What is the taphonomic agent responsible for the avian accumulation? An approach from the Middle and early Late Pleistocene assemblages from Payre and Abri des Pêcheurs (Ardèche, France)

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A B S T R A C T

The acquisition of quick-flying small prey has been a widely discussed topic over the last decades, especially since the emergence of archaeological bird collections more ancient than expected, with evidence of anthropogenic processing. Residue analyses carried out on stone tools at the Payre site in France (MIS 8–5) suggest human activity on birds; however, no direct analyses have been carried out on avian specimens from the site. Similarly, no detailed data from numerous bird bones have been obtained from a nearby site, Abri des Pêcheurs (MIS 5–3), which could also provide important information about subsistence strategies in the region. Bird bones from both sites were analyzed here within the framework of the taphonomic methodology and identified a wide variety of avian specimens, suggesting nocturnal raptors and small mammal carnivores as main accumulator agents. Despite the anthropogenic activity at Payre proposed from lithic residue and use-wear analyses, bird bones do not reveal any hominid intervention. Our attempt here is to explain this apparent contradiction and discuss possible hypotheses regarding the presence of avian specimens at both archaeological sites.

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1. Introduction

The study of bird bone remains and their implication in human behavior and subsistence strategies has often been tackled from a palaeoenvironmental perspective, largely because it is generally accepted that birds did not play an important role in the pre-Upper Paleolithic human diet. It has been mainly discussed with respect to caves and shelters, where the presence of bird remains can be associated with mammalian carnivores and/or raptors that commonly occupied these places. In general, anthropogenic activities on small prey remains are usually under-represented in the archaeological record because these could be consumed without using tools (Lyman, 1994; Laroulandie, 2001; Steadman et al., 2002). For this reason, other characteristics are needed to distinguish accumulations produced by hominids, as previously attempted (Bochenski et al., 1998, 1999; Laroulandie, 2001, 2002, 2005; Laroulandie et al., 2008); these include human tooth marks, patterns of breakage, and/or burning. Other valid criteria to identify the origin of avian remains can be the skeletal representation, as Mourer-Chauviré (1979, 1983), Vilette (1983), Bramwell et al. (1987), and Díez Fernández-Lomana et al. (1995) pointed out. These authors argue that the abundance of some skeletal parts,
such as coracoids, humeri, and femora, is related to human activity, while the predominance of tarsometatarsi and carpometacarpi is mainly associated with raptor accumulations. Even if these methods are relevant, they are subject to criticism and should be used with caution as additional proxies (e.g. Livingston, 1989; Laroulandie, 2010).

The presence of hominid processing marks on bird bones during the pre-Upper Paleolithic is still scarce, but cut marks have been documented in some localities, such as the Early Pleistocene sites of Sima del Elefante (Spain) (Huguet, 2007) and Dursunlu (Turkey) (Güleç et al., 1999) or those framed within the Middle Pleistocene such as Lazaret (France) (Lumley et al., 2004; Roger, 2004) and Bolomor Cave (Blasco and Fernández-Peris, 2009, 2012; Blasco et al., 2013). In later periods, avian processing can be found in Salzgitter-Lebenstedt in Germany (Gaudzinski-Windheuser and Niven, 2009), the French Mousterian sites of Pech de l’Azé I (Mourer-Chauviré, 1979; Soressi et al., 2008), Pech de l’Azé IV (Dibble et al., 2009), Mandrin Cave (Romanini et al., 2014), Combe-Grenal, and Les Fieux (Morin and Laroulandie, 2012), as well as at the Mousterian sites of Grotta di Fumane and Grotta del Rio Secco in Italy (Fiore et al., 2004; Peresani et al., 2011; Romanini et al., 2014), and Krapina in Croatia (Radovič et al., 2015). Some of these localities attests to the exploitation of non-edible avian products, such as talons of raptors, which seem to have been used as ornamental elements. In addition, new results from Gibraltar sites (Finlayson et al., 2012; Blasco et al., 2014) also indicate the presence of cut marks on avian remains during the Mousterian, confirming that bird processing for feathers and consumption is not as strange as previously thought. Even though solid evidence supports avian consumption, its systematic acquisition is still debated.

In past years, archaeological sites such as Payre (Ardèche, France, MIS 8–5) took an active part in this discussion through analysis of lithic residue and use-wear, which show a processing of small fast prey (rabbits and birds) earlier than 125 ka (Hardy and Moncel, 2011). No further analyses on small prey specimens from this site have been carried out since to support this hypothesis. The present work attempts to present new data about bird processing in the cave, based on a taphonomic approach. In addition, an assemblage as a reference within the region is obtained by including the Middle Paleolithic site of Abri des Pêcheurs (Ardèche, France, MIS 5–3) in this study. At Abri des Pêcheurs, human activity is evident on larger fauna (Moncel et al., 2010), but, as in the case of Payre, bird remains still have not been studied from a taphonomic perspective. New analyses at both sites could provide further knowledge about hominid subsistence and diet within the region. In that sense, three main objectives were set out: 1) to detect what taphonomical agents act on the avian specimens; 2) to demonstrate whether birds were consumed by hominids at Payre; and 3) to establish processing patterns if anthropogenic consumption of birds is evident.

2. Materials and methods

2.1. Payre

Payre is an archaeological site situated 25 km from Valence, on the right side of the Rhône River. It is part of an active karstic system located 60 m above the Payre River, at a confluence point with the Rhône Valley (Ardèche region, France). Its location results in a convergence of different environments, which makes it a strategic point for the exploitation of different ecosystems (Fig. 1). The sequence, which is 5 m thick and comprises eight archaeological levels, is in turn divided into sub-levels. It has been systematically excavated since 1990 to 2002 by a team led by M.-H. Moncel (Fig. 2).

The sediment characterization allows us to distinguish three different phases from the top to the bottom (Moncel et al., 2002):

a) Final phase (levels A and B), 5–60 cm thick, characterized by silty, pulverulent, and breached sediment at the base and fragmented at the walls of the remaining eastern tunnel.

b) Second phase (levels C and D), 50–80 cm thick, with dark-grey (C) and dark-red (D) sediments, very stony and with local breaches from autochthonous and allochthonous origin. The base of this phase presents many bioturbations. Human occupations are located in these levels, corresponding to temperate moments with high humidity and open landscapes, typical of end of MIS 6/beginning of MIS 5. They took place under shelter.

c) First and main phases of occupation into a cave (levels E to H). Level E (20 cm thick) has three sub-levels that present small...
Fig. 2. Stratigraphy of Payre (A) and Abri des Pècheurs (B). The one of Payre includes some paleoecological data and stands out different sediment slices (F1 to G5-6).
grey-white blocks, slightly altered and without matrix, probably
responding to a decay of the cave ceiling. Level F (1 m-thick)
is composed by grey sediments locally breached with, at least,
four different human occupation phases (Fa to Fd). They corre-
spond to a Mediterranean environment with semi-open land-
scapes, typical from MIS 6–5 or MIS 8/7. Level J (1 m thick), only
present in the north-west part of the site, is highly breached,
with an unreliable archaeological context. Level G (ca.1 m thick)
is formed by stony orange sediments, almost breached and with
two main phases of occupation (Ga and Gb). The climate of this
period was probably dry and cold, corresponding to the MIS 6 or
MIS 8/7. Level H (MIS 7) is formed by a flowstone formation,
which stretches up to the end of the sequence (level I), totally
breached and sterile.

