Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain)

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ABSTRACT

Birds are abundant in fossil assemblages of Quaternary sites; they can be used in landscape reconstruction as they are well adapted to the environment. Here we present the analysis of the avian assemblage from the Middle Paleolithic levels of the Llonin Cave, where 558 bird remains have been recovered from levels G-VI and CP-VIII, belonging to at least ten different taxa: Aves indet., Galliformes indet., Lagopus lagopus Linnaeus, 1758, Tetrao bonasia Linnaeus, 1758, Columba livia oenas Gmelin, 1789/Linnaeus, 1758, Passeriformes indet., Alaudidae indet., Motacilla sp., Turdus sp., Corvidae indet., Garrulus glandarius Linnaeus, 1758, Pyrrhocorax sp., Pyrrhocorax pyrrhocorax Linnaeus, 1758, Pyrrhocorax graculus Linnaeus, 1766 and Corvus cornix Linnaeus, 1758. This assemblage is similar to other assemblages from the Upper Pleistocene of the north of the Iberian Peninsula, and it reflects a mixed landscape, with open areas and woodland. The taphonomic analysis points to a mixed origin of the accumulation, mainly formed by medium-sized corvids dying in the cave, and also raptors accumulating their prey.

KEY WORDS
Avifauna, karstic system, Middle Paleolithic, Iberian Peninsula, Lagopus, Tetrao.
INTRODUCTION

The Marine Isotopic Stage 3 (between 60 and 27 ka ago) is a period within the Upper Pleistocene with strong climatic fluctuations, showing both warming (Dansgaard et al. 1993) and cooling events (Heinrich 1988). In this context, fossil birds play a key role in the paleoecological and paleoenvironmental reconstruction, as they appear as direct remains in paleontological and archaeological sites, but also could have participated as main actors in the accumulation of small vertebrates (Andrews 1990). Also, birds have interacted with the Paleolithic human populations, having been used as a nutritional source and also for ornamental/symbolic purposes (e.g. Laroulandie et al. 2016; Blasco et al. 2019; Rodríguez-Hidalgo et al. 2019). For these reasons, the analysis of the MIS3 fossil avifauna is a main step towards the understanding of the past environment and ecology, and also human subsistence and behavior.

The Upper Pleistocene avifaunas from the northernmost part of the Iberian Peninsula have been thoroughly analyzed in recent years (Elorza 1990, 2000; Sánchez-Marco 2005; Margalida & Marín-Arroyo 2013; Eastham 2017; Moreno-Garcia 2017; Núñez-Lahuerta et al. 2018b; Demarchi et al. 2019; Suárez-Bilbao et al. 2020, among others). The paleontological record of birds during that period is abundant, but relatively scarcer than the record of other vertebrates. In the case of the middle part of MIS3 in this area, the present data is diverse regarding the accumulating agents and the human exploitation thereof (Gómez-Olivencia et al. 2018; Marín-Arroyo et al. 2018). In this context, the Lonín Cave contains an archaeofaunal assemblage where Neandertals and carnivorans also show interaction, so it is interesting to go further in depth into their interrelations with other faunal species such as birds, which are quite numerous in the assemblage. This study focuses on the two excavated sectors of the cave (Galería and Cono Posterior) where the Middle Palaeolithic is documented, both containing Mousterian lithic remains (Rasilla & Santamaría 2011-2012; Sanchis et al. 2019; Rasilla et al. 2020).

The main objectives of this work are the identification of the taxa present in the avian association, the palaeoecological analysis of the avifauna remains, and the characterization of the origin of the accumulation, in order to ascertain the characteristics of the environment during this part of the MIS3 (as also including the interaction of the birds with the rest of the faunal specimens, and any possible exploitation by Neandertals).

