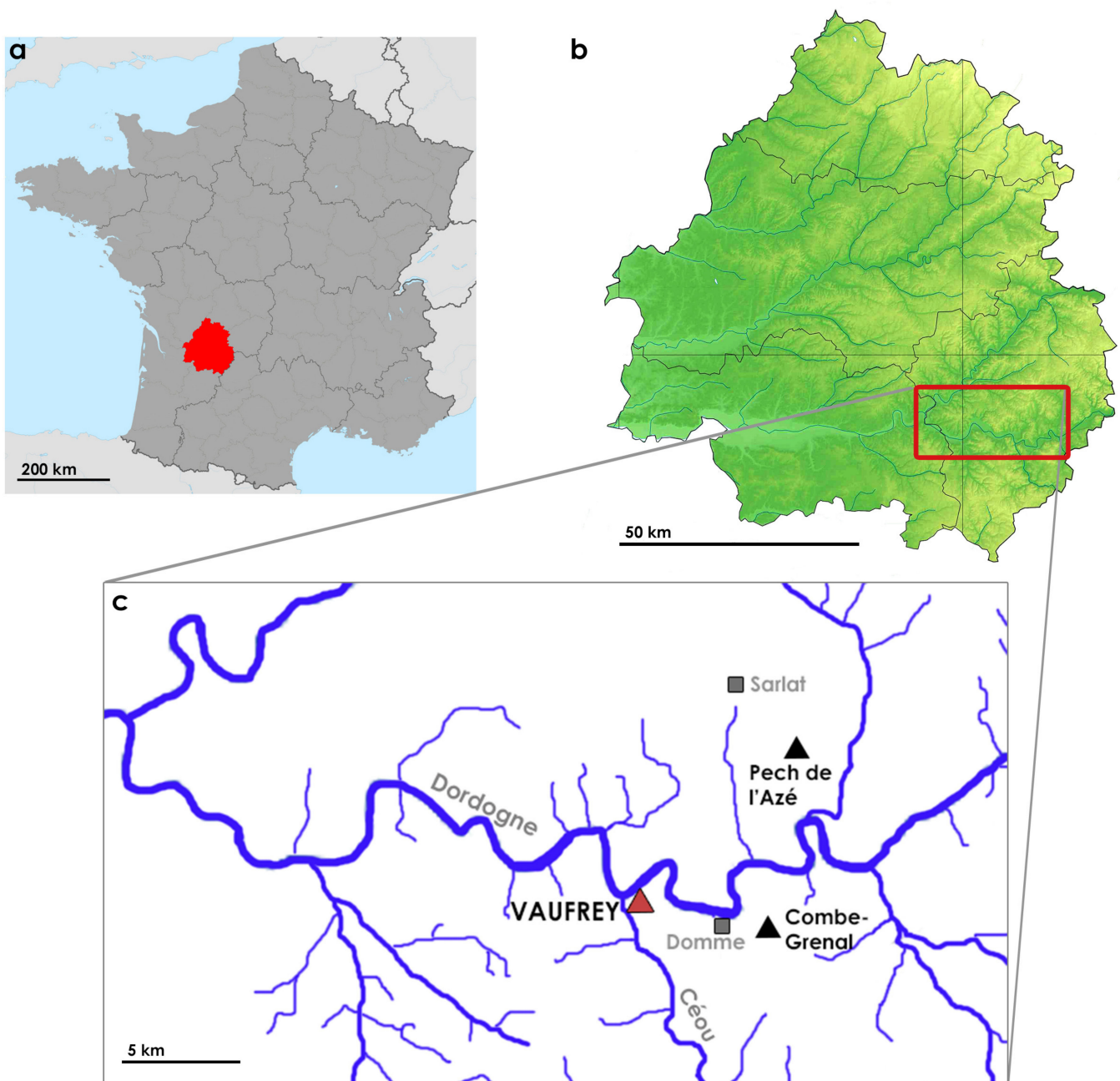
of the Sima del Elefante site (Spain), where a large bird radius bearing cut marks was identified [77]. At the Dursunlu site (Turkey), a tarsometatarsus of a large-sized bird also had cut marks in the context of 0.9 Ma [78]. Other rare evidence was documented at the Achelo-Yabroudian Lower Palaeolithic of Quesem Cave (Israel), where three bones presented cut marks on their surfaces and a humerus of starling (*Sturnus* sp.) had possible human modifications related to chewing activities. One of the cut-marked bones was a swan (*Cygnus* sp.) carpometacarpus, which also bore peeling on its proximal area [12]. Five bones were also documented at the Middle Pleistocene of the Gran Dolina site (four at unit TD10-1 and one at TD10-2) [79,80]. At the site of Payre (MIS 8–5), bird use was proposed because of the presence of some feather barbules on a stone tool [81], even though the taphonomic study of bird remains does not confirm this hypothesis [82]. In more recent chronologies, anthropogenic activity on Alpine chough (*Pyrrhocorax graculus*) bones was suggested in the “Acheulean cabin” of the Lazaret in France [56], even if no direct evidence on bones was confirmed. At the same site, a rock dove (*Columba livia*) cut-marked humerus was found at UA24 [83].

Apart from this evidence, a remarkable case was documented at Bolomor Cave (Spain), where bird use seemed to occur systematically during the Middle Pleistocene (MIS 9–5e). The processing of bird body parts in this site was confirmed along the sequence (levels VI, XI, XII and XVII), affecting a variety of bird bones from both aquatic and terrestrial species [79,84,85]. During these ancient periods, the procurement of birds seemed to be mostly related to their use as food. Nevertheless, the handling of inedible products possibly involved in symbolically mediated behaviour and aesthetical expressions is documented in some cases [12], in particular at the end and after the MIS 5 [3–10,74–76].

In this line, we would like to explore the bird bone assemblage at Grotte Vaufrey (Dordogne, France), analysing part of the remains recovered from J.-P. Rigaud’s excavations.

#### *La Grotte Vaufrey*

The Grotte Vaufrey, or Grotte XV, is one of the 22 caves conforming to the karstic system at Falaise du Conte (Cénac-et-Saint-Julien, Dordogne, France), a cliff overlooking the Céou River, at its confluence with the Dordogne river (Figure 1). The cave has a large entrance and is composed of a 22-metre-long principal room, NE oriented, which joins with a little chamber of 4 × 3 metres. Raymond Vaufrey discovered the cave in 1930 and conducted the first archaeological excavations in the site. Two test pits were performed during this period, confirming the archaeological potential of the site. However, the works were dropped out. The Direction des Antiquités Préhistoriques closed the entrance of the cave to protect it from destruction and plundering suffered since the end of Vaufrey’s excavation. In 1969, J.-P. Rigaud restarted the works in the cave, which lasted until 1982 and uncovered fifteen archaeo-paleontological layers (I–XV). After this work, Texier refined the stratigraphy by identifying five lithostratigraphic units that included the previously stated layers. From them, twelve archaeological layers remained (I–XII), while the others only had a paleontological component [86,87].



**Figure 1.** Location of Grotte Vaufrey (or Grotte XV) within Dordogne area. (a) Map of France with the location of the Dordogne region marked in red; (b) Dordogne region with the specific area of interest along the Dordogne river; (c) location of Grotte Vaufrey, at Céou and Dordogne confluence.