The dating compiled by ESR, U-Th series, TL, and TIMS methods
provide a chronology for the end of MIS 8 and the beginning of MIS
7 for levels Gb to Fa that spreads up to the end of MIS 6 and the
beginning of MIS 5 for levels D and E (Moncel et al., 2002; Valladas
et al., in press). Lithic tools and faunal remains agree with the dating
obtained, establishing the sequence in the Early Middle Paleolithic.
Neanderthals seemed to have occupied the place during interglacial
periods, when more temperate conditions took place (Moncel,
2008; Rivals et al., 2009).

The lithic technology is characterized by flint from local or semi-
local outcrops and the main core technologies are discoid- and
orthogonal-type (Fernandes et al., 2008; Moncel et al., 2009; Baena
et al., in press). The faunal remains in the archaeological assem-
blage mainly consist of large herbivores (Cervus elaphus, Equus
caballus, and large bovids) that were hunted and carried to the cave
entirely or as parts (Moncel, 2008). Other large mammals, such as
rhinoceros and elephants, were apparently scavenged (Moncel
et al., 2002).

Human occupations alternated with carnivores (bear, hyena,
fox), but seem more intense at the lower levels, with the pres-
ence of macro-faunal remains with evidence of human modifi-
cations (bone breakage, cut marks, and burnt bones) as well as
abundant lithic tools and hearths in level Ga. Anthropogenic
activity is higher at level G, as a result of occupations that spread
throughout the year, or from short but repeated seasonal occu-
pations. Level F also has anthropogenic activity in the form of
records of short-term seasonal occupations, even if bears mainly
used the site during its formation (Moncel, 2008). In addition,
human remains were recovered from levels D, E, F, and G— all
belonging to infant or juvenile individuals (Moncel and Condemi,

Therefore, the macro-faunal remains indicate anthropogenic
activity; furthermore, a study carried out by Hardy and Moncel
(2011) on stone tools also suggests the processing of small mam-
mals, fish, and birds by hominids. For these reasons, bird remains
recovered from levels A, D, F, and G have been analyzed to
corroborate this hypothesis.

2.2. Abri des Pecheurs

The Abri des Pecheurs site is a ditch-cave of around 15–20 m²
located 30 km from Vallon Pont d’Arc (Chassezac Valley, Ardèche
region) — Fig. 1. It is composed of a 7 m sediment package formed
by vertical diacasis. Its excavation exposes different levels that
stretch from the Middle to the Upper Paleolithic, corresponding
to a total of four sectors (1–4, from the top to the bottom), with some
later occupation events at the top of the sequence (Sector 1)
(Fig. 2). From 1973 to 1988, it was excavated by G. Lhomme, but in
2005, the excavation was resumed to obtain a better understanding
of human occupations during the Middle Paleolithic (Moncel et al.,
2010). Its sediments consist of an alternation of limestone stony
levels, fine or coarse sands, and collapsed blocks (Debard, 1988).

The results from macro-faunal, microfaunal, and palynological
analyses distinguish two different phases:

1) A lower phase (Sector 4), with semi-open landscape typical of a
warm and humid Mediterranean climate, from the MIS 6
interstadial period and MIS 5.
2) An upper phase (Sectors 3 to 2), where the environment of the
site deteriorates to drier and colder periods; it is characterized
by steppe vegetation for the upper part of the Middle Paleolithic
sequence (MIS 4).

C14, ESR, and U–Th series methods date the site around 24.4
and 31 ka BP (Evin et al., 1985) and 120 ka (Masaoudi et al.,
1994; Valladas et al., 1999), from the end of MIS 5 to MIS 3 (Table 1).

Table 1
Radiocarbon, ESR and U/Th dates for the Abri des Pecheurs sequence (Evin et al., 1985; Masaoudi et al., 1994; Moncel et al., 2015).

<table>
<thead>
<tr>
<th>Sectors</th>
<th>14C sample</th>
<th>Level</th>
<th>Sample</th>
<th>Industries</th>
<th>Depth</th>
<th>14C (BP)</th>
<th>U–Th ka (LU)</th>
<th>ESR ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sector 2</td>
<td>Ly-2337</td>
<td>F9</td>
<td>bone</td>
<td>Aurignacian</td>
<td>210–230</td>
<td>26,760 ± 1000</td>
<td></td>
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<tr>
<td></td>
<td>Ly-2338</td>
<td>F11-12</td>
<td>bone</td>
<td></td>
<td>225–230</td>
<td>29,400 ± 900</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Ly-2339</td>
<td>F10-11</td>
<td>bone</td>
<td></td>
<td>230–240</td>
<td>23,880 ± 750</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sector 3</td>
<td>Ly-2341</td>
<td>F13</td>
<td>bone</td>
<td>Middle Paleolithic</td>
<td>240–250</td>
<td>28,440 ± 1280</td>
<td>49 ± 2</td>
<td>21 ± 1</td>
</tr>
<tr>
<td></td>
<td>PECH 1</td>
<td>F14 F15</td>
<td>bone</td>
<td></td>
<td>250</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH 2</td>
<td>F16</td>
<td>bone</td>
<td></td>
<td>260</td>
<td>&gt;31,000</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ly-2343</td>
<td>L1-2</td>
<td>bone</td>
<td></td>
<td>270–300</td>
<td>29,700 ± 900</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH 3</td>
<td>F20-21</td>
<td>bone</td>
<td></td>
<td>330</td>
<td>50 ± 3/–2</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>PECH 4</td>
<td>S-base</td>
<td>bone</td>
<td></td>
<td>395–420</td>
<td>24,940 ± 680</td>
<td>51 ± 2</td>
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</tr>
<tr>
<td>Sector 4</td>
<td>PECH CA1</td>
<td>S4</td>
<td>breccia</td>
<td>Middle Paleolithic</td>
<td>430</td>
<td>39 ± 3/–2</td>
<td>95 ± 14</td>
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<tr>
<td></td>
<td>PECH 5</td>
<td>bone</td>
<td></td>
<td></td>
<td>445</td>
<td>47 ± 2</td>
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<td></td>
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<tr>
<td></td>
<td>PECH 6</td>
<td>bone</td>
<td></td>
<td></td>
<td>445</td>
<td>56 ± 5/–4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH 7</td>
<td>bone</td>
<td></td>
<td></td>
<td>445</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH CA2</td>
<td>breccia</td>
<td></td>
<td></td>
<td>450</td>
<td>80 ± 5</td>
<td>118 ± 19</td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH 8</td>
<td>bone</td>
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<td></td>
<td>450</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PECH 9</td>
<td>bone</td>
<td></td>
<td></td>
<td>570</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The assemblage is defined by relatively few lithic tools, mainly made from local quartz collected at the foot of the cave along the river, which was normally used as a secondary raw material in the region. Flint is rare and principally represented by non-retouched flakes and a Levallois core introduced already knapped. It was collected from a 10–20 km perimeter area (Fernandes et al., 2010; Moncel, 2010).