LLÓNIN CAVE

The Lonín Cave is located in Peñamellera Alta, Asturias, in the north of Spain (Fig. 1A). The karstic system opens at 112 m above sea level, in the Cares-Devá rivers basin, surrounded by mountainous relief (Fig. 1B), with the Cuera Range at the north, the Picos de Europa central massif at the south, and the Peñamellera peak at the center. The archaeological research carried out reveals an important cultural sequence, including rock and portable art (Fortea et al. 1992, 1995, 1999, 2007; Fortea 2001; González-Pumariega 2007; Ríos et al. 2007; Rasilla & Santamaría 2011-2012; Rasilla 2014; Rasilla et al. 2014, 2016, 2020). The archaeological sequence contains: Middle Palaeolithic (Mousterian dated around 43,000 uncalBP), Upper Palaeolithic/Mesolithic (Gravettian, Upper Solutrean, Badegoulian, Middle and Upper Magdalenian, Azillian dated between c. 28,000-10,000 uncalBP), and Bronze Age remains (c. 1,800-700 BC).

The cave consists of a small vestibule which bifurcates into a narrow dead-end gallery at the right, and a big chamber with a vast dejection cone at the left. The excavation works have been carried out at several sectors of the cave (Fig. 1C): Galería (G), Vestíbulo (V), Cono Anterior (CA) and Cono Posterior (CP), each of which presents a different stratigraphical setup. However, only Middle Palaeolithic levels were recovered in Galería (G-VI) and Cono Posterior (CP-VIII), and they constitute the occupational base of the cave. G is located in the highest part of the cave and near the vestibule area (the actual entrance), while CP is in the lower part of the cave but its entrance is different and nowadays collapsed (Fig. 1D, E). Here we analyzed the bird fossil remains recovered in G-VI and CP-VIII.
The archeological assemblage of the Middle Paleolithic levels (G-VI and CP-VIII)

The macromammalian faunal remains recovered in the analyzed levels reveal a diverse association with six different ungulate species (highlighting Rupicapra pyrenaica, Capra pyrenaica and Cervus elaphus) and seven carnivore species (highlighting Ursus spelaeus, Crocuta spelaea, Canis/Cuon and Panthera pardus), all of them present in both levels (except Crocuta spelaea, which only appears in CP-VIII). The taphonomic analyses of these levels reveal a predominant use of the cave as a den by hyenas and leopards. Human presence in the cave is sporadic, given their limited interaction with deer, and the scarce lithic toolkit (N = 159). The leopards accumulated the caprines, and the hyenas introduced the bears and scavenged over the remains left by the Neandertals.

The micromammals (Microtus agrestis-arvalis group, Sorex araneus-coronatus, Microtus lusitanicus, Pliomys lenki, Arvicola sapidus, Arvicola terestris, Talpa europaea, Apodemus flavicollis) show an habitat of open forests, with abundant shrubbery and open areas, humid environments, and with Atlantic or Central European climates. The flora analysis points in that direction as well, representing open forests and an Atlantic mild or Central European climate. The anthracological analysis shows a predominance of species whose current optimum environment includes montane and subalpine environments; thus, it suggests that the conditions at the moment of the accumulation would have been cooler and arid. A deer ulna with cutmarks recovered in CP-VIII has been radiocarbon dated using ultrafiltration pretreatment (43.539 ± 2419 BP) (Rasilla & Santamaria 2011-2012; Sanchis et al. 2019; Rasilla et al. 2020).

Fig. 1. — Llonin Cave geographical and stratigraphic context: A, geographical location of the site; B, view from the entrance (photo: J. Fortea); C, cave plan and location of the different sectors (study areas shown in grey); D, stratigraphic cross-section of Galería; E, stratigraphic cross-section from Cono Posterior.

From Sanchis et al. 2019.
METHODOLOGY

The fossil remains were recovered by using two sieves with a mesh size of 2.38 and 1.41 mm, respectively. The analyzed bird remains were measured with a digital caliper (Mitutoyo Digil, Japan, with a theoretical precision of 0.01 mm) and photographed. The general nomenclature used is that of Baumel & Witmer (1993). For the systematic study, the identification keys are those from Erbersdobler (1968), Kraft (1972), Fick (1974), Jánossy (1983), Gilbert et al. (1985), Tomek & Bochenski (2000, 2009), Wójcik (2002), Bochenski & Tomek (2009) and Kessler (2015). The reference collection was the Gabinete de Fauna Cuaternaria Innocenç Sarrión, located in the Museu de Prehistòria de València. For the analysis of the fossil record of the taxa the works of Elorza (1990), Hernández-Carrasquilla (1993) and Tyrberg (2007) have been used. For the paleoenvironmental reconstruction, the current distribution of each identified taxa has been analyzed, and the results have been compared with the other groups present in the assemblages.