Considering chronology, Vaufrey's sequence has commonly provided inconsistent results [86–91]. The first dating was performed using the U-Th technique on speleothems, providing a chronological range from  $246 \pm 76$  ka BP (layer X) to  $74 \pm 18$  ka BP (layer I). However, the extremely low content of uranium and the high presence of detrital impurity only delivered some estimations [86,91]. Delpech, using biostratigraphy, and Texier, based on the presence of cryosols and radiometric data, tried to estimate the chronology of different strata, situating the formation of unit I during MIS 4. The chronology for the lowermost layers was more inconsistent, proposing variability in dating between MIS 7 and MIS 11 for layers IX to XI [86,88,91]. New TT-OSL dating performed in the cave by Hernandez and colleagues suggests that the sequence spreads from MIS 14 ( $545 \pm 47$  ka BP) at layer XIII to a minimum age of  $109 \pm 7$  ka BP (layer II) [89]. No new absolute

dates were made for layer I, as it was attributed to MIS 4, based on paleontological data, which is consistent with the environmental data available [89,91]. Considering cultural assignments, layer I contains the Quina Mousterian industry. Layers from II–VIII are assigned to the Typical Mousterian, with a significant Levallois component. In layers IX to XII, Levallois products are limited or absent, and an increasing number of tools are typically assigned to the Acheulean [86]. Faunal remains show a wide diversity of species all along the sequence, where ungulates stand out: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), reindeer (*Rangifer tarandus*), horse (*Equus ferus*), aurochs (*Bos primigenius*), steppe bison (*Bison priscus*), Bonal tar (*Hemitragus cf. bonali*), chamois (*Rupicapra rupicapra*), and wild boar (*Sus scrofa*), among others. Leporid remains are abundant and comprise an important component of the faunal assemblage [92]. Carnivores are also present: dhole (*Cuon sp.*), fox (*Vulpes/Alopex*), wolf (*Canis lupus*), cave lynx (*Lynx spelaea*), bear (*Ursus sp.*), and the European badger (*Meles meles*).

During Rigaud's excavations, many multidisciplinary studies were performed in the cave. As a result, a monograph dedicated to the cave was published in 1988 [86]. According to it, layer VIII is the richest among all the archaeo-stratigraphic sequence. Its formation took place during a temperate and humid period, probably from MIS 7 [89]. This layer preserves abundant Mousterian lithic industry from different raw materials that were collected in a radius of 50 km. The faunal assemblage is mainly composed of ungulates, where red deer stands out. Tahr, horse, chamois, and roe deer are present to a lesser extent. Rabbits (*Oryctolagus cuniculus*) are numerous and are probably accumulated by the action of the dhole [92]. Several carnivore remains were also discovered belonging to dhole, fox, wolf, lynx, bear, and badger [86,93]. First analyses carried out by Binford on the ungulate remains from the cave proposed that human activity in layer VIII was mainly related to scavenging activities [86]. This hypothesis was later criticized and rejected by Grayson and Delpech, who proposed that these animals were hunted and that the subsistence strategies observed from faunal remains pointed towards hominid–carnivore alternation, where humans performed short but repeated occupations [93]. In addition to mammal remains, fish and bird remains were recovered during the excavation [42,94]. In the case of the birds, their study was first assigned to P. Vilette for a paleontological determination. However, this work was not finished. After him, one of us (VL) reviewed the corvid remains from unit VIII, taking them as an example of the natural contribution of birds in archaeological assemblages [42,95]. No further studies have been conducted on the bird assemblage until now. Thus, the purpose of this study was to analyse bird bones from layer VIII (those previously studied by VL and those from other bird species) from a taphonomic point of view. Different objectives were pursued: (a) to find out other possible accumulations of birds in the site to see the different taphonomic stories that could have happened in the cave and (b) to search for traces of human activities so that they could help to unveil the role of humans in this assemblage. These data will provide information on the occupation dynamics of layer VIII and will help to understand the role of small animals, such as birds, in archaeological accumulations.

## 2. Materials and Methods

Bird remains from Grotte Vaufrey were reviewed in December 2019 during a stay at Musée National de Préhistoire (MNP) at Les Eyzies-de-Tayac, where the material is currently housed. The whole bird bone assemblage (from layers I to XI) was analysed and identified anatomically and taxonomically at the family, genus, or species level by using both osteological atlases [96–99] and the osteological bird collection from the PACEA (De la Préhistoire à l'Actuel: Culture, Environnement et Anthropologie) laboratory, Université de Bordeaux. No bird remains underneath layer XI were documented. When detailed determination was not possible, the bones were classified by size and followed the same criteria as mentioned below. The degree of ossification of cortical tissue was used to determine immature individuals [54]. The sex determination was occasionally possible by the presence of medullary bone in some long bones. The medullary bone is a granular

dense tissue of calcium formed within the bones during the laying period [54,100,101]. The remaining bones were quantified according to the number of identified specimens (NISP), the minimum number of elements (MNE), and the minimum number of individuals (MNI).

At this point, further analyses were performed only for the layer VIII collection, as it was the richest in the number of remains to obtain detailed results. The percentage of relative abundance (%RA) was computed to assess possible biases in the assemblage [102]. This formula was applied by dividing the MNE found for each bone category by the total number of elements expected to be found, based on the MNI represented, and is expressed as a percentage. After the initial identification, the remains were classified, taking into account six larger categories according to the bird's weight [40]: size 1 (<50 g); size 2 (51–150 g); size 3 (151–250 g); size 4 (251–500 g); size 5 (501–1500 g); and size 6 (>1501 g). This allowed for the calculation of different indexes with more precision. The wing-to-leg ratio and the proximal-to-distal element ratio were calculated for the principal size categories and for the medium-sized (msz) Corvidae group to assess possible differences in anatomical representation. Medium-sized corvids were the only taxa considered in addition with its size category, as other taxa were not representative enough to establish reliable statistics. The wing-to-leg ratio was calculated by dividing wing remains (humeri, ulnae, and carpometacarpi) by the sum of the wing and leg specimens (femora, tibiotarsi, and tarsometatarsi) [55]. The proximal-to-distal element ratio was calculated by dividing the proximal bones (scapulae, coracoides, humeri, femora, and tibiotarsi) by the sum of the proximal and distal bones (ulnae, radii, carpometacarpi, and tarsometatarsi). Additionally, the proximal and distal fragment ratio was estimated for long bones from size 4, as the number of remains was large enough to compute it. This ratio is obtained by dividing the total proximal parts (whole bones and proximal ends) by the sum of proximal and distal parts (whole bones and distal ends) [30]. These ratios are expressed as a percentage and allowed us to assess possible biases in anatomical representation. Bone fractures were classified by green, dry, and modern fractures. Green fractures are usually distinguished by the presence of oblique angles and smooth edges, while dry and modern fractures usually have rough and irregular edges. In addition, modern fractures can be identified because the edges do not present other post-depositional modifications at the fracture points, and the fractures usually preserve the internal colouration of the bone [42,103].

All layer-VIII bird bone surfaces were analysed using an Euromex stereomicroscope (Nexius Zoom NZ 1902-P) with magnification up to 45×. Bones were observed to search for any kind of modification related to the different taphonomic agents involved in their accumulation. Mechanical modifications produced by mammalian carnivores or raptors (tooth marks/beak and claw marks) were observed in the form of pits and punctures [64,104], and their location (proximal/distal end, shaft) and distribution (isolated, concentrated, unilateral, bilateral) were considered. Chemical alterations produced by the ingestion of the bones were documented, distinguishing among the five degrees of corrosion stated by Andrews [105]: 0—no corrosion; 1—light; 2—moderate; 3—strong; and 4—extreme. The distribution of damage along the bone was also considered (proximal/distal end or fracture edge). On the other hand, cut marks have been documented as anthropic modifications on bones [106,107]. The distribution (isolated, concentrated), orientation (oblique, longitudinal, transversal), morphology (straight, curved), and dimensions were registered. In addition, the degrees of colouration were documented for burned bones from 0 (no burned, no specific colouration) to 5 (calcined, white) [65]. A small selection of remains was borrowed from the MNP to perform further analyses using an environmental scanning electron microscope (ESEM) Zeiss EVO operated in a low vacuum and with magnification up to 100×.