On the other hand, faunal remains are present throughout the sequence, with the base levels presenting a higher density of complete elements. Carnivores represent a third of the total faunal remains, with bear (Ursus spelaeus) and wolf (Canis lupus) the best represented. Alpine ibex (Capra ibex) is the most important herbivore in the sequence, especially at the lower part, and represented C. ibex as castor (Moncel et al., 2008; Moncel, 2010). Other animals, such as castor (Castor fiber), fish, birds, and an abundant number of avian species are represented (Daujeard, 2008; Moncel et al., 2010).

Anthropogenic activity on the site has been attested by the faunal remains showing the presence of cut marks and bone breakage. Nevertheless, cut marks are scarce, and mainly on Alpine ibex (4%). On the contrary, wolf activity is higher (5.7%), suggesting that C. ibex died naturally in a trap, where it was consumed by hominins and wolves (Moncel et al., 2008, 2010). In addition, a 1 m² hearth has been registered at the upper part of the Middle Paleolithic sequence (Moncel, 2010).

Globally, Abri des Pêcheurs could be considered to have supported a succession of short-term human occupations (bivouac-type), where herbivore hunting was combined with carnivore activity. This is denoted by the low presence of anthropogenic activity in the site, the presence of local raw materials, as well as the importance of carnivores in the assemblage (Moncel et al., 2008, 2010; Moncel, 2010).

Bird specimens are present in the whole sequence (from Sector 1 to Sector 4). Sectors have been defined from the top of the sequence (sector 1) to the bottom (sector 4). Sectors 3 and 4 characterize the Middle Paleolithic levels. Although bird remains have not been analyzed taphonomically in detail, raptors have been suggested as possible accumulators within the site (Moncel, 2010).

2.3. Methods

The analysis of bird remains from Payre (seasons 1990–2002) and Abri des Pêcheurs (from the 2005 intervention) was carried out by applying a methodology based on Taphonomy (Binford, 1981; Brain, 1981; Lyman, 1994; Reitz and Wing, 1999). Bird remains have been recovered from the excavation fieldwork using a 3D location system. The smallest elements were recovered by water-screening the sediments on a superimposed mesh from 5 to 0.5 mm. In the case of Payre, a distinction of different sublevels was taken into account to present and analyze the data. Nevertheless, some remains of level F could not be classified in any subdivision, and for this reason they were grouped as “F.”

Most specimens from Abri des Pêcheurs were previously identified at a taxonomical level (Moncel et al., 2010). Nevertheless, species were grouped by families for the analyses, owing to the scarce number of individuals assigned to each species (in some cases only rendered by one individual). Bones with no specific categorization were classified by size: large (e.g., wood grouse), medium (e.g., partridge) and small (e.g., most of the Passeriformes). A distinction between immature and adult individuals has been established on the basis of epiphyses formation and by the degree of ossification of cortical tissues (Hargrave, 1970; Lefèvre and Pasquet, 1994). All complete and fragmented remains were quantified to calculate the Number of Identified Specimens (NISP), the Minimum Number of Elements (MNE), the Minimum Number of Individuals (MNI), and the Minimal Anatomical Units (MAU), which allowed estimation of the proportion of the recovered fragments to those expected to be found (Brain, 1981; Lyman, 1994).

The MNE was computed using the age profiles as well as the repeated anatomical portions of identified specimens (Schmidt, 1972). The total MNI is estimated considering the laterality. Some elements only represented in size categories were computed as possible individuals, because they could not correspond to any other species of the level. For example, one level contained a medium-sized bone and a small-sized one, so a minimum of two individuals must be computed in the final counting, although they do not have a taxonomical attribution. They are understood not to correspond to the same individual by the differences in their size. No other calculations have been taken into account to evaluate differential conservation since the large variability of bird specimens complicates the assessment of bone density on all taxa. For the general evaluation of each level, all species have been taken as a whole, since important distinctions among species have not been observed.

The ratio of wing to leg bones suggested by Ericson (1987) does not always work and it is criticized by some authors (Livingston, 1989; Laroulandie, 2010), but this was computed for the Abri des Pêcheurs accumulations as an additional approach (e.g., Serjeantson et al., 1993; Laroulandie, 2000, 2001; Bochenski, 2005). This ratio is the result of dividing the total number of wing remains (humerus, ulna, carpometacarpus) by the sum of wing and leg (femur, tibiotarsus, tarsometatarsus) remains, giving a percentage of representation (*100). In the same way, core/limb ratio was computed (Bramwell et al., 1987; Bochenski, 2005), dividing the total core elements (sternum, coracoid, pelvis, scapula) by the sum of core and limb elements (humerus, femur, radius, ulna, tibiotarsus, carpometacarpus, and tarsometatarsus), also expressed as a percentage. Proximal/distal ratio was included as another element to enrich the discussion (Bochenski and Nekrasov, 2001), this was calculated using the number of proximal remains (scapula, coracoid, humerus, femur, and tibiotarsus) divided by the sum of proximal and distal ones (ulna, radius, carpometacarpus, and tarsometatarsus). Nonetheless, the fact that these ratios may cause controversy if they are used independently should be taken into account. Accumulations produced by different predators may overlap with others due to equifinality processes, as stated by different authors (Louchart and Soave, 2002; Laroulandie, 2010). This emphasizes the importance of working with a combination of different variables.

