

SPECIAL ISSUE PAPER

Accumulation agents and bird assemblages: The case of the TE9d level at Sima del Elefante (Sierra de Atapuerca, Spain)

Mario Marqueta^{1,2}  | Rosa Huguet^{1,2,3}  | Carmen Núñez-Lahuerta^{1,2,4} 

¹Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Avinguda de Catalunya 35, Tarragona, 43002, Spain

²Institut Català de Paleocologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), Tarragona, 43007, Spain

³Unit associated to CSIC, Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, c/José Gutiérrez Abascal 2, Madrid, 28006, Spain

⁴Aragosaurus-IUCA, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, c. Pedro Cerbuna, 12, Zaragoza, 50009, Spain

Correspondence

Mario Marqueta and Rosa Huguet, Institut Català de Paleocologia Humana i Evolució Social Campus Sescelades URV (Edifici W3), Zona Educacional 4, 43007 Tarragona, Spain. Email: mariomarqueta@hotmail.com and rhuguet@iphes.cat

Funding information

The research technical support of Maria Dolors Guillén was supported by the Spanish Ministry of Science and Innovation through the “María de Maeztu” excellence accreditation (CEX2019-000945-M); This research was conducted as part of competitive projects PGC2018- 093925-B-C32 (MICINN-FEDER); AGAUR SGR 2017-1040; URV 2014, 2015 and 2016 PFR-URV-B2-17; (100576, 2014), C.N.-L. is the recipient of a Juan de la Cierva-Formación contract (FJC2020-044561-I), supported by the MCIN and co-financed by the NextGenerationEU/PRTR; Juan de la Cierva-Formación, Grant/Award Number: FJC2020-044561; Spanish Ministry of Science and Innovation, Grant/Award Number: CEX2019-000945-M.

Abstract

Bird assemblages can be found in archeological sites throughout the Pleistocene. Taphonomy studies are key to understanding how such assemblages were formed. These assemblages can be generated by various agents, including human groups, animals, and natural death. In this paper, we analyzed the avifaunal assemblage from level TE9d at the Sima del Elefante site, where corvid (Corvidae) remains are the most abundant taxa, as reported in previous studies from that deposit. The remains of smaller birds (Charadriiformes, Rallidae) and large raptors (*Aquila cf. heliaca/adalberti*, *Haliaeetus albicilla*) have also been documented. Our taphonomic analysis shows that birds of prey were the main accumulators of bird remains at the site. The presence of modifications such as beak/talon marks and different degrees of digestion reinforce the idea that both diurnal and nocturnal raptors were involved. Nevertheless, we cannot rule out the accumulation by natural death of those species that could have nested in the rocky walls of the cave. The absence of evidence of anthropogenic activity on the bird remains from level TE9d therefore indicates that hominins were not involved in this accumulation. These results can be considered a new contribution to the discussion on the origin of avifaunal accumulations in Pleistocene archeological contexts.

KEYWORDS

bird accumulations, Early Pleistocene, raptor, Sima del Elefante, taphonomy

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *International Journal of Osteoarchaeology* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Avifaunal studies carried out at Pleistocene sites have shown that bird remains are frequent in archeological deposits (e.g., Laroulandie, 2010; Lloveras et al., 2020; Núñez-Lahuerta et al., 2016; Rufà et al., 2016). In these contexts, the remains may have several origins, involving human action, non-human agents, or natural death. It is at this point where taphonomy plays a key role in distinguishing the origin of the remains at archeological sites, making it possible to assess the role played by humans and other predators on bird remains.

Throughout prehistory, it has been observed that anatids, phasianids, columbids, and corvids were the most widely consumed taxa by human groups (Blasco et al., 2014; Blasco & Fernández Peris, 2009; Finlayson et al., 2012; Laroulandie, 2005). It has also been reported that human groups as *Homo neanderthalensis* and *Homo sapiens* captured birds for other purposes, such as symbolic reasons, or technological purposes (Blasco et al., 2019; Laroulandie et al., 2016; Morin & Laroulandie, 2012; Peresani et al., 2011; Rodríguez-Hidalgo et al., 2019; Romandini et al., 2014). In fact, there are some evidences of *Homo neanderthalensis* using elements such as bones, feathers and claws of large raptors as ornaments (Fiore et al., 2004; Gaudzinski-Windheuser & Niven, 2009; Mourer-Chauviré, 1989; Peresani et al., 2011; Rodríguez-Hidalgo et al., 2019; Romandini et al., 2014; Soressi et al., 2008). These findings have helped to reinforce the idea that Neanderthals had symbolic expressions and, therefore, that their cognition could have been just as complex as that of *H. sapiens*. In sites closer to the Holocene, technological uses including the manufacture of needles, tubes and flutes are more abundant than in earlier chronologies (García & Menéndez, 1998; Mannermaa & Rainio, 2020; Vilette, 1983, 1999).