For the taphonomic analysis, the state of the remains has been studied in order to infer the origin of the accumulation of bird bones (Andrews 1990; Louollandie 2000). For this purpose, the presence of modifications related to human action, mainly cutmarks, and modifications related to the action of other predators (digestion, pits, punctures, beak or claw marks, etc.) has been taken into account. Also, the percentage of complete bones has been calculated (Bochen ski 2005), with the wing versus leg elements (Ericson 1987) and proximal versus distal elements (Bochenski & Nekrasov 2001) parameters calculated additionally.

RESULTS

A total of 558 avian remains recovered from the G-VI and CP-VIII levels have been analyzed. The remains belong to at least ten taxa, albeit some of them were not identified beyond the Aves class (Table 1). The number of remains recovered in each level strongly differs, with 44 remains in G-VI and 514 in CP-VIII. The remains identified as Aves indet. represent a similar proportion in both levels, with 29.5% in G-VI and 32.6% in CP-VIII.

Concerning the groups identified within each level, only the family Corvidae is present in the G-VI level. The diversity in level CP-VIII is slightly more varied, with the family Corvidae also being the most common in the assemblage (representing the 56.8% of the NISP), but with other groups also having been identified, such as the order Galliformes (representing 1.8%), the Columbiformes (0.4%), and the non Corvidae Passeriformes (8.5%). The differences in the number of remains recovered in G-VI and CP-VIII could be due to the structure of the cave, as a similar scenario can also be found in the macromammal remains, where a larger amount of remains were recovered in level CP-VIII, and with a lesser presence of anthropic modifications and more evidence of carnivores in level G-VI (Sanchis et al. 2019). The Cono Posterior area had a different entrance at a lower level, which is inaccessible nowadays, and could have been less exposed than the Galería sector, which is accessible from the current main entrance of the cave. Evidence of human occupation was found in the outer part of the main entrance, although it has to be taken into account that the human occupation of the cave was sporadic (Sanchis et al. 2019; Rasilla et al. 2020), and that humans and birds would not have frequented the cave at exactly the same time.

SYSTEMATICS

Order GALLIFORMES Temmink, 1820

Galliformes indet.

Material. — Six remains have been recovered: CP-VIII: left diaphysis fragment of a carpometacarpus, two sternum fragments, proximal femur, a left proximal ulna and a distal tibiotarsus.

Family PHASIANIDAE Horsfield, 1821

Genus Lagopus Linnaeus, 1760

Lagopus lagopus Linnaeus, 1758

Material. — CP-VIII: complete left tarsometatarsus and right distal tarsometatarsus (Fig. 2A).

DESCRIPTION

The two tarsometatarsus are the same size. The total length of the tarsometatarsus (38.6 mm) fits several representatives of the order Galliformes but allows to rule out the larger-sized taxa (Erbersdobler 1968). The proximal (7.5 mm) and distal length (8.2 mm for both remains) fits both Lagopus lagopus and Perdix perdix Linnaeus, 1758 (Kraft 1972). Morphologically,

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**Table 1.** Avifaunal spectrum expressed as number of identified specimens (NISP) and minimum number of individuals (MNI) for levels G-VI and CP-VIII dated from MIS3.