In any case, neither of the ratios suggested above was used in the example of Payre. The results would not be statistically significant due to the low number of specimens in the site; therefore, only a general trend of representation was taken into consideration. Fragmentation has also been considered in our analyses. The completeness of the bones was inferred by classifying the fractures as dry fractures (produced after the bone lost all collagen, with transverse forms and straight rough edges) or green fractures (with generally smoothed edges and oblique angles) (Steadman et al., 2002; Laroulandie and Lefèvre, 2014).
Euromex with magnification up to 45 was used to detect surface modifications produced by both hominids and carnivores. Hominid damage considered includes cut marks (Shipman, 1981; Shipman and Rose, 1983), bone breakage (Steadman et al., 2002; Cochard et al., 2012; Sanchis, 2012), and burnt bones, classified on a scale of six coloration degrees (Stiner et al., 1995; Blasco and Fernandez Peris, 2009), from 0 (no-coloration) to 5 (white/char). Modifications including carnivore tooth-mark (pits, punctures and scores) and bird beak-marks were considered, as well as their distribution, orientation, and measurements. Notches, crenulated edges, and pitting were also observed as a result of a consumption process. Other chemical alterations produced by digestion processes were documented, differentiating five degrees of corrosion (Andrews, 1990): 0) no damage; 1) light; 2) moderate; 3) strong; 4) extreme.

Experimental and archaeological studies made on bird and other small game accumulations were taken into account as a reference to identify possible hominid (Laroulandie, 2000, 2001, 2004, 2005; Laroulandie et al., 2008; Blasco and Fernandez Peris, 2009; Blasco et al., 2014) and carnivore accumulations within the region. The previous studies of bird accumulations focused on birds of prey as the main accumulator agents: eagle owl (Bochenski et al., 1993; Bochenski and Tomek, 1997; Laroulandie, 2000, 2002), snowy owl (Baales, 1992; Bochenski, 1997), tawny owl (Bochenski et al., 1993; Bochenski and Tomek, 1997; Laroulandie, 2000, 2002), gyrfalcon (Bochenski et al., 1998; Bochenski and Tornberg, 2003), golden eagle (Bochenski et al., 1997, 1999, 2009); imperial eagle (Bochenski et al., 1997), and white-tailed eagle (Mlikovsky, 1996; Bochenski et al., 2009). Referring to mammalian carnivores, accurate studies on bird accumulations do not exist. This problem was overcome by using these modifications produced on leporids — which are widely studied — as a model of potential damage. These studies include fox (Hocket, 1999; Sanchis, 1999, 2000, 2012; Laroulandie, 2000; Mondini, 2000; Hocket and Haws, 2002; Cochard, 2004a, 2004b; Sanchis and Pascual, 2011; Krajcarz and Krajcarz, 2012; Lloveras et al., 2012), coyote/dog (Payne and Munson, 1985; Schmitt and Juell, 1994), or lynx and wildcat (Laroulandie, 2000; Lloveras et al., 2008; Rodriguez-Hidalgo et al., 2013, 2015). Nevertheless, the possibility should be considered that the peculiar composition of bird bones could produce different damage on bones than expected.

### 3. Results

#### 3.1. Payre

A total of 57 remains were recovered from the Payre site for all archaeological levels (Table 2). Levels A and D are the most abundant in terms of numbers of remains and in MNE (21 and 19 for each level, respectively), with sublevels Fb, Fc, Fd, and Gb being the lowest in NR and MNE (from 3 to 1 bones). At least four different family groups are represented, but Corvidae and Phasianidae stand out. Nonetheless, among non-identified specimens, medium-sized bones play an important role, surpassing the number of identified elements in most of the levels and, in the case of level Fb, representing the only group found. All together, we determined an MNI estimate of 18. Corvids are the best represented group (MNI = 2, in level D). The remaining categories are represented at most by one individual in each level. Adult individuals are predominant in all the archaeological levels. Only one bone corresponds to an immature individual from a medium-sized category at level D.

The anatomical representation is complicated by the scarcity of remains in most of the levels, which adds difficulty to obtaining an accurate interpretation of the assemblage. Hand and limb bones predominate in all levels, composing from 50 to 100% of the preserved elements. Girdles are also important at level A, while cranial and axial skeletons are completely absent in the whole assemblage.

The real anatomical representation was assessed by using % MAU, and revealed important biases in all taxa skeletal representation. The long bones (stylopodials, zeugopodials, and metapodials) are generally well represented, but their presence is not continuous in all groups and some individuals can only be documented through posterior phalanges (Table 3). The presence of acropodials is high considering the NR in the assemblage, but their relative representation is lower than expected, at 23.4% representation at level A and never surpassing 6.3% in the remaining levels. The limited number of remains in each level creates difficulty in establishing a possible pattern of representation rather than that announced. However, in level D, which has a wider spectrum of elements, a trend is apparent where hind limbs are more abundant than forelimbs on the other hand, level A, which has less variety but higher NR, has more forelimbs than hind limbs (Table 4).
### Table 3

NME and (%MAU) of the elements present at Payre assemblages by Family/size groups.

<table>
<thead>
<tr>
<th>Taxa/Size categories</th>
<th>Phasianidae</th>
<th>Corvidae</th>
<th>Accipitriformes</th>
<th>Large-sized</th>
<th>Medium-sized</th>
<th>Small-sized</th>
</tr>
</thead>
<tbody>
<tr>
<td>Levels</td>
<td>A</td>
<td>D</td>
<td>F</td>
<td>Fa</td>
<td>A</td>
<td>D</td>
</tr>
<tr>
<td>Furculum</td>
<td>1 (33.3)</td>
<td></td>
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</table>

Those undetermined fragments (NR = 2) are not included in the table due to the %MAU cannot be computed. A relative %MAU has been computed for those taxa classified by size, due to its representation in NR is significant. A, D, F, Fa, Fb, Fc, Fd, Gb correspond to archaeological levels. Cmc (carpometacarpus). Tmt (tarsometatarsus). Post. Phx. (posterior phalanx). Term. Phx. (terminal phalanx).

### Table 4

General characteristics of Payre and Abri des Pêcheurs assemblages, considering the parameters described here for each archaeological level. The possible accumulator agent is also proposed.