In addition to human activity, bird remains may be accumulated by other agents. Birds of prey tend to generate skeletal accumulations of hunted prey; among these remains, ingested and uneaten bones may be found. These remains are usually accumulated mainly in roosting areas such as cliffs, caves, or shelters. Their taphonomic signature involves beak modifications and degrees of digestion observed on bone surfaces (Bochenski et al., 1993; Bochenski & Nekrasov, 2001; Lloveras, Cosso, et al., 2018; Lloveras, Moreno-García, et al., 2014; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Rufà & Laroulandie, 2019). Moreover, the natural death of the birds themselves can also generate accumulations, particularly the skeletons of immature individuals and eggshells (Laroulandie, 2010).

Carnivores such as foxes and lynxes also accumulate bird bones in the cavities they use as dens (Krajcarz & Krajcarz, 2014; Rodríguez-Hidalgo et al., 2016). These kind of accumulations have been documented at different archeological sites, such as Grotte Vaufrey (Rufà & Laroulandie, 2021) or Arbreda Cave (Lloveras et al., 2020; Lloveras, Garcia, et al., 2018).

There are several Early Pleistocene sites where the presence of birds has been documented. In most of these deposits, the avifaunal remains have been studied from a purely palaeontological perspective, without considering taphonomic aspects (Louchart et al., 1998; Sánchez-Marco, 2004).

The aim of this work is to characterize and determine the origin of the avifaunal assemblage from level TE9d at Sima del Elefante, in order to identify whether human groups or other predators were involved in the accumulation of these remains.

2 | ARCHEOLOGICAL CONTEXT

Sima del Elefante is one of the sites located in the Sierra de Atapuerca (Burgos). It has the largest number of avifaunal remains of all the Sierra de Atapuerca sites, most of them accumulated in the Early Pleistocene levels (TE14-TE7) (Huguet et al., 2017; Núñez-Lahuerta et al., 2021). These levels represent an interval from 1.5 to 1.1 million years ago (Cuenca-Bescós & García, 2007; Parés et al., 2006; Rosas et al., 2001). Some bone remains with anthropic modifications and stone tools, have been recovered from these units (Carbonell et al., 2008; Huguet et al., 2013, 2017; Ollé et al., 2013) (Figure 1). Additionally, a bird radius with a cut mark was recovered from level TE9a (Huguet et al., 2013). This is the only evidence of anthropogenic contribution to the bird remains at the site.

Level TE9d is characterized by sedimentary beds formed of weathered limestone blocks and brown-red gravelly clays. Birds are the most widely taxonomic group represented in this level, but some remains of macro and micromammals have also been recovered. Human activity in this level is evidenced by a few chert stone tools (Ollé et al., 2013) and anthropic modifications (cut marks and breakage) on some macrofaunal bones, which are currently under study. The TE9c level, immediately above the TE9d level, has been dated yielding an age of between 1.3 and 1.1 million years. Human remains assigned to *Homo* sp. have been recovered from this level, representing the oldest human fossils recovered in Western Europe (Bermúdez de Castro et al., 2011; Carbonell et al., 2008).

The taxonomic list of birds includes a great variety of species and some of them also represent the first fossil evidence in the Iberian Peninsula (Núñez-Lahuerta et al., 2021; Rosas et al., 2001; Sánchez-Marco, 2018).

3 | MATERIALS AND METHODS

In this work, all mapped bird remains from level TE9d of the Sima del Elefante were examined.

The taxonomy was determined using the osteological collections of the *Institut Català de Paleoeologia Humana i Evolució Social* and the *Museu de Ciències Naturals de Barcelona*, as well as anatomical descriptions (Cohen & Serjeantson, 1996; Driesch & Boessneck, 1976; Louchart et al., 2005; Tomek & Bochenski, 2000). The remains were classified into three different weight classes considering the species identified in this study (Núñez-Lahuerta et al., 2021) (Table 1).