### 3. Results

#### 3.1. Spectrum and Population Structure

More than two thousand specimens, organised among eleven different layers, compose the bird assemblage of Grotte Vaufrey (Table A1). Layer VIII is the most representative of

the number of remains, with 1181 bones (55.5% of the total assemblage). The assemblage is composed of at least fifteen bird species, where corvids are the most abundant (Table 1). The Corvidae family is represented by at least two different species (*Corvus corone/fragilegus* and *Pyrrhocorax graculus*), which together represent 59.4% of the total MNI of the assemblage (MNI = 60). Most of the corvid remains were attributed to Alpine chough (*P. graculus*). Other elements could not be assigned to a specific corvid species because they belong to young individuals or because distinctive characters are absent on the bones. Thus, firstly, the birds were classified separately as “medium-sized Corvidae.” However, some of these remains complement the absences perceived for the Alpine chough group and have a similar size. Therefore, they could belong to the same group. For this reason, we assumed that part of the non-assigned corvid remains were choughs, and they were finally included within the same category. To avoid further confusion in this field, all corvid remains that have the same size and morphology as the Alpine chough (this species included) were classified as “medium-sized Corvidae.”

The medium-sized Corvidae group comprised 57.4% of the total MNI ( $n = 58$ ), followed by other medium and small Passeriformes (8.9% and 6.9% of the total individuals, respectively). Seven individuals are partridges (*Perdix* sp.) that could be assigned to the species *P. perdix* or *P. palaeoperdix*. Six more individuals were classified as pigeons of the species *Columba livia/oenas* (6% of the MNI). The remaining species are only represented by one or two MNI. One medium-sized Charadriiformes was included in the individuals counted, as it could not be included in any other species (it is larger than the snipe—*Gallinago* sp.—identified in the same layer). The grouse family was documented by three identified elements. One of them corresponded to the rock ptarmigan (*Lagopus muta*), while the others were included in the *Lagopus* sp. group because non-distinctive criteria were detected. Nevertheless, *Lagopus* sp. remains were counted as another different individual, as their size does not fit with the *L. muta*, and they would belong to another *Lagopus* individual.

If only the size of the specimens is considered, the size 4 category is the most important in MNI, representing nearly three-quarters of the total assemblage (Table A2). Within this category, 17.8% are immature individuals, but nearly all belong to medium-sized corvids ( $n = 15$ ; 28.8% of medium-sized corvid remains). Five long bones from the medium-sized Corvidae group also contained medullary bone, indicating the presence of females who died during the laying period.

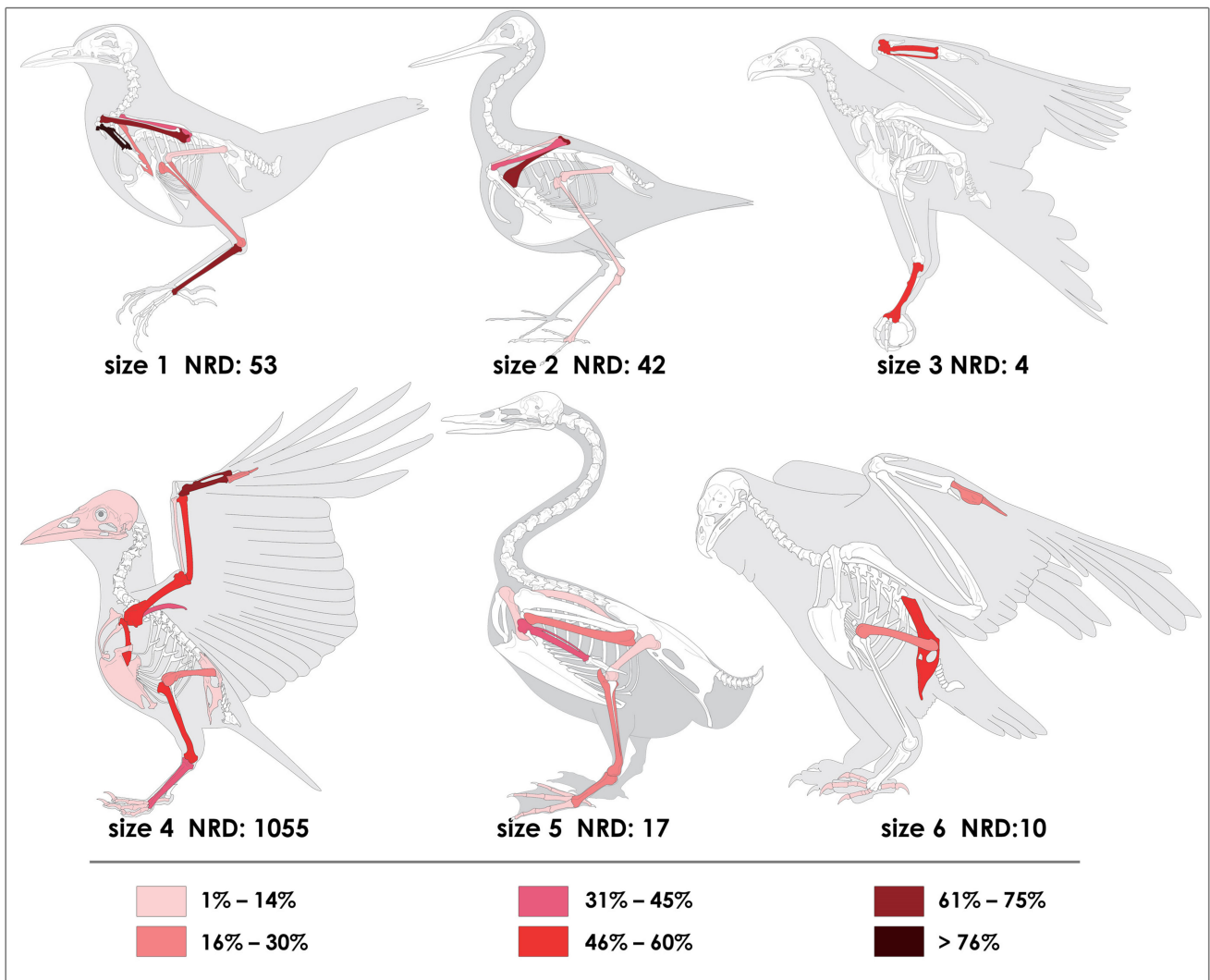


**Table 1.** NISP and MNE present at layer VIII of Grotte Vaufrey. MNE indicated inside the brackets. MNI indicated in the last column, specifying the number of immature (im) individuals. Bek: beak; man: mandible; ste: sternum; fur: furcula; cor: coracoid; ver: vertebra; sca: scapula; syn: synsacrum; hum: humerus; rad: radius; uln: ulna; cmc: carpometacarpus; whp: wing phalanx; fem: femur; tib: tibiotarsus; tmt: tarsometatarsus; pph: posterior phalanx (talon excluded); tal: talon. Lsz: large size; msz: medium size; ssz: small size.