|          | G-VI | CP-VIII | TOTAL |
|----------|------|---------|-------|
|          | NISP | MNI     | NISP  | MNI  | NISP  |
| Aves indet. | 13   | –       | 168   | –    | 181   |
| Galliformes indet. | –    | 6       | –     | 2    | 6     |
| Lagopus lagopus | –    | 2       | –     | 2    | 2     |
| Tetraastes bonasia | –    | 1       | –     | 1    | 1     |
| Columba livia/oenas | –    | 2       | –     | 1    | 2     |
| Passeriformes indet. | 5    | 31      | –     | 36   | –     |
| Alaudidae indet. | –    | 1       | –     | 1    | 1     |
| Motacilla sp. | –    | 1       | –     | 1    | 1     |
| Turdus sp. | –    | 10      | –     | 3    | 13    |
| Corvinae indet. | 11   | 114     | –     | 125  | –     |
| Gammals glandarius | –    | 1       | –     | 1    | 1     |
| Pyrrhocorax sp. | 4    | 33      | –     | 37   | –     |
| P. pyrrhocorax | 8    | 2       | 115   | 13   | 128   |
| P. graculus | 3    | 1       | 26    | 3    | 29    |
| Corvus corax | –    | 3       | 1     | 1    | 3     |
| TOTAL     | 44   | 514     | 558   | –    | –     |
Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave

the tarsometatarsus recovered shows round epicondyles in trochlea metatarsi II; also, the trochleae are spread. That, along with the proportions of the smallest width of the shaft (3.6 mm) and the total length (Fig. 3), allows us to assign these remains to *Lagopus lagopus* (Kraft 1972).

**REMARKS**

The current European distribution of the willow grouse is limited to Scandinavia and Scotland (Juana et al. 2019); nevertheless, during the Pleistocene it expanded its habitat southwards, outranging its current distribution (Sánchez-Marco 2004; Holm & Svenning 2014). The contraction of their refuges during the Holocene explains the current distribution of the species (Lagerholm et al. 2017). Nowadays the distribution of the willow grouse is related to tundra areas and openings of boreal forests (Juana et al. 2019). In the Iberian Upper Pleistocene, the willow ptarmigan appears in Aitzbitarte IV (Elorza 1990), Ermitia (Elorza 1993), Urratxa III (Elorza 1997), Laminak II (Hernández-Carasquilla 1993), Abauntz (Altuna et al. 2002), Praileaitz 1 (Moreno-García 2017) and Santa Catalina (Elorza 2014; Laroulandie 2014).

**Genus Tetrastes Linnaeus, 1758**

*Tetrastes bonasia* Linnaeus, 1758

**MATERIAL.** — CP-VIII: complete right coracoid (Fig. 2B).

**DESCRIPTION**

The coracoid shows the morphology of Galliformes, the medial length of the coracoid (33.7 mm) fits the size of *Tetrastes bonasia*, *Perdix perdix* and *Alectoris graeca* Meisner 1804. The acrocoracoid shows a tuberculum craniale more laterodistally positioned than the tuberculum caudale. The foramen pneumaticum, is well developed, unlike in *Alectoris* Kaup, 1829 (which presents a hump in that position) and is
located further from the articulation with the sternum than in *Perdix* Brisson 1760. Those characters allow the assignation of the bone to *Tetrastes bonasia* (Kraft 1972).

**Remarks**
The hazel grouse breeds in mixed coniferous woodland with understory (Juana & Kirwan 2019). It currently inhabits forests and mountain systems in the northern areas of Europe (Bergman & Klaus 1994). In the Iberian Peninsula its presence is limited to sporadic observations (Catusse et al. 1992). In the north of the Iberian Peninsula the hazel grouse has been identified in the Holocene of the B-8 cave (Núñez-Lahuerta et al. 2018b).

Order COLUMBIFORMES Latham, 1790
Family COLUMBIDAE Leach, 1820
Genus *Columba* Linnaeus, 1758
*Columba livia* Gmelin, 1789/ *Columba oenas* Linnaeus, 1758

**Material.** — CP-VIII: complete right ulna (Fig. 2C); complete left distal ulna.

**Description**
Both ulnae present a similar size and the morphology of Columbiformes, with a prominent straight crista pectoralis in the proximal end, and a scar located more proximally than the proximal end of the condylus dorsalis in the distal end. The total length of the bone (51.4 mm) fits both *Columba livia* and *Columba oenas* (Fick 1974).