<table>
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<th>Level/sub-level</th>
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<th>Abri des Pêcheurs</th>
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<td>Mechanical modifications</td>
<td>Pits/punctures (%)</td>
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<td>Digestion</td>
<td>General</td>
<td>%</td>
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<td>Scores (%)</td>
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<td>G1 (%)</td>
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<td>5 (21.7)</td>
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<td>G2 (%)</td>
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<td>G3 (%)</td>
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<td>Accumulator agent</td>
<td>Nocturnal raptors (principal); mammal carnivore (secondary)</td>
<td>Nocturnal raptors (principal); mammal carnivore (lynx)/nocturnal raptor (secondary)</td>
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</table>

Fragmentation degree is clearly conditioned by the low number of remains in the assemblage. In general, it is moderate to high in levels A and D (52.4% and 15.8% of remains complete, respectively), which have larger numbers of bones. At level F, the total number of complete elements is 37.5%, although the entire package (from F to Fd) is considered as a unique unit. Nonetheless, some sub-levels have a high survival rate of complete elements as they contain a low number of bones. The same happens at sub-level Gb, where the only bone present is complete. All complete elements are phalanges, with an exception of a carpometacarpus from level A and a coracoid from level D. This agrees with the fact that bird remains are more susceptible to breakage due to their fragility. In that sense, smaller and/or compact bones such as articular bones and phalanges are less susceptible to break because of (1) their higher density, (2) their small size; and (3) their low or almost total absence of marrow content.

Fracture planes from fragmented bones could be analyzed in 16 cases (2 from level A, 7 from level D and 7 from level F). At levels A and F, all the fractures observed seemed to have been produced when the bone was still fresh, while at level D, one of the fractures analyzed (14.3%) took place when the bone was dry.

Carnivore modifications were observed in 47.6% of the remains in level A (NR = 10), 43.5% from level D (NR = 6), and 40% of the bones from level F, without sublevel attribution (NR = 2). Of these, mechanical modifications are mainly represented by tooth marks – pits and punctures (Table 4). They represent 13–50% of the total carnivore activity. Crenulated edges and pitting are also present on some of those bones. Mechanical modifications can be found on the whole surface of the bones, being more frequent on the epiphyses and diaphyses (Fig. 3). They can be located on one bone face or on opposite faces.

Other carnivore modifications are presented as corrosions produced by digestion (Fig. 3). These affect more than 20% of the remains from levels A, D, and F. Some of them present a moderate degree of corrosion (40% of digested bones from level D), but the majority are slightly digested (Table 4).

Otherwise, no other modifications that could be associated with human activity were found in the whole Payre assemblage.

3.2. Abri des Pècheurs

The site of Abri des Pècheurs provides a total of 727 bird remains, distributed among 4 archaeological units: Sector 1 (S1), Sector 2 (S2), Sector 3 (S3), and Sector 4 (S4), situated at different depths. Of these units, S4 has the highest number of remains (NR = 374); while S2 the fewest (NR = 36). All the sectors present a wide variety of species, grouped by family, especially in S3 and S4 (Table 5). Corvidae and Columbidae groups are present throughout the sequence, with Corvidae being the most abundant identified taxa in the site. Phasianids are also important in the lower part (S3 and S4). However, a significant number of remains cannot be classified by species and they were categorized by size. Medium and small-sized remains surpass the number of identified specimens of the assemblage. An estimation of 74 MNI had been done (S1 = 7; S2 = 5; S3 = 20; S4 = 24).

![Fig. 3. Pits/punctures (A) and digestive damage (B) on Payre avian remains. A1: left pelvis of Gallus gallus from level A. A2: left ulna of Gallus gallus from level A. A3: left tarsometatarsus of a small-sized bird from level D.](image)
S4 = 42), where adult individuals predominate. Nonetheless, at least one immature individual is found in each sector, never exceeding 20% of the total MNI (S1 = 14.3%; S2 = 20%; S3 = 10%; S4 = 4.8%).

The %MAU provides the real anatomical presence regarding the expected MNI. In that sense, long bones (stylopodials, zeugopodials and metapodials) are the best represented, reflecting a bias among bones with lower density (Table 6). Humeri are relevant in all the archaeological levels. They can exceed 50% in Fringillidae, Passeridae, and small-sized groups. Metapodials are also important in Columbidae and small-sized groups, especially in S3 and S4. Tarsometatarsi, which are one of the most represented elements, are 50% rendered among the Columbidae group in S4; and from 66.7% (S3) to 72.2% (S4) in the small-sized category. Girdles are significant at S1, S3, and S4 by the high presence of coracoids. They are important in Phasianidae family (33.3% and 42.9% of representation in S3 and S4, respectively) and in small-sized groups (S3: 33.3%; S4: 88.9%). Pelvises also have a high representation in medium-sized (60% in S3) and small-sized categories (66.7% in S1). Wing to leg ratios show a similar proportion of both extremities in their representation (S1: 64.8%; S2: 53.8%; S3: 48.8%; S4: 49.7%). Only in S1 did wing fragments predominate over

![Fig. 4. Mechanical modifications (A) and digestive damage (B) produced on bird bones from Abri des Pêcheurs. Pits/punctures (A1, A2). Scores (A3). A1: right proximal humerus of Tetrax tetra from sector 3. A2: right proximal humerus of Pyrrhocorax graculus from sector 4. A3: right proximal femur of Pyrrhocorax pyrrhocorax from sector 4. B1: left proximal femur of Asio flammeus from sector 4. B2: right distal tibiotarsus of Tetrao tetrix from sector 4.](image)

![Fig. 5. Hole on a right distal humerus of Pyrrhocorax graculus from sector 2 (A), probably result from carnivore activity, and a left distal humerus of Pyrrhocorax graculus with burning damage from sector 4 (B). All the remains come from Abri des Pêcheurs site.](image)
the leg fragments, but not much difference was observed between them. On the contrary, core elements are clearly under-represented (S1: 20%; S2: 3.7%; S3: 19.1%; S4: 20.6%). Proximal/distal ratios show a predominance of proximal fragments over the distal ones in all the units (S1: 59.4%; S2: 62.9%; S3: 54.7%; S4: 61.3%).

Fragmentation ranges from high to moderate in all the archaeological units. The completeness oscillates around 34–38%, with an exception at S1, where the fragmentation is more severe, with only 19.4% complete elements (Table 4). Articular bones (100%) and phalanges (80–92.6%) are almost unbroken. Some long bones attributed to small Passeriformes and small-sized groups are also found complete, especially at S4, where humeri of small birds are abundant. Fragmentation especially affects long bones. Despite this, shaft fragments can be found in the archaeological record, although proximal and distal ends are more common, representing more than 75% of the total remains.

In addition, 72 fracture planes were analyzed (19 from S1; 11 from S2; 26 from S3; and 16 from S4). In all levels, green fractures predominate in the analyzed fractures (from 62.5% in S4 to 68.4% in S1). No other modifications could be associated with fresh breakage.