NISP (MNE)	bek	man	ste	fur	cor	ver	sca	syn	hum	rad	uln	cmc	wph	fem	tib	tmt	pph	tal	Total	MNI
<i>Anas crecca</i>																1 (1)			1 (1)	1
<i>Tadorna tadorna</i>							1 (1)					1 (1)			2 (2)				4 (4)	2
Anatinae																2 (2)			2 (2)	-
<i>Perdix</i>					10 (10)		3 (3)		3 (3)	1 (1)	2 (2)	3 (3)			1 (1)	4 (4)			27 (27)	6 + 1 im = 7
<i>perdix/palaeoperdix</i>																1 (1)			1 (1)	1
<i>Lagopus muta</i>																			2 (2)	1
<i>Lagopus</i> sp.					1 (1)							1 (1)							2 (2)	1
Phasianidae					2 (2)						1 (1)	1 (1)			3 (3)				7 (7)	-
<i>Columba livia/oenas</i>			1 (1)		3 (3)		1 (1)		5 (5)	3 (3)	2 (2)	5 (5)	2 (2)		1 (1)	1 (1)			24 (24)	4 + 2 im = 6
<i>Gallinago</i> sp.					1 (1)														1 (1)	1
Charadriiformes msz					1 (1)				2 (2)										3 (3)	1
Charadriiformes ssz									1 (1)			1 (1)							2 (2)	-
<i>Aquila chrysaetos</i>																	2 (1)		1 (1)	1
<i>Buteo</i> sp.																	1 (1)		1 (1)	1
Accipitridae													1 (1)				1 (1)	2 (2)	4 (4)	-
Accipitridae/Strigidae								1 (1)									1 (1)		2 (2)	-
<i>Falco tinnunculus</i>												1 (1)				2 (2)			3 (3)	2
<i>Bubo bubo</i>																	2 (2)	1 (1)	3 (3)	1
Strigidae												1 (1)							1 (1)	-
<i>Corvus corone/frugilegus</i>											3 (3)	2 (2)		1 (1)					6 (6)	2
Corvidae msz					74 (65)		45 (42)		106 (51)	18 (12)	132 (70)	135 (96)	37 (37)	52 (34)	95 (63)	71 (43)			765 (513)	43 + 15 im = 58
Passeriformes msz					2 (2)				21 (12)	1 (1)	8 (8)	2 (2)		1 (1)	1 (1)	3 (3)			39 (30)	9
Passeriformes ssz					4 (4)				6 (5)		14 (10)	12 (12)		3 (2)	4 (3)	10 (9)			53 (45)	7
Aves lsz													1 (1)			3 (3)			4 (4)	-
Aves msz	2 (2)	2 (2)	3 (3)	4 (3)	4 (3)	9 (9)		6 (6)	5 (2)	1 (1)	4 (4)	1 (1)	2 (2)	1 (1)	13 (8)	6 (3)	134 (132)	17 (17)	214 (199)	-
Total	2 (2)	2 (2)	4 (4)	4 (3)	107 (93)	9 (9)	50 (47)	7 (7)	151 (81)	24 (18)	167 (100)	167 (127)	42 (42)	59 (40)	120 (82)	105 (72)	141 (138)	20 (20)	1181 (886)	101

### 3.2. Anatomical Representation and Completeness of the Assemblage

In general, long bones are the most rendered. Ulnae and carpometacarpi are the best represented in categories from size 1 to size 5, presenting remarkable values in size 1 (%RA 71.4 and 85.7, respectively) and size 4 (58.1% and 66.9%, respectively). Tarsometatarsi are well documented in size 1 (66.2%), while in size 4, ulnae and carpometacarpi are followed by humeri (49.3%), tibiotarsi (48.6%), and coracoides (48%). Tarsometatarsi are also well represented in this latter category, but with values under 38% (Figure 2). In other categories (sizes 2, 3, 5, and 6), the values of relative abundance are low. However, it should be taken into account that these groups have few specimens, which makes the percentages difficult to interpret. Considering the wing-to-leg ratio, wing elements dominate, and the values calculated for the main categories (size 1: 65.3%; size 2: 86.8%; size 4: 62%; Corvidae msz: 61.1%) differed significantly from the expected value, based on the MNI, except for size 1 (Table A3). As for the proximal to distal elements ratio, the calculated values (size 1: 32.1%; size 2: 64.3%; size 4: 52.4%; Corvidae msz: 51.1%) are not different from the expected ratio except for size 1, where distal remains are significantly more numerous than proximal ones.



**Figure 2.** Percentage of relative abundance of bird remains at Grotte Vaufray layer VIII classified by size. NRD: number of remains determined. See Materials and Methods for “size” definition.

The degree of fragmentation in layer VIII is high (79.9% of the remains), which means that only 237 of the total 1181 remains were complete. This trend is true for all size

categories present in the assemblage. Sizes 3 and 6 present higher completeness, but the low number of remains (four and ten, respectively) led us to consider this result with caution. The most complete elements are phalanges—including wing phalanges, posterior phalanges, and talons. In size 4, which is the most representative in terms of the number of remains, wing phalanges raised 63.4% of complete elements, while pedal phalanges and talons had values of 83.6% and 84.2% of completeness, respectively. The small dimensions, morphology, and robustness of these bones probably facilitate its preservation.

Nevertheless, the values of fragmentation obtained at Grotte Vaufrey layer VIII were difficult to assess, as most of the fractures observed on bones are modern fractures, caused during the process of excavation or later. This was particularly evident when observing fragmentation on long bones; 81.5% of the total fracture edges revised present modern fractures, and they could not be analysed from a zooarchaeological point of view. Only 13.8% of the bone fractures were produced when the bone was still fresh. The low proportion of ancient fractures hinders the calculation of significant fracture indexes.

The calculation of proximal ends with respect to the distal ends of long bones show that, in general terms, the proximal and distal ends are both well preserved. Only in the case of tibiotarsi, there is a clear predominance of distal ends (27.6%). In some cases, there is a slight preponderance of proximal (e.g., omal coracoides, with values of 61.9%) or distal ends (e.g., radii—40%, and tarsometatarsi—41.6%).

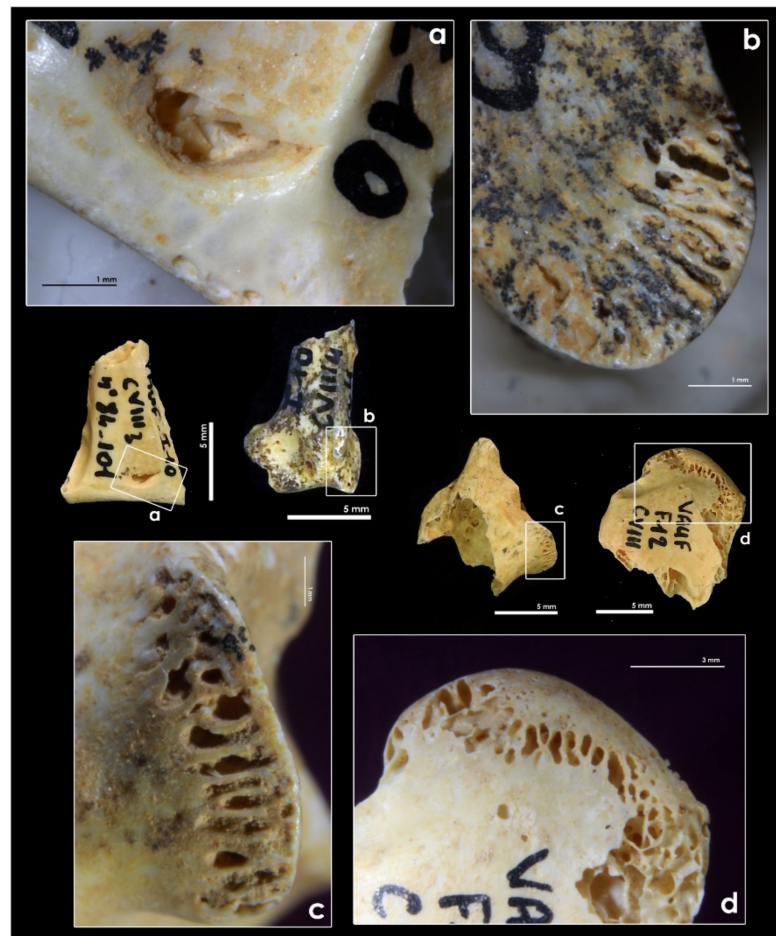
### 3.3. Bone Surface Modifications

#### 3.3.1. Traces of Non-Human Activity

Only 4.4% of the bones present evidence of alteration ( $n = 52$ ) resulting from non-human predators. Most of the damage is from digestion, and only five elements present mechanical modifications. The latter occur on a humerus of a medium Passeriformes, a carpometacarpus of a common kestrel (*Falco tinnunculus*), and three elements of medium-sized corvids (Table 2). Teeth/beak and claw mechanical damage (pits, punctures, or beak/claw marks) are isolated and unilateral (Figure 3). The only exception is a corvid tibiotarsus, which has five pits concentrated on its proximal end at the anterior face.

**Table 2.** Predatory-induced damage on bones at layer VIII of Grotte Vaufrey and its final percentage of representation.