**Remarks**
Both the rock and the stock doves can be found nowadays in the Iberian Peninsula. The rock dove breeds in caves and cliffs while the stock dove breeds mainly in open country and punctually in open woodland (Baptista et al. 2019a, b). In the Upper Pleistocene of the northern Iberian Peninsula the remains attributed to *Columba livia oenas* are very common. They are registered among others in the Abric Romani, Aven del Gegant (Sánchez-Maro 2004), Brechas de la Cantera de l’Altissent, Cueto de la Mina, Valdegoba, Cueva del Toll (Sánchez-Maro 2005), and Praileaitz 1 (Moreno-García 2017).

Order PASSERIFORMES Linnaeus, 1758
Passeriformes indet.

**Material.** — 36 remains have been recovered: five from G-VI and 31 from CP-VIII.

Family ALAUDIDAE Vigors, 1825
Alaudidæ indet.

**Material.** — CP-VIII: right humerus.

Family MOTACILLIDAE Horsfield, 1821
Genus *Motacilla* Linnaeus, 1758

*Motacilla* sp.

**Material.** — CP-VIII: a right humerus.

**Description**
Humerus with two confluent fossae, nearly not separated by the cruss dorsale fossae, with a narrow habitus and a reduced wall of cruss dorsale fossae and a prominent epicondylus ventralis in ventral view (Jánossy 1983).

Family TURDIDAE Rafinesque, 1815
Genus *Turdus* Linnaeus, 1758

*Turdus* sp.

**Material.** — CP-VIII: three complete femora, three complete humeri, two complete coracoids, a tibiotarsus fragment and a tarsometatarsus.

**Description**
The size and morphology of these bones fits a medium-sized Passeriform. The coracoids show a distinct spine-shaped facies articularis claviculares, with a short and pointed processus acrocoracoideus (Gilbert et al. 1985; Kessler 2015). The humeri show the two fossae confluent, and a reduced medial bar (Jánossy1983; Wójcik 2002). The femora show a well-developed condylus fibularis and a rounded muscle attachment proximal to it (Gilbert et al. 1985), and the epicondylus medialis is not arching (Kessler 2015). The comparison with the comparative anatomy collection specimen of *Turdus philomelos* (TUPH-001) allowed the assignation of the remains to *Turdus* sp.

Family CORVIDAE Leach, 1820

**Material.** — 125 remains were analyzed: 11 from the G-VI, and 114 from CP-VIII (Table 2).

**Description**
The family Corvidae is the best represented in Llonin MIS3 MP levels. 319 corvid remains have been analyzed, 26 from G-VI, and 292 from CP-VIII (Table 2), representing 59% and 56.8% of the assemblages respectively.

Corvidae indet.
Genus *Garrulus* Brisson, 1760

*Garrulus glandarius* Linnaeus, 1758

**Material.** — CP-VIII: right carpometacarpus.

**Description.**
A complete carpometacarpus with a cranial length of 22.6 mm with Corvidae morphology. The size, along with the slender shape of the processus extensorius and the straight ventral edge of the trochlea carpalis allows the assignment of the bone to *G. glandarius* (Tomek & Bochenski 2000).

**Remarks.**
The Eurasian jay is currently present in the Iberian Peninsula; it inhabits woodlands and forests (Madge et al. 2019). It is common in the Upper Pleistocene sites of the Iberian Peninsula, as in El Castillo (Sánchez-Marco 2018), L’Arbreda, Reclau Viver (García i Petit 2002), La Riera (Sánchez-Marco 2005) and El Esquilleu (Baena et al. 2005).