Carnivore activity is important in all the archaeological sequence. It affects 38.1% of the remains in S1 (NR = 48), 25% (NR = 9) from S2, 29.3% (NR = 56) at S3, and 32.9% (NR = 126) from S4. Both mechanical and digestive modifications can be observed on the bone surfaces (Fig. 4).

Mechanical modifications associated with mammalian carnivores affect between 11.9 and 9.4% of the remains in each sector (Table 4). They are mainly represented by tooth marks (pits/punctures and scores). Nevertheless, other modifications such as notches, crenulated edges, and pitting are present on some of these bones, but these do not usually exceed 2% of the unit remains. Most of the tooth marks are located on the epiphyses and diaphyses of long bones, on one or more faces of the bone. On some occasions, scores display sharp bottoms usually associated with infantile mammal carnivores, which have sharp and non-worn teeth. Of the bones presenting mechanical modifications, two remains from S1 show pits that may be associated with beak-marks rather than mammal carnivore tooth marks. Their morphology is more triangular than the others. Furthermore, other mechanical modifications produced by raptors cannot be discounted, because of their irregular morphology.

Corrosions caused by digestion are also important in all the assemblage, affecting more than 16.7% of the remains in all levels (Table 4). Corrosion mainly consists of loss of cortical tissue, accentuated on the epiphyses, and it could modify all long, flat, or irregular bones. Slight digestion was more abundant in all sectors (from 88.8 to 100% of the digested remains). However, a moderate degree of digestion could be detected on some remains, as indicated by higher porosity on the bone ends. Only in S1 were more severe digestions observed, but never surpassing 3% of all the digested remains.

In reference to anthropogenic activity, two remains may cause controversy (Fig. 5). A distal humerus of *Pyrrhocorax* (Corvidae family) found at S2 presented a hole similar to that described by Laroulandie (2000, 2005) and Laroulandie et al. (2008), associated with overextension of the elbow. This hole is quite rounded and a bit lateralized and presents two scores on a side. On the other hand, anthropogenic damage could be observed on a distal humerus of a *Pyrrhocorax graculus* from S4, which is completely burnt to a high degree (grade 3, marked by Stiner et al., 1995).

Nonetheless, natural burning cannot be excluded as a possible cause.

4. Discussion

The data obtained from the taphonomical study on bird bones at Payre and Abri des Pecheurs indicate that hominids do not seem to play any significant part in these accumulations. The number of specimens is much lower at Payre than at Abri des Pecheurs, but the remains share some common characteristics that allow us to link both avian accumulations. Firstly, an important number of anatomical elements are absent, especially those of the cranial and axial skeleton—only some beaks were recovered in S1 and S4 of Abri des Pecheurs. The absence of cranial bones may have been related to the decapitation of prey by some birds of prey such as eagles, falcons, or eagle owls (Bochenski and Tomek, 1994, 1997). Nevertheless, we have to take into account that these bones are the most likely to disappear due to post-depositional processes related to their differential conservation that depends on bone density; thus, their underrepresentation or absence in the assemblage might not be explained by predation strategies (Moncel et al., 2015). Additionally, excavation techniques could also affect these specific bones, which are fragile and tend to break easily. Nonetheless, not all the absences can be explained on this basis and further analyses should be undertaken.

The possibility that the birds come naturally to the cave and die there seems unlikely (at least in the major part of the studied sample) because most of the bones are fragmented in a fresh state and anatomical connections have not been found. The high moderate fragmentation present in the assemblages is usually associated with raptor pellets, as well as mammalian carnivore activity (e.g., Bochenski et al., 1993, 1997, 1998; Bochenski, 1997; Hockett, 1999; Sanchis, 1999, 2000, 2012; Laroulandie, 2000, 2002; Cochard, 2004a, 2004b; Ulleras et al., 2008; Krajcarz and Krajcarz, 2012; Rodriguez-Hidalgo et al., 2016). Digestive damage to bones, hardly ever manifested on un eaten remains, determines the probable ingestion of bones by mammal carnivores and/or birds of prey in the site. This could explain the high level of fragmentation. Non-ingested remains generated by birds of prey are normally only slightly fragmented (e.g., Bochenski et al., 1993, 1997, 1999, 2009; Bochenski and Tomek, 1997; Laroulandie, 2000, 2002), which does not match completely with the previous cases. In addition, the importance of regurgitation pellets from nocturnal birds of prey should not be under-valued. These predators usually nest in caves, which increases the possibility they perform an important role in accumulations from archaeological sites.

The intense modifications of bones (tooth marks and digestion) indicated what were possibly small mammalian carnivore and raptor activities, as no anthropogenic damage was observed on bird bones in the form of cut marks or patterns of burning or breakage. This evidence leads to the proposal that non-human predators could have brought in birds and could have inhabited the cave/rock shelters when hominids were not occupying them. To contrast this statement, a comparison of actual bird accumulations produced by different agents has been carried out and is summarized in Table 7. This could provide more accurate data about possible agents accumulating in both sites. The studies made on avian remains produced by raptors have provided a wide number of bibliographic data, for example, by Bochenski et al. (1993, 1997, 1998, 1999, 2009), Bochenski and Tomek (1994),
Laroulandie (2000, 2002), Bochenski and Nekrasov (2001), Bochenski and Tornberg (2003), and Bochenski (2005), among others. Nonetheless, no reference is made to mammalian carnivores. Only a few preliminary studies have dealt with this problem (Laroulandie, 2000; Rodríguez-Hidalgo et al., 2016) and most of these are difficult to assess. For instance, leporid accumulations produced by mammalian carnivores were examined in order to provide a wider data set for comparison (Payne and Munson, 1985; Hockett and Haws, 2002; Cochard, 2004a, 2004b; Lloveras et al., 2008, 2012; Mallye et al., 2008; Sanchis and Pascual, 2011; Rodriguez-Hidalgo et al., 2013). We are aware, however, that their measurements. Tooth mark dispositions or locations are also difficult to assess. For instance, leporid accumulations produced by mammalian carnivores were examined in order to provide a wider data set for comparison (Payne and Munson, 1985; Hockett and Haws, 2002; Cochard, 2004a, 2004b; Lloveras et al., 2008, 2012; Mallye et al., 2008; Sanchis and Pascual, 2011; Rodriguez-Hidalgo et al., 2013). We are aware, however, that carnivores, foxes present higher percentages of heavy corrosion by digestion.