		Pits/Punctures	Digestion	Cut Marks	Burning
Size 1	Passeriformes ssz		1		
Size 2	Passeriformes msz	1	2		
Size 3	<i>Falco tinnunculus</i>	1			
Size 4	<i>Perdix perdix/palaeoperdix</i>		5		
	Phasianidae		1		
	Accipitridae		1		
	Corvidae msz	3	21		3
	Aves msz		10		
Size 5	<i>Tadorna tadorna</i>		1		
	<i>Corvus corone/frugilegus</i>		1		
	Aves lsz		1		
Size 6	<i>Aquila chrysaetos</i>		1		
	Accipitridae		1	1	
	<i>Bubo bubo</i>		1		
Total		5 (0.4%)	47 (4%)	1 (0.1%)	3 (0.3%)



**Figure 3.** Non-human alterations observed at Grotte Vaufrey layer VIII: pit (a) and digestive damage (b–d). (a) Left sternal coracoid of *P. graculus*. (b) Left distal medium-sized *Corvidae* ulna. (c) Right proximal ulna of *C. corone/fragilegus*. (d) Left humerus of *P. graculus*.

Digestive damage is attested in all size categories, except for size 3, and the number of affected remains is low (4% of altered remains). Size 4 is the most representative, affecting different skeletal elements from different species: medium-sized corvids, phasianids, and an Accipitridae. Alterations were slight (grade 1) on most of the digested remains (85.1%). Only seven remains (14.9%) have moderate damage (grade 2), and no strong or extreme degrees were documented. Digestion mainly affects the proximal and distal ends of long bones (Table 3), while it is less extended at fracture edges—only detected on two coracoides and a radius.

It is important to remark that, although there are few digested remains, if we look at the species affected, the remains of corvids—which are nesting species in caves and shelters—have a low percentage of bones digested, representing 2.7% of the total remains of medium-sized corvids. On the other hand, if we focus on the non-habitual inhabitants of these areas (including Phasianidae, Anatidae, and Charadriiformes), we see that the percentage of digested elements is much higher, reaching values of 14%. A statistical Z-test ( $Z$ -value = 4.233) was applied between these two groups, providing a  $p$ -value < 0.001 and confirming that the difference is significant between them.

**Table 3.** Digestion grades observed at layer VIII of Grotte Vaufrey by skeletal elements. cor: coracoid; hum: humerus; rad: radius; uln: ulna; cmc: carpometacarpus; fem: femur; tib: tibiotarsus; tmt: tarsometatarsus; pph: posterior phalanx (talon excluded); tal: talon.

	Element	Grade 1	Grade 2	Total Digested
Size 1	cmc	1		1
Size 2	hum	2		2
Size 4	cor	3		3
	hum	2		2
	uln	5	2	7
	rad	2		2
	fem	4	2	6
	tib	5		5
	tmt	4		4
	pph	7	1	8
	tal	1		1
Size 5	tib	1		1
	tmt	1		1
	uln	1		1
Size 6	pph	1	2	3
Total		40	7	47

### 3.3.2. Traces of Human Activity

Anthropogenic activity was documented on four avian remains (0.3% of the assemblage). Three posterior elements of medium-sized corvids present burning damage. They correspond to a femur and two tibiotarsi, which have homogeneous brown and black colourations over their entire surface, a consequence of fire exposure.

Apart from these, a group of cut marks was identified on a shaft fragment of the femur of a large diurnal raptor (Figures 4 and 5). As it is a small fragment, it was not possible to make a taxonomical determination. However, the curvature of the bone and the positioning of the anterior intermuscular line—straight with respect to the longitudinal axis of the bone—indicate that it is a taxon belonging to the Accipitridae family. No other bird of similar size has these characteristics. This fragment, broken into two parts, probably during the excavation process, is 3.3 cm long and 1.6 cm wide. The fragment could not be joined together because of recent damage.

Two groups of three and five incisions can be observed on the largest portion of the fragment. The first group is composed of deep parallel striae and seems to be the result of the same action. Next to them, another group of five incisions is present. The deepest incision in this group slightly overlapped with one of the previous incisions described and could be interpreted as an extension of the previous mark. However, this group of striations was more oblique than the first group and possibly indicates another gesture.

The second and smallest portion of the fragment also has two short and parallel cut marks on its surface. They are deep and oblique. This notwithstanding, the fragment was marked after the excavation with its reference number. Even if the reference is removed, the marks are more difficult to observe.

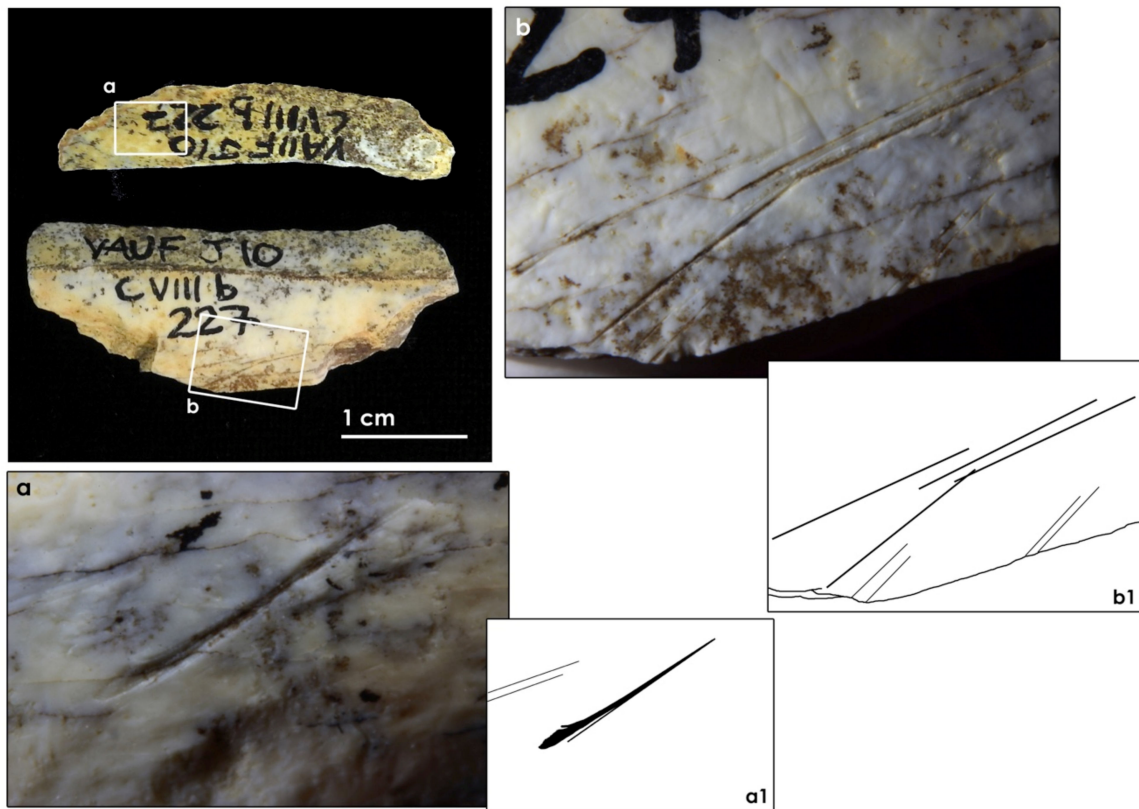


Figure 4. Photo of the large raptor femur shaft with the location (a,b) and the scheme (a1,b1) of the cut marks.