Genus *Pyrrhocorax* Tunstall, 1771

*Pyrrhocorax pyrrhocorax* Linnaeus, 1758

**Material.** — 123 remains were analyzed: eight from G-VI and 115 from CP-VIII (Figs 2D-I; 4; Table 2).

**Description.**
All the remains have the morphology of a medium sized Corvidae, with osteological features that fit with several species, as *Pyrrhocorax* spp. and *Corvus monedula*. Several characters allow the assignation of the remains to the genus *Pyrrhocorax*, such as the lack of a depression at the base of the acrocoraoid, and the shape of the bony crest in the coracid, or the presence of two openings in the plantar surface of the tarsometatarsus. The size of the bones also allowed the assignation of the remains to the genus *Pyrrhocorax*, specifically to *P. pyrrhocorax*, which is in general slightly bigger than the sister species *P. graculus* Linnaeus, 1766 (Tomek & Bochenski 2000) (Fig. 4).

**Remarks.**
The red billed chough appears in the south of Europe, and it breeds in cliffs and high mountain pastures with rocky areas (Madge 2019a). It is one of the most common species in the Upper Pleistocene of Europe (Tyberberg 2007), and *P. pyrrhocorax* underwent expansions in both cold and warm pulses during the last part of the Pleistocene (Holm & Svenning 2014). It has been found among others in Aitzbitarte, Ermitxia, Urriaga (Elorza 1990), Abauntz (Altuna et al. 2002) Prailieitz 1 (Moreno-García 2017), B-8 cave (Núñez-Lahuerta et al. 2018b), Artazu VII (Suárez-Bilbao et al. 2020) and Azlor (Gómez-Olivencia et al. 2018).

*Pyrrhocorax graculus* Linnaeus, 1766

**Material.** — 27 remains were analyzed, three from G-VI and 26 from CP-VIII (Table 2; Figs 2J-L; 4).
**DESCRIPTION**
The remains have the morphology of a medium sized Corvidae. As with the remains assigned to *P. pyrrhocorax*, the various bones show features that allow their assignation to the genus *Pyrrhocorax*. The size of the remains allows their assignation to *P. graculus*, which are generally smaller than those of *P. pyrrhocorax* (Tomek & Bochenski 2000) (Fig. 4).

**REMARKS**
The yellow billed chough appears nowadays in the south of Europe, as does its sister species *P. pyrrhocorax*, but it is confined to high mountain areas with rocky crags (Madge 2019b). For this reason, it has been used as a cold climate indicator; nevertheless, as it happens with the red billed chough, *P. graculus* is practically a cosmopolitan species, and its use as climate indicator must be done taking into account the other taxa present in the associations (Núñez-Lahuerta et al. 2018a). It has been recorded among others in Olha, Aitzbitarte (Elorza 1990), Prailleitz 1 (Moreno-García 2017), B-8 cave, D-2 cave, Los Batanes (Núñez-Lahuerta et al. 2018b) and Artazu VII (Suárez-Bilbao et al. 2020).

**Corvus corax** Linnaeus, 1758

**MATERIAL.** — Three remains were analyzed from CP-VIII (Table 2).

**DESCRIPTION**
The remains show the features of a large-sized Corvidae. The species *Corvus corax* is the largest species of the genus *Corvus* in the Palearctic, and the size of the two ulnae and the tarsometatarsus fits this species (Tomek & Bochenski 2000).

**REMARKS**
The raven is the biggest passerine bird. It appears throughout the Iberian Peninsula, and is a generalist bird. It can appear in a wide range of habitats, generally in more open habitats (Marzluff 2019). It appears among other sites in the Iberian Upper Pleistocene sites of Urtiaga, Aitzbitarte, Santimamiñe (Elorza 1990), Amalda (Eastham 1989) El Castillo (Sánchez-Marco 2018), Prailleitz 1 (Moreno-García 2017) and Axlor (Gómez-Olivencia et al. 2018).