On the other hand, the assemblages composing Abri des Pécheurs show a higher proportion of specimens. In the uppermost sector (S1), the anatomical representation and the moderate degree of fragmentation seem close to those accumulations generated by nocturnal raptors from their ingested bones (Table 4, Table 7). The modest predominance of wing elements suggests that nocturnal raptors could have intervened on the assemblage (Bochenski et al., 1993, 1997; Laroulandie, 2000, 2002). Diurnal raptors could also produce a higher proportion of wings on uneaten remains, but the difference in wing/leg ratio is usually even greater (Bochenski and Tomek, 1997; Bochenski et al., 1997, 2009; Laroulandie, 2002). Diurnal raptors could also produce a higher proportion of wings on uneaten remains, but the difference in wing/leg ratio is usually even greater (Bochenski and Tomek, 1997; Bochenski et al., 1997, 2009; Laroulandie, 2002). Following the criteria established by Bochenski (2005), the proportion of proximal to distal remains also coincides with accumulations produced by birds of prey included in group II (with around 60% of proximal elements). This group includes accumulations produced by owl pellets and non-ingested remains of diurnal raptors, but the presence of digested remains pointed to nocturnal raptors as a possible input rather than diurnal birds of prey. The results from S1 differ even more from hominid accumulations, which usually present a predominance of legs, as determined by Ericson (1987). Digestions, with a clear supremacy of slight corrosions, also pointed to nocturnal raptors as accumulators. According to Andrews (1990), the percentage of bones showing digestions in S1 fits with the typical range attributed to eagle owl (Bubo bubo) accumulations, where damage to bones affects between 20 and 25% of the remains. It may likewise be supported by the possible presence of beak-marks on at least two remains. Nevertheless, this data are not sufficient to assess the agent producing the marks. If they are compared with that damage described by Laroulandie (2002) for eagle owl, they are out of line, especially concerning their measurements. Tooth mark dispositions or locations are also not definitive. In addition, the possible contribution of other mammal carnivores cannot be dismissed by the presence of pits and scores.

Sector 2 has the lowest NISP in the site. Its anatomical representation reflects a similar proportion of wings in relation to leg

Table 6
NME and (%MAU) of the elements present at Abri des Pécheurs site, classified by Family groups.

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A relative %MAU has been computed for those taxa classified by size, due to its representation in NR is significant. S1, S2, S3 and S4 refer to archaeological units used for the study. Cnx (carpometacarpus). Tmt (tarsometatarsus). Phx (phalanx). Posterior. Terminal. It continues at the next page.
Table 7
Comparison of bird accumulations produced by different predators (raptors and mammalian carnivores), adapted from Bochenski (2005).

<table>
<thead>
<tr>
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<th>Species</th>
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<th>Core/limb</th>
<th>Prox/dist</th>
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<th>Mechanical modifications (%)</th>
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<tbody>
<tr>
<td>Bird accumulations</td>
<td>Eagle owl, Ingested</td>
<td>30–60 (moderate)</td>
<td>wing, leg, core, limb</td>
<td>prox, dist</td>
<td>Tmt, humerus/tmt, cmc (&gt;90%)</td>
<td>19.6</td>
<td>Light-moderate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tawny owl, Ingested</td>
<td></td>
<td>wing, leg</td>
<td></td>
<td>Cranium, mandible, humerus, ulna (&gt;80%)</td>
<td></td>
<td>Light-moderate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Long-eared owl, Ingested</td>
<td></td>
<td>wing, leg</td>
<td></td>
<td>Humerus, ulna (&gt;95%)</td>
<td></td>
<td>Light</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gryfalcon, Non-ingested</td>
<td>&lt;30 (low)</td>
<td>wing, leg</td>
<td>prox, dist</td>
<td>Cmc, cranium, mandible (&gt;85%)</td>
<td></td>
<td>Heavy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Imperial eagle, Non-ingested</td>
<td>wing, leg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-ingested Peregrine falcon</td>
<td>&gt;60 (high)</td>
<td>wing, leg</td>
<td>prox, dist</td>
<td>Humerus, ulna</td>
<td>3.8</td>
<td>No damage</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gryfalcon</td>
<td>core, limb</td>
<td></td>
<td></td>
<td>Sternal, coracoid, humerus (&gt;90%)</td>
<td>0.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Imperial eagle</td>
<td>core, limb</td>
<td></td>
<td></td>
<td>Sternal, humerus (&gt;84%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Golden eagle</td>
<td>core, limb</td>
<td></td>
<td></td>
<td>Sternal (100%), coracoid, humerus (&gt;65%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-tailed eagle</td>
<td>core, limb</td>
<td></td>
<td></td>
<td></td>
<td>9.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammal carnivores</td>
<td>Cat, Non-ingested</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>No damage</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Red fox</td>
<td>85</td>
<td>wing, leg</td>
<td>core, limb, prox &gt; dist</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lynx</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ingested Genet intensively</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>Heavy</td>
<td></td>
</tr>
<tr>
<td>Leporid accumulations</td>
<td>Red fox</td>
<td>&lt;50</td>
<td>ant, post core, limb</td>
<td>-</td>
<td>girdles and proximal appendicular skeleton, axial skeleton</td>
<td>1.7–32</td>
<td>Mainly heavy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coyote/dog, 7 (ingested);</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.3–0.9</td>
<td>Heavy-extreme</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Iberian lynx</td>
<td>20 (non-ingested)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mainly heavy</td>
<td></td>
</tr>
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<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
</tbody>
</table>

Bird accumulations produced by mammalian carnivores were added, considering Laroulandie (2000) and Rodríguez-Hidalgo et al. (2016). Leporid accumulations produced by small mammalian carnivores were included as a reference to complement the scarce examples existing on birds (Payne and Munson, 1985; Schmitt and Juell, 1994; Hockett, 1999; Sanchis, 1999, 2000, 2012; Hockett and Havas, 2002; Cochard, 2004a, 2004b; Lloveras et al., 2008, 2012; Mally et al., 2008; Sanchis and Pascual, 2011; Rodríguez-Hidalgo et al., 2013). Prox(inal), Dist(al), X (presence).
bones, which is typical of mammal carnivore accumulations (e.g., Mallye et al., 2008). The high fragmentation in the assemblage suggests that lynxes (ingested remains) might play an important role in that level (Lloveras et al., 2008; Rodríguez-Hidalgo et al., 2013). Nevertheless, the digestions do not support this, as they are light and not really abundant. This could be due to the presence of nocturnal raptors that could intervene on the remains. Raptors often gobble down small prey entirely if the prey is small enough. If not, the prey is dismembered and/or fragmented for digestion. However, this argument fails to explain the high degree of fragmentation in the level. No other data referring to mammalian carnivores such as genet are available for comparison (Table 7).