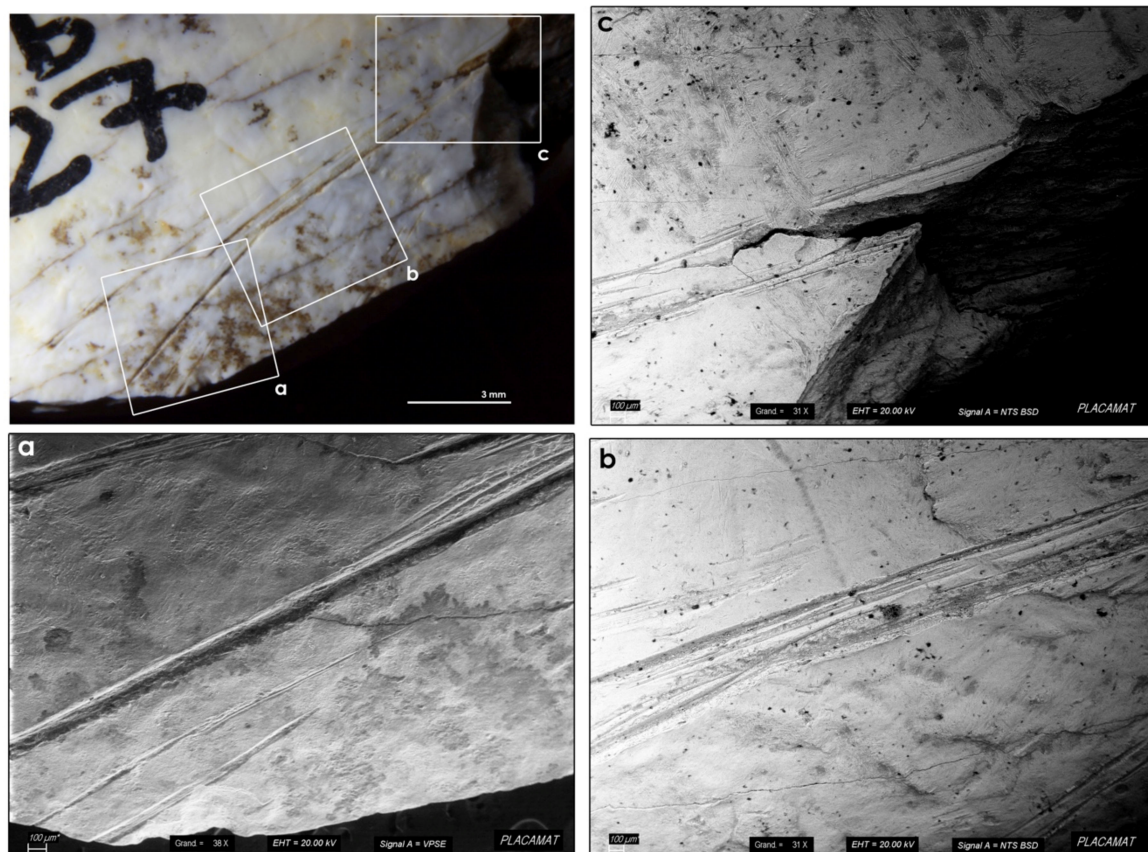


Figure 5. Detail of the cut marks observed on the large raptor femur (a–c).

#### 4. Discussion

In archaeological sites, many inputs can be involved in the accumulation of bone remains. Determining their origin is sometimes an arduous task, but it allows us to understand the dynamics of occupation, as well as the functionality of these places [104,108]. Similarly, the presence of some agents at a site does not necessarily imply that they were the accumulators of the assemblage as a whole, and many factors must be taken into account when assessing the possible causes of accumulation. The bird bone assemblage recovered from Grotte Vaufrey layer VIII provides new data on a complex taphonomic story at the site. This accumulation has a mixed origin in which the natural dynamics of accumulation themselves play a prominent role.

First, the results of the present study show that medium-sized corvids are the predominant category in Vaufrey's assemblage, where the Alpine chough is the only identified species. In the preliminary study carried out on Alpine chough remains at the site [42,95], it was determined that the origin of their accumulation was due to the natural death and deposition of these birds on the site's soil. These inferences were established by the significant presence of immature individuals, the anatomical representation of the assemblage, and the absence of predator marks on the remains. Our results corroborate previously established hypotheses for corvids while introducing some nuances.

According to several studies, the mortality rate of chicks during the breeding season is high among Alpine choughs [109,110]. Thus, as corvids are frequent inhabitants of caves and shelters, it is not surprising that some of them die in these spaces, including adult individuals but also a high percentage of juveniles. The existence of some corvid remains with medullary bone indicates that some females died at the site during the laying period [54,100], which supports the hypothesis that the cavity was used as a nesting site for this taxa.

It is theoretically expected that remains generated by natural deaths should be found in anatomical connection or associated together. At Vaufrey, there are no data from Rigaud's excavation about the spatial distribution of the bird remains, probably because most of the elements were recovered during the sieving process [86]. Thus, if there were any anatomical associations, they have not been documented. Nevertheless, no important biases in the anatomical representation of the assemblage, except those that can be explained by small size (phalanx, carpals) and weakness (sternum, skull, pelvis), suggest other possible agents intervening in the assemblage. The wing-to-leg ratio indicates a predominance of wing elements among Corvidae. This value supports Ericson's hypothesis [55], arguing that an equal amount or predominance of wing bones is often associated with natural accumulations. Moreover, the proximal-to-distal ratio is close to the expected value [30].

Although there is a percentage of corvid bones with possible tooth/beak and claw marks (0.4%) and digestive alterations (2.7%), it is marginal. If the whole accumulation had been generated by a mammalian carnivore or a raptor, we would expect a higher percentage of remains with mechanical modifications (in the case of non-ingested remains) or a higher proportion of digestions (for the ingested ones) [20–44]. In general terms, it is stated that nocturnal birds of prey tend to ingest their prey. As a consequence of this process, an important number of remains present digestive corrosion in light or moderate degrees. They could also have mechanical modifications in percentages from 0.1% to 7.7%, depending on the prey [20–22,39–42]. In the case of diurnal birds of prey, if the prey is ingested, digestive damage is intense or extreme to most of the bones. Mechanical modifications are not frequent and when present they are under 1.2% [22,25,35,36,42]. On the contrary, on non-ingested diurnal raptor waste, digestive damage is absent, while mechanical modifications are frequent, in percentages that can reach up to 35.1%, depending on the species [23,25,26,28,33,35,36,42,43]. Concerning mammalian carnivores, studies have mainly focused on non-ingested remains, where mechanical modifications usually raise values of 48%. The mastication process is intense on long bones, with an abundance of multiple and bilateral pits and punctures. Crenulated edges are common, mainly affecting the bone extremities and causing the loss of part of the bone in these areas.

Ingested remains produced by mammalian carnivores are characterized by intense bone corrosion [31,34,38,42,44,47].

We also observed that corvid remains are less affected by non-human predator marks than other species that do not inhabit the karst (including related size class species such as the partridges). This result supports the hypothesis that both groups have different taphonomic stories.

Based on the above, all the arguments mainly point to an accumulation of natural origin, to which an unknown predator might have contributed either by bringing a corvid carcass or by scavenging some of the remains already deposited in the cavity [45,46]. The same explanation could be applied to other possible cave-dwelling bird species present in the assemblage, such as small Passeriformes or pigeons [111,112]. Nevertheless, none of these remains show evidence of predation, which supports this argument.

Second, apart from corvids, other taxa not inhabiting caves and shelters also compose the avifaunal assemblage at Vaufrey layer VIII. These species, such as phasianids, anatids, or Charadriiformes, usually occupy open spaces in grassy and scrubby areas (phasianids) or spaces close to aquatic resources (anatids and Charadriiformes) [113,114]. Therefore, the fact that these taxa are found at Vaufrey indicates that they were introduced into the cavity by an external agent. In this group of prey, mechanical modifications to the remains were not observed. However, the proportion of digested bones is higher than that documented for corvids, and all the corruptions are slight. The small number of damaged remains prevents us from identifying a potential accumulator, but the absence of anthropogenic marks on bones and the digestive damage observed point to a raptor or a small mammalian carnivore.