**TAPHONOMICAL REMARKS**

Most of the anatomical elements have been recovered in the Llonin MIS3 levels. As remarked above, the family Corvidae is the most represented in the two analyzed levels, followed by the Galliformes (Fig. 5C; Table 1). As discussed previously, the number of remains for each level is clearly different (44 remains in G-VI and 514 in CP-VIII), and those...
Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave

No cutmarks have been detected on the remains. The digestion is scarce in the sample. In G-VI, five elements (11% of the G-VI Aves sample) show light or medium digestion (an undetermined fragment and a coracoid and three femora assigned to corvids); and in CP-VIII five remains (1% of the CP-VIII Aves sample) present light or medium digestion (ulna, proximal femur and a tibiotarsus assigned to undetermined Aves, and two femora assigned to Corvidae). Some of the bones present punctures that could be due to the action of birds of prey (Bochenski et al. 2018). In the level CP-VIII four long bones show punctures (one undetermined, three corvid long bones, representing the 0.7% of the remains). The presence of carbonate crusts in the remains could hide some modifications, but only a low percentage of remains present crusts (6% of the CP-VIII birds sample and 9% of the G-VI birds sample), thus, the effect of the crusts in the taphonomic interpretation is not very relevant. Most of the modification appears in undetermined Aves or corvids, which are the most abundant remains in the assemblages.

The percentage of complete bones varies in each level, and is apparently higher in level CP-VIII, nevertheless the differences are not statistically representative (31.6% in CP-VIII, with an Confidence interval of 95%, between 27%-36.6%; and 21.4% in G-VI, CI 95%: 9%-41.4%) (Fig. 5D). The low number of remains recovered in G-VI prevents the calculation of proportions and therefore to perform deeper taphonomic analyses. For this reason, the wing versus leg and proximal versus distal were calculated only for the CP-VIII level assemblage. In this level, the data from Corvidae and the rest of the Aves taxa have been analyzed separately. The small amount of remains of non-corvid groups hampers the possibility of analyzing each group separately.

The wing versus leg results of CP-VIII shows approximately a 50% ratio for both corvids and non-corvids, and the wing elements are more abundant in both groups (Fig. 5E), but this abundance is not significative (p = 0.8). These results are similar to those given for uneaten remains from diurnal birds of prey and pellets from nocturnal birds of prey. The predominance of wing elements and the absence of cutmarks allow for discarding the human processing of the bird remains (Ericson 1987). The results of the proximal
versus distal analysis shows a 56–44% ratio between them for the corvids and 57–44% for the rest of the bird remains (Fig. 5F), and these proportions correspond to a group II predator, also including pellets from nocturnal birds of prey and uneaten remains from diurnal birds of prey (Bochenśki & Nekrasov 2001). The results need to be interpreted carefully, as these ratios have been criticized (Livingston 1989; Laroulandie 2010), and also, some authors proposed that the predominance of wing elements in Neanderthal sites reflects the use of the feathers by the humans (Finlayson et al. 2012).

**DISCUSSION**

**ORIGIN OF THE ACCUMULATION**

Both groups (corvids and non-corvids) yielded similar results in the analyzed parameters. The high proportion of broken bones in the assemblage could be due to postdepositional processes, such as trampling produced by the animals and humans occupying the cave (Sanchis et al. 2019).

The clear domination of cave dwelling corvids in the assemblage (Fig. 5C), the presence of fragile remains such as skulls and sternums (Fig. 5A), together with the presence of juvenile remains of this group (1%) (Fig. 5B) and the scarce amount of modifications on the assemblages, points to a natural accumulation of the corvids inhabiting the cave. Nevertheless, it has been shown that the processing of corvids by Neanderthals does not necessarily leave anthropic marks, due to the small size of the birds, and because the exploitation of corvids by humans is an extended activity (Finlayson et al. 2012), and the sporadic presence of humans in the Llionin Cave is clear (Sanchis et al. 2019; Rasilla et al. 2020). Also, corvids are well-known scavengers that could have visited the cave following the carcasses which had been left by the different predators that acted in the cave.
The evidence points to a mixed origin of the accumulation of birds: with some individuals of medium-sized corvids (P. pyrrhocorax and P. graculus) mostly dying naturally in the cave, representing the majority of the assemblage, and other groups of birds being sporadically accumulated by birds of prey. But a Neanderthal role in this accumulation cannot be ruled out with the available data.