Lower sectors S3 and S4 have similar percentages of digestion, fragmentation, and proximal/distal ratio as S1, but the wing/legs proportion is closer to the accumulations generated by mammalian carnivores, as pointed out in S2 (Tables 4 and 7). This is not incongruous with the bibliography. As already mentioned, some mammal carnivores, such as foxes, can produce moderate percentages of fragmentation that resemble ingested nocturnal raptor assemblages (Sanchis, 1999, 2000, 2012; Cochard, 2004a, 2004b; Lloveras et al., 2012). Genet or felid inputs are discarded because, according to the published studies made on ingested remains (Laroulandie, 2000; Lloveras et al., 2008; Rodríguez-Hidalgo et al., 2013), the damage they produce is more severe. If this was a case of non-ingested remains (Rodríguez-Hidalgo et al., 2015, 2016), digestive corrosion should not be present in the assemblage. In addition, as pointed by Laroulandie (2000) in a preliminary study, genet activity may cause damage to extremities of long bones, making them disappear. Nevertheless, these data should be taken with caution as they refer to immature individuals. Abri des Pêcheurs assemblages generally preserve the extremities of bones, which are mainly from adult individuals. The presence of clear tooth marks on bones reinforces the idea of mammalian carnivores as main agents. Foxes seem to fit well with the variables. In addition, the thin sharp scores present on bones might suggest the use of the cave as a den when hominins did not occupy it. These kinds of tooth marks are typical of cubs, which do not have dental erosion at the beginning of their life. On the contrary, the slight digestions attest to the probable presence of nocturnal raptors during some periods of sedimentary formation of the levels. Mammalian carnivores — including foxes — do not produce the patterns of digestion seen in S3 or S4. Their damage is more intense (moderate-heavy) than the ones observed. Therefore, nocturnal raptors could have used the shelter in alternation with mammal carnivores.

What seems clear, even though hominid presence was demonstrated at both sites by the presence of lithic tools and cut marks on larger-sized fauna, is that anthropogenic activity does not happen on bird specimens. Only two bones might argue with that at Abri des Pêcheurs. On the one hand, the hole on a distal humerus of Pyrrhocorax at S2 may be associated with anthropogenic activity by overextension of the elbow. However, its possible association with hominid activities was discarded for various reasons. First of all, the morphology and the disposition of the hole are not like those described by Laroulandie (2000, 2005) and Laroulandie et al. (2008). Secondly, no other signs associated with overextension have been found on the same or on other bones (wrenching of the medial part of distal humerus, breakage of the proximal joints of the radius and ulna). Lastly, two scores associated with one pit pointed to probable mammalian carnivore activity (Fig. 5). Those modifications could be used as examples of equifinality processes at Abri des Pêcheurs, due to the disarticulation of the elbow by mammalian carnivores or simply damage induced by non-human predators during their consumption sequences. In line with these processes, the burnt humerus of Pyrrhocorax graculus from S4 could have been generated by natural causes or resulting from anthropogenic activity. Intentional human activity seems unlikely because no other bird remains have been recovered with possible burning damage or human traces. Nonetheless, accidental combustion by contact with a hearth could be possible. Fireplaces documented at the site are from different levels, including an upper level and the sector 4 (Moncel et al., 2008). In that sense, a possible punctual perturbation cannot be dismissed.

The Payre site revealed no sign of hominid activity on birds, which seems to be incongruent with the lithic functional analyses carried out by Hardy and Moncel (2011), who claim the processing of birds and other small prey based on residues and use-wear on stone tools. However, this duality is not necessarily contradictory. The unique stone tool that supports bird processing comes from sub-level Ga. However, no bird remains were recovered in that sub-level. Only one bird bone has its origin on level G, but it belongs to sublevel Gb. Thus, different scenarios may clarify this fact:

1. The tool found at sublevel Ga was used outside the site and, after that, carried to the cave, as suggested by Hardy and Moncel (2011) for fish. This would explain the absence of bird specimens, as well as the human-induced damage on their bones.

2. Bird bones may exist at sub-level Ga, but the area where they are located remains unexcavated. Although the current dig zone shows high intensity of human activity — including lithic tools with evidence of feather processing (Hardy and Moncel, 2011; Baena et al., in press), a differentiation of activity areas may exist that would lead to accumulation of birds in specific areas of the cave. This scenario could only be tested with the excavation of other different zones or the entire surface of the site — circumstances not always possible due to external factors beyond our control. For example, the entrance and back areas are not totally preserved, due to sediments that collapsed in the slope. This situation was taken to select the excavation zone in the middle part of the cave, where the bird specimens come from.

Despite the open hypotheses left around the Payre assemblages, the general results of these analyses are congruent with the outcomes previously published for both sites. In the case of Payre, the presence of mammalian carnivores and raptors fits with the general trend of short-term human occupations (Moncel et al., 2008; Rivals et al., 2009). Carnivores, especially raptors, do not use caves when occupied by humans, and the presence of bones modified by these predators in alternation with others modified by hominids seems to reflect this kind of occupation, as well as the palimpsest character of these deposits. Additionally, the cave morphology in levels such as F should be taken into account when interpreting the assemblages. During the sedimentary formation of level F, the cave entrance seems to outline a smaller morphology than that observed in other archaeological units, suggesting a favorable environment for the establishment of carnivore dens. This situation could have accentuated the sporadic character of human occupations and explain the low anthropogenic activity detected. The link between karstic morphology and carnivore activity is often used to explain, together to other environmental and ecological factors, the significant presence of non-human predators in a specific place (e.g., Blasco et al., 2011). In case of Abri des Pêcheurs, previous hypotheses about the accumulations pointed to the significant role of carnivores in the formation of the assemblages (Daujeard, 2008; Moncel, 2010; Moncel, 2013).
et al., 2010). The results presented here support this approach, as the intense activity of non-human predators is also supported by avian remains and the sporadic human activity seems to be focused on macro-faunal remains. This is in agreement with short-term occupations established for the site (Moncel, 2010; Moncel et al., 2010).

5. Conclusions

Taphonomical analysis carried out on avian specimens from Payre and Abri des Pécheurs shows visible absence of anthropogenic activity on birds. The assessment of anatomical representation, the level of fragmentation, and mechanical and digestive modifications pointed to a mixture of mammalian carnivore and nocturnal raptor accumulations at different intensities, depending on the level. Nevertheless, the scarcity of bird specimens recovered at Payre makes further assessment difficult. The results obtained from this study raise questions regarding residue analyses carried out at level G3. No avian bones have been found at that level; therefore, previous studies cannot be supported by taphonomical analysis on bird bones. However, this brings up the necessity of widening the sample in order to obtain new data and to determine the existence or absence of bird remains along the stratigraphical sequence of Payre.

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