The number of identified specimens (NISP), the minimum number of elements (MNE), and the minimum number of individuals (MNI) were calculated (Lyman, 1994a, 1994b). The ages of the individuals were estimated based on bone porosity (Baumel et al., 1993;

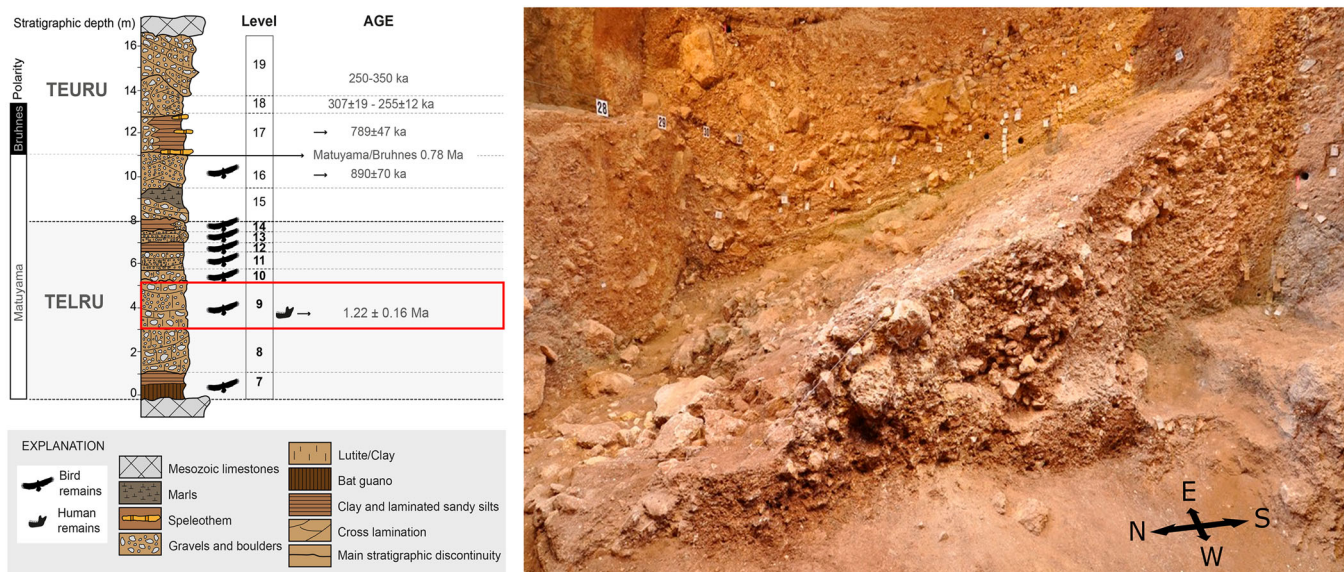


FIGURE 1 Synthetic stratigraphic column of the Sima del Elefante site and image of level TE9d. Modified from Carbonell et al., 2008 and Núñez-Lahuerta et al., 2021. Age data from Parés et al. (2006), Van der Made (2001), Rosas et al. (2006), López-García et al. (2011), Arnold and Demuro (2015), Cuenca-Bescós et al. (2015), and de Lombera-Hermida et al. (2015) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3185)]

TABLE 1 Weight sizes of birds identified at TE9d at Sima del Elefante site

| Weight sizes | Taxa |
|---------------------------------------|---|
| Large size (over 2 kg) | <i>Haliaeetus albicilla</i> , <i>Aquila heliaca</i> / <i>adalberti</i> , <i>Aquila/Hieraetus</i> |
| Medium size (between 0.1 and 2 kg) | <i>Corvus plicicaeus</i> |
| Small size (between 0.02 and 0.09 kg) | Scolopacidae, Rallidae |

Serjeantson, 2002, 2009). The presence of medullary bone tissue (Lentacker & Van Neer, 1996) and the identification of ancient and modern fractures (Steadman et al., 2002) has been diagnosed.

In order to estimate the integrity of the sample, the percentage of relative abundance (%RA) was performed (Binford, 1978; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Rufà et al., 2016). Different anatomical ratios were calculated using the MNE: (1) the wing/leg ratio, (Ericson, 1987); (2) the core/limb ratio, (Bochenski, 2005; Bramwell et al., 1987), and (3) the proximal and distal ratio (Bochenski & Nekrasov, 2001) (Figure S1).