During the Upper Palaeolithic and even the Late Middle Palaeolithic period, certain medium-sized taxa, such as phasianids and anatids, were recurrent human prey [75,115–121]. However, Vaufrey layer VIII is a clear example that this is not always the case. Our results differ from those obtained at other sites of similar chronologies and thus confirm that the use of birds in ancient chronologies is not systematised. Many factors can influence their exploitation. In fact, the recurrent use of medium-sized birds for this period has only been confirmed in the case of Bolomor Cave [84].

Actually, other birds that are not typically consumed by humans have direct or indirect anthropogenic modifications at Vaufrey layer VIII. A few corvid bones present colourations related to bone exposure to fire. Despite being the most abundant taxon at the layer, there are no other finds with evidence of anthropic activity among them. This suggests that the presence of these burned bones could be accidental, which means it is not linked to direct human activity on the bones themselves. Although no combustion structures have been recognised in layer VIII, Binford pointed in his zooarchaeological analysis to the presence of some burned macrofauna bones as an indicator of the use of fire in the cavity [86]. Therefore, the occasional existence of hearths in the cave cannot be discarded. It would be possible that some bird bones already deposited on the soil of the site had contact with the hearths, thus producing thermoalterations on some remains [65,122,123].

The raptor cut-marked bone recovered at Vaufrey is the only bone with direct evidence of human activity. The fact that this is the bone of a large bird of prey is of remarkable importance, as in Eurasia, there are a few birds of prey found in the Middle Palaeolithic with clear evidence of human processing. The peculiarity of this finding has two noteworthy aspects. The first is the association of the remains with butchery activities linked to meat removal. The second is related to the age of the find itself. Although the use of diurnal raptors during the Middle Palaeolithic period is a known phenomenon, much of the existing evidence is limited to the presence of striae on wing bones or phalanges/talons [3–7], which have little or no meat content. This has been interpreted as the use of large raptors to obtain non-edible products, such as feathers or claws. However, the cut marks observed at Vaufrey are on a femur, a bone from the fleshy area of the leg. Furthermore, the location of the cut marks, on the shaft, suggests activities related to meat procurement.



Defleshing activities potentially linked to obtaining food on raptor bones are rare and restricted to MIS 3 [5,74,76,124,125], with the exception of Cova Negra (Table 4). In this site, a scapula of lesser kestrel (*Falco naumanni*) has striae on its shaft [76]. At Axlör, a golden eagle (*Aquila chrysaetos*) femur and tibiotarsus have striae in the proximal and distal areas, respectively, which have been attributed to the procurement of meat [74]. At Les Fieux, a golden eagle femur is cut-marked in the proximal and articular areas of the bone [124,125]. Apart from these cases, a kestrel distal humerus also presents longitudinal striae in Le Noisetier [5], but it is difficult to interpret whether they are associated with meat or feather procurement [126]. At unit IV of Gorham's Cave (Gibraltar), a femur of *Gyps* with marks on its proximal end and a tibiotarsus of a black kite (*Milvus migrans*) with cut marks on the shaft were probably used for food. However, some other wing bones of golden eagle and red kite (*Milvus milvus*) in the site bearing cut marks have been interpreted as the possible procurement of feathers [4]. Thus, the Vaufrey femur could be one of the oldest raptor remains associated with the procurement of edible products to date.

**Table 4.** Sites with evidence of possible raptor use for food. mid (middle), prox (proximal), dist (distal), ant (anterior), post (posterior), lat (lateral), art (articular). hum: humerus; sca: scapula; fem: femur; tib: tibiotarsus. FR: France; ES: Spain; GIB: Gibraltar (United Kingdom).

Site	Layer/Unit	Chronology	Taxon	Element	Striae Location	Reference
Vaufrey, FR	VIII	MIS 7	Accipitridae	fem	mid shaft	Present study
Cova Negra, ES	IIIb	MIS 5-3	<i>Falco naumanni</i>	sca	mid shaft	[76]
Axlör, ES	IV	MIS 3	<i>Aquila chrysaetos</i>	fem	prox end (post and art)	[74]
	V	MIS 3	<i>Aquila chrysaetos</i>	tib	dist end (ant)	
Les Fieux, FR	K	MIS 3	<i>Aquila chrysaetos</i>	fem	prox end (post, lat and art)	[125]
Le Noisetier, FR	-	MIS 3	<i>Falco</i> sp.	hum	dist end (ant)	[5]
Gorham's, GIB	IV	MIS 3	<i>Gyps melitensis/fulvus</i>	fem	mid shaft (caudal)	[4]
			<i>Milvus migrans</i>	tib	prox shaft (lat)	

In this sense, we can ask what could have driven humans to exploit this type of prey. The find did not seem to have occurred during a period of food shortage, as there are other much larger prey at the site—mainly ungulates—with evidence of anthropogenic activity [93]. Likewise, as attested by the numerous remains of corvids and other birds found at the site, other avian resources were available and of potential interest. Taking into account that animals such as corvids and pigeons nest in cave environments, they would have been easily captured, especially during egg-laying and the breeding of chicks, when adults stay in the nest [127,128]. However, none of these taxa appeared to interest humans in Vaufrey.

Large raptors are attractive animals for humans, impressive, and often associated with symbolism and power [129], which could lead to their capture. Regular or occasional scavenging birds—including large Accipitriformes—when feeding, gorge themselves to the point that they are unable to fly after the meal. Humans could have taken advantage of this behavior to capture these birds of prey without too much difficulty [130]. Although this scenario could have occurred at Vaufrey, we have only one undetermined Accipitridae element bearing cut marks, which limits the interpretation scope.

Besides the femur fragment identified, several posterior phalanges of Accipitriformes were identified at the site, some of which show light or moderate digestion. No particular human interest in these anatomical elements is known at Vaufrey, unlike those documented in several more recent Middle Palaeolithic assemblages [5–9,124]. The data obtained demonstrate the necessity of accurate taphonomic analysis and contribute to a better knowledge of past human relationships with birds.

## 5. Conclusions

The bird assemblage from layer VIII at Vaufrey is a clear example of complex taphonomic story in which there are natural contributions mixed with those of other agents. Corvids are the most represented taxa in the assemblage, and they seem to be mainly deposited in the site naturally, possibly with other species used to inhabit karstic or rocky environments. Predator intervention on these remains is almost non-existent or could be the result of scavenging.

Contrary to corvids, other bird species that are not cave-dwelling inhabitants (e.g., partridges) seem to have been brought to the site by external agents, such as small mammalian carnivores or birds of prey. However, the small number of remains recovered does not allow accurate identification of the predator.

It is noteworthy that despite the scarce presence of anthropic activity on the remains, the raptor bone with cut marks recovered in the cavity is one of the oldest recorded in Europe so far and is not directly associated with possible aesthetic or symbolic purposes. This case in itself demonstrates that the populations inhabiting Europe during MIS 7 were capable of exploiting a wide variety of animal resources. Nevertheless, it also indicates that the use of birds in ancient chronologies is not systematic, and other factors beyond resource availability need to be considered.

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## Appendix A

**Table A1.** Synthetic table with the NISP, MNE, and MNI for each archaeological layer of Grotte Vaufrey. NISP (MNE); \* = presence of immatures; # = presence of females (medullary bone). Lsz: large size; msz: medium size; ssz: small size. NRD: number of remains determined. The classification by size has been included considering six categories according to bird's weight (see Section 2). Note that the MNI is very low in all the layers, with the exception of layer VIII.