Paleoenvironmental reconstruction

Several species that have been considered interesting due to their climate-related behavior (Sánchez-Marco 2004; Holm & Svenning 2014) appear in the assemblage: the willow ptarmigan (Lagopus lagopus), the hazel grouse (Tetrastes bonasia) and the choughs (Pyrrhocorax pyrrhocorax and Pyrrhocorax graculus). The current distribution of the willow ptarmigan (L. lagopus) does not include the Iberian Peninsula (Juana et al. 2019). Nevertheless, it expanded its habitat southwards during the Pleistocene, and then contracted its geographical range back during the Holocene, remaining at some punctual areas outside its current range as a relict (Sánchez-Marco 2004; Holm & Svenning 2014). This contraction of its refuge during the Holocene explains the current distribution of the species, which is nowadays related to tundra areas and openings of boreal forests (Lagerholm et al. 2017). The hazel grouse (B. bonasia) inhabits mixed coniferous woodland with understorey in the north of Europe (Juana & Kirwan 2019), and its occurrence in the Iberian Peninsula is limited to sporadic observations (Catússe et al. 1992). During the Late Pleistocene these three species show a strong relation with forested areas (Núñez-Lahuerta et al. 2018a).

Both chough species (Pyrrhocorax pyrrhocorax and Pyrrhocorax graculus) inhabit similar areas in Europe, although the yellow billed chough (P. graculus) appears at higher altitudes than the red-billed chough (P. pyrrhocorax). It has been proposed that this difference is due to a higher tolerance to low temperatures by the yellow billed chough (Tyrberg 1991). Due to its current distribution, the presence of P. graculus has been interpreted as an indicator of a colder climate; nevertheless, the yellow billed chough was present in all of Europe during both cold and warm periods of the Late Pleistocene (Tyrberg 2007). In summary, the avian association points to a mixed landscape, composed of open areas and woodlands, with understorey.

Concerning the other faunal elements identified in the analyzed levels, the small vertebrate assemblage also points to a landscape mainly composed of open areas, such as meadows, grasslands, and rushes, with low density forests. This presence of open forest has been also confirmed by the anthracological analysis. Additionally, the small mammal assemblage points to a humid environment, and the presence of permanently wet areas, which is reflected by the presence of semiaquatic taxa such as the Pyrenean desman (Galemys pyrenaicus Geoffroy, 1811) and the southwestern water vole (Arvicola sapidus Miller, 1908) (Sanchis et al. 2019). The presence of water bodies in the surroundings of the cave is not so strongly reflected by the avian association, but nevertheless, one remain assigned to a genus generally related to water bodies has been identified: Motacilla sp.

Both the small mammal association and the anthracological analysis point to a colder climate in the Llonin Cave area. Although most of the avian taxa identified in the levels are present nowadays. The existence of some taxa (today absent in the Iberian Peninsula and only inhabiting the northern part of Europe) can be justified due to this past colder climate, which is reflected by the mammals and anthropological analysis, although it has to be taken into account that birds tend to reflect more middle temperatures rather than other proxies, and their distribution also strongly depends on the landscape (Lorenc 2007).

Conclusions

The analyzed remains (N = 558) have revealed at least ten different taxa: Aves indet., Galliformes indet., Lagopus lagopus, Tetrastes bonasia, Columba livia/oenas, Passeriformes indet., Alaudidae indet., Motacilla sp., Turdus sp., Corvidae indet., Garrulus glandarius, Pyrrhocorax sp., Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus and Corvus corax. The assemblage is similar to others of the Upper Pleistocene of the north of the Iberian Peninsula. The scarcity of modifications (digestion, punctures), and the absence of cutmarks, together with the presence of juvenile remains, point to a mixed origin of the accumulation, with small corvids naturally dying in the cave, and raptors accumulating their preys.

Despite the presence of species considered typical of colder areas (Lagopus lagopus and Tetrastes bonasia), the whole avian association present in the levels under study points to an environment similar to that of today. A mixed landscape with open and woodland areas occurred near the cave during the accumulation of the Middle Paleolithic levels, with this landscape interpretation correlated by the small mammal association and the anthropological data present.

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