Bone surface modifications (BSM) were examined using an Olympus SZ1144TR binocular microscope (magnification 15X and 40X), and an HIROX KH8700 3D digital microscope both located in the IPHES facilities. These analyses were performed according to already published taphonomic methods (Andrews & Cook, 1990; Bochenski, 2005; Laroulandie, 2000; Lloveras, Moreno-García, et al., 2014; Lyman, 1994a).

The diurnal and nocturnal raptors signature was identified by the presence of certain modifications on the analyzed remains, characteristic of their activity, such as digestion damage and beak or talon marks (Bochenski et al., 1993; Bochenski & Nekrasov, 2001;

Bochenski & Tornberg, 2003; Laroulandie, 2001, 2002; Lloveras, Cosso, et al., 2018; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Rufà & Laroulandie, 2019). Digestion damage was classified into different degrees according to Lloveras, Moreno-García, et al. (2014). Bird beak/talon modifications were categorized as depressions, perforations, pecking, scratches, and chipping (Table S1 and Figure S2). Scratches and chipping are considered raptor damage in this study due to their association with other raptor modifications. In fact, linear marks produced by the beaks of raptors have already been described by Fernández-Jalvo and Andrews (2016).

4 | RESULTS

A total of 1877 remains were analyzed, 1763 of which were anatomically and taxonomically identified, mostly belonging to the family Corvidae (91.9% of the assemblage). Also, five different groups of Accipitriformes, and unidentified Charadriiformes, Scolopacidae and Rallidae aves were identified in the assemblage (Table 2). The total minimum number of individuals (MNI) was 109.

4.1 | Taxonomic and age estimation

All the remains, except four undetermined, have been divided into three weight sizes (Table 2). The medium-sized bird group, composed by the Corvidae family, is the most abundant in the assemblage, with 96 individuals (MNI); the large bird group is less abundant (MNI = 8) than the medium-sized group but shows a greater diversity of taxa. Among the large birds, the species *Haliaeetus albicilla* (MNI = 2) has been identified. Within the genus *Aquila*, a distinction has been made between *Aquila* cf. *heliaca/adalberti* (MNI = 2) and *Aquila/Hieraetus*

TABLE 2 Number of individual specimens (NISP) (numbers without parentheses) and minimal number of elements (MNE) (numbers with parentheses) by species, sizes, and skeletal elements