Layers	Size Category	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Total
<b>MNI</b>		15	21	11	38	5	13	16	101	10	8	6	159
<i>Anas crecca</i>	4	-	-	-	-	-	-	-	1 (1)	-	-	-	1 (1)
<i>Tadorna tadorna</i>	5	-	-	-	-	-	-	-	4 (4)	-	-	-	4 (4)
Anatinae	4, 5	1 (1) #	-	-	-	-	1 (1)	1 (1) *	2 (2) *	1 (1)	1 (1)	-	7 (7)
Anseriformes	5	-	-	-	-	-	-	-	-	-	1 (1)	-	1 (1)
<i>Coturnix coturnix</i>	2	-	1 (1)	-	-	-	-	-	-	-	-	-	1 (1)
<i>Perdix perdix/palaeoperdix</i>	4	1 (1)	2 (2)	-	6 (6)	1 (1)	1 (1)	-	32 (27) *	1 (1)	2 (2)	-	46 (41)
<i>Lagopus muta</i>	4	-	-	-	-	-	-	-	1 (1)	-	-	-	1 (1)
<i>Lagopus sp.</i>	5	-	-	-	-	-	-	-	2 (2)	-	-	-	2 (2)
Phasianidae	4	2 (2) *	2 (2)	1 (1)	5 (5)	-	3 (3)	2 (2)	8 (7) *	-	-	2 (2)	25 (24)
<i>Columba livia/oenas</i>	4	-	4 (4)	-	34 (29) *	-	3 (3)	5 (5)	28 (24) *	6 (6)	6 (6)	2 (2)	88 (79)
<i>Gallinago sp.</i>	2	-	-	-	-	-	-	-	1 (1)	-	-	-	1 (1)
Charadriiformes msz	4	-	-	-	3 (3)	-	-	-	3 (3)	1 (1)	-	-	7 (7)
Charadriiformes ssz	2	-	-	-	-	-	1 (1)	-	2 (2)	-	-	-	3 (3)
<i>Aquila chrysaetos</i>	6	-	-	-	-	-	-	-	2 (1)	-	-	-	2 (1)
<i>Buteo sp.</i>	5	-	-	-	-	-	-	-	1 (1)	-	-	-	1 (1)
Accipitridae	4, 6	-	6 (6)	-	4 (4)	-	-	4 (4)	4 (4)	1 (1)	-	1 (1)	20 (20)
Accipitridae/Strigidae	6	-	-	-	-	-	-	-	2 (2)	-	-	-	2 (2)
<i>Falco tinnunculus</i>	3	-	-	-	-	-	-	-	3 (3)	-	-	-	3 (3)
<i>Bubo bubo</i>	6	-	-	-	-	-	-	-	3 (3)	-	-	-	3 (3)
Strigidae	3	-	-	-	-	-	-	-	1 (1)	-	-	-	1 (1)
<i>Corvus corone/frugilegus</i>	5	1 (1)	-	-	-	-	-	-	6 (6)	-	-	-	7 (7)
<i>Corvus monedula</i>	4	-	1 (1)	-	1 (1)	-	-	-	-	-	-	-	2 (2)
<i>Pyrrhonorax pyrrhonorax</i>	4	-	-	-	1 (1)	-	-	-	-	1 (1)	-	-	2 (2)
<i>Pyrrhonorax graculus</i>	4	13 (9) *	97 (69) *	33 (29) *	218 (167) *#	20 (17)	78 (58) *	99 (70) *#	-	25 (20) *#	10 (9)	-	946 (738)
Corvidae msz	4	-	3 (3) *	1 (1)	5 (5) *	1 (1)	-	-	765 (513) *#	3 (3) *	-	1 (1)	426 (273)
Passeriformes msz	2	4 (4)	10 (10)	1 (1)	15 (15) *	1 (1)	4 (4)	5 (5)	39 (30)	3 (3)	1 (1)	1 (1)	84 (75)
Passeriformes ssz	1	34 (33)	7 (7)	1 (1)	22 (21)	3 (3)	3 (3)	11 (11)	53 (45)	-	1 (1)	4 (4)	139 (129)
Aves lsz	5, 6	-	1 (1)	-	1 (1)	-	-	-	4 (4)	-	2 (2)	-	8 (8)
Aves msz	4	1 (1)	10 (10) *	-	28 (28)	5 (5)	16 (16)	13 (13)	214 (199)	3 (3)	3 (3)	-	293 (178)
Aves ssz	1	-	-	-	1 (1)	-	-	-	-	-	-	-	1 (1)
NISP (NRD) Total		57 (52)	144 (116)	37 (33)	344 (287)	31 (28)	110 (90)	140 (111)	1181 (886)	45 (40)	27 (26)	11 (11)	2127 (1647)

**Table A2.** Representation of Grotte Vaufrey layer VIII remains by size. The classification of remains by size has been evaluated considering the bird's weight (see Section 2). NRD: number of remains determined. Bek: beak; man: mandible; ste: sternum; fur: furcula; cor: coracoid; ver: vertebra; sca: scapula; syn: synsacrum; hum: humerus; rad: radius; uln: ulna; cmc: carpometacarpus; whp: wing phalanx; fem: femur; tib: tibiotarsus; tmt: tarsometatarsus; pph: posterior phalanx (talon excluded); tal: talon.

NRD	Size 1 (MNI = 7)	Size 2 (MNI = 10)	Size 3 (MNI = 2)	Size 4 (MNI = 74)	Size 5 (MNI = 6)	Size 6 (MNI = 2)	Total (MNI = 101)	% Size 1	% Size 2	% Size 3	% Size 4	% Size 5	% Size 6
bek				2			2	0.0	0.0	0.0	0.2	0.0	0.0
man				2			2	0.0	0.0	0.0	0.2	0.0	0.0
ste				4			4	0.0	0.0	0.0	0.4	0.0	0.0
fur				4			4	0.0	0.0	0.0	0.4	0.0	0.0
cor	4	3		99	1		107	7.5	7.1	0.0	9.4	5.9	0.0
ver				9			9	0.0	0.0	0.0	0.9	0.0	0.0
sca				49	1		50	0.0	0.0	0.0	4.6	5.9	0.0
syn				6		1	7	0.0	0.0	0.0	0.6	0.0	10.0
hum	6	22		123			151	11.3	52.4	0.0	11.7	0.0	0.0
rad		1		23			24	0.0	2.4	0.0	2.2	0.0	0.0
uln	14	8		142	3		167	26.4	19.0	0.0	13.5	17.6	0.0
cmc	12	3	2	146	4		167	22.6	7.1	50.0	13.8	23.5	0.0
wph				41		1	42	0.0	0.0	0.0	3.9	0.0	10.0
fem	3	1		53	1	1	59	5.7	2.4	0.0	5.0	5.9	10.0
tib	4	1		113	2		120	7.5	2.4	0.0	10.7	11.8	0.0
tmt	10	3	2	86	4		105	18.9	7.1	50.0	8.2	23.5	0.0
pph				134	1	6	141	0.0	0.0	0.0	12.7	5.9	60.0
tal				19		1	20	0.0	0.0	0.0	1.8	0.0	10.0
Total	53	42	4	1055	17	10	1181	4.5	3.6	0.3	89.3	1.4	0.8

**Table A3.** Wing-to-leg (WL) and proximal-to-distal (PD) bone ratios, considering the total observed and expected remains. The classification by size was evaluated considering the bird's weight (see Section 2). The ratios were only calculated for those categories for which the number of remains was large enough to obtain reliable results. A Z-test was calculated to see if the differences between the observed and expected elements are significant. \* Significant. Msz: medium size.

	Observed			Expected (Based on the MNI)			Z-Test	p-Value
	Wing	Leg	Ratio WL	Wing	Leg	Ratio WL		
Size 1	32	17	65.30	42	42	50	1.713905298	0.08 < p < 0.09
Size 2	33	5	86.8	60	60	50	4.022140631	p < 0.01 *
Size 4	411	252	61.9	444	444	50	4.69715692	p < 0.01 *
Corvidae msz	373	218	63.1	348	348	50	4.723087674	p < 0.01 *
	Proximal	Distal	Ratio PD	Prox	Distal	Ratio PD	Z-Test	p-Value
Size 1	17	36	32.1	70	56	55.55	-2.869431268	p < 0.01 *
Size 2	27	15	64.3	100	80	55.55	1.02966479	0.30 < p < 0.31
Size 4	437	397	52.4	740	592	55.55	-1.435548179	0.15 < p < 0.16
Corvidae msz	372	356	51.1	580	464	55.55	-1.851106305	0.06 < p < 0.07

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