| NISP (MNE) | Rallidae | Scolopacidae | Charadriiformes | <i>Aquila cf. heliaca/adalberti</i> | <i>Aquila sp.1</i> (big-sized) | <i>Aquila sp.2</i> (medium-sized) | <i>Aquila/Hieraetus albicilla</i> | Accipitridae | Corvidae | Total | Large size | Medium size | Small size | Aves indet. | Total |
|--------------|----------|--------------|-----------------|-------------------------------------|--------------------------------|-----------------------------------|-----------------------------------|--------------|-------------|-------------|------------|-------------|------------|-------------|-------------|
| cra | | | | | | | | | 6 (2) | 6 (2) | | 6 (2) | | | 6 (2) |
| quad | | | | | | | | | 7 (7) | 7 (7) | | 7 (7) | | | 7 (7) |
| mand | | | | | | | | | 7 (4) | 7 (4) | | 7 (4) | | | 12 (7) |
| vert | | | | | | | | | 88 (88) | 88 (88) | | 88 (88) | | | 93 (93) |
| rib | | | | | | | | | 3 (3) | 3 (3) | | 3 (3) | | | 3 (3) |
| ste | | | | | | | | | 18 (13) | 18 (13) | | 18 (13) | | | 20 (15) |
| fur | | | | | | | | | 4 (3) | 4 (3) | | 4 (3) | | | 4 (3) |
| cor | | | | | 1 (1) | | | | 115 (77) | 117 (79) | 3 (2) | 115 (77) | 3 (3) | | 121 (82) |
| sca | | | | | 2 (2) | | 1 (1) | | 50 (45) | 53 (48) | 3 (3) | 50 (45) | | | 53 (48) |
| hum | | | | | 1 (1) | | | | 156 (90) | 157 (91) | 3 (2) | 156 (90) | 4 (4) | | 163 (96) |
| uln | | | | | 1 (1) | | | | 287 (185) | 289 (187) | 8 (5) | 287 (185) | 6 (5) | | 301 (195) |
| rad | | | 1 (1) | | | | | | 89 (68) | 90 (69) | 1 (1) | 89 (68) | 1 (1) | | 91 (70) |
| ulnr | | | | | | | | | 7 (7) | 7 (7) | | 7 (7) | | | 8 (8) |
| radl | | | | | | | | | 2 (2) | 2 (2) | | 2 (2) | | | 3 (3) |
| cmc | | | | | | 1 (1) | 2 (2) | 3 (3) | 170 (149) | 176 (155) | 6 (6) | 170 (149) | 3 (3) | | 179 (158) |
| pel | | | | | | | | | 34 (26) | 34 (26) | 1 (1) | 34 (26) | | | 35 (27) |
| fem | 1 (1) | | | | | | | 1 (1) | 129 (106) | 132 (109) | 4 (3) | 129 (106) | 5 (4) | | 138 (113) |
| tbt | | | | | 2 (2) | | 1 (1) | | 147 (110) | 150 (113) | 3 (3) | 147 (110) | 2 (2) | | 152 (115) |
| fib | | | | | | | | | 13 (13) | 13 (13) | | 13 (13) | | | 13 (13) |
| tmt | | | 2 (2) | | 3 (3) | 1 (1) | | 2 (3) | 177 (138) | 189 (148) | 13 (8) | 177 (138) | 11 (9) | | 201 (155) |
| calc | | | | | | | | | | | 1 (1) | | | | 1 (1) |
| ant ph | | | | | | | | | 41 (40) | 41 (40) | | 41 (40) | | | 41 (40) |
| post ph | | | | | | | | 5 (5) | 82 (80) | 87 (85) | 33 (29) | 82 (80) | | | 115 (109) |
| claw | | | | | | | | | 22 (22) | 22 (22) | 15 (15) | 22 (22) | | | 37 (37) |
| indet | | | | | | | | | 71 | 71 | 3 | 71 | 2 (2) | 4 | 80 (2) |
| Total | 1 (1) | 1 (1) | 3 (3) | 3 (2) | 6 (6) | 6 (6) | 2 (2) | 4 (4) | 1725 (1278) | 1763 (1314) | 111 (91) | 1725 (1278) | 37 (33) | 4 | 1877 (1402) |
| MNI | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 96 | 108 | 8 | 96 | 5 | | 109* |

Note: The last row shows the minimal number of individuals (MNI) by species and sizes. cra: cranium; quad: quadrates; rib: rib; ste: sternum; fur: furcula; cor: coracoid; sca: scapula; hum: humerus; uln: ulna; rad: radius; ulnr: ulnare; cmc: carpometacarpus; pel: pelvis; fem: femur; tbt: tibiotarsus; fib: fibula; tmt: tarsometatarsus; ant ph: anterior phalanx; post ph: posterior phalanx; claw: claw; indet: indeterminate. The first "Total" column includes only taxonomically identified remains. The second "Total" column includes all taxonomically identified remains and those not taxonomically identified. (*): immature small-sized individual added.

(MNI = 1). In addition, two groups of *Aquila* sp. have also been identified: *Aquila* sp. 1 (MNI = 2), which includes large eagles that are smaller than *Aquila claudgerini* (Mourer-Chauviré & Bonifay, 2018); and *Aquila* sp. 2 (MNI = 1), which includes eagles smaller than *Aquila* sp.1, such as *Aquila fasciata* or *Aquila heliaca/adalberti*. Some of the remains have been assigned to Accipitridae indet. Due to a lack of identifiable anatomical features. Among the small birds, the least abundant group (MNI = 5), we identified some remains as belonging to the order Charadriiformes and the families Scolopacidae and Rallidae (Table 2).

The sample is mainly composed of adult individuals (MNI = 98), representing 89.9% of the avian assemblage. Immature individuals are less abundant (MNI = 11), representing 10.1% of the entire sample, including one large-sized individual, one small-sized individual, and

9 medium-sized individuals. In relation to the sex of the individuals, we were only able to identify the presence of one corvid ulna with medullary bone tissue, indicating that this individual was a female.

4.2 | Anatomical representation

Almost all avian skeletal elements are represented in the assemblage (Table 2). All three weight sizes follow similar patterns, with a high presence of long bones, such as ulnae or tarsometatarsi (Figure 2). The cranial and axial skeleton are poorly represented throughout the sample. The number of elements of medium-sized birds clearly outnumbers those of the other weight size categories. A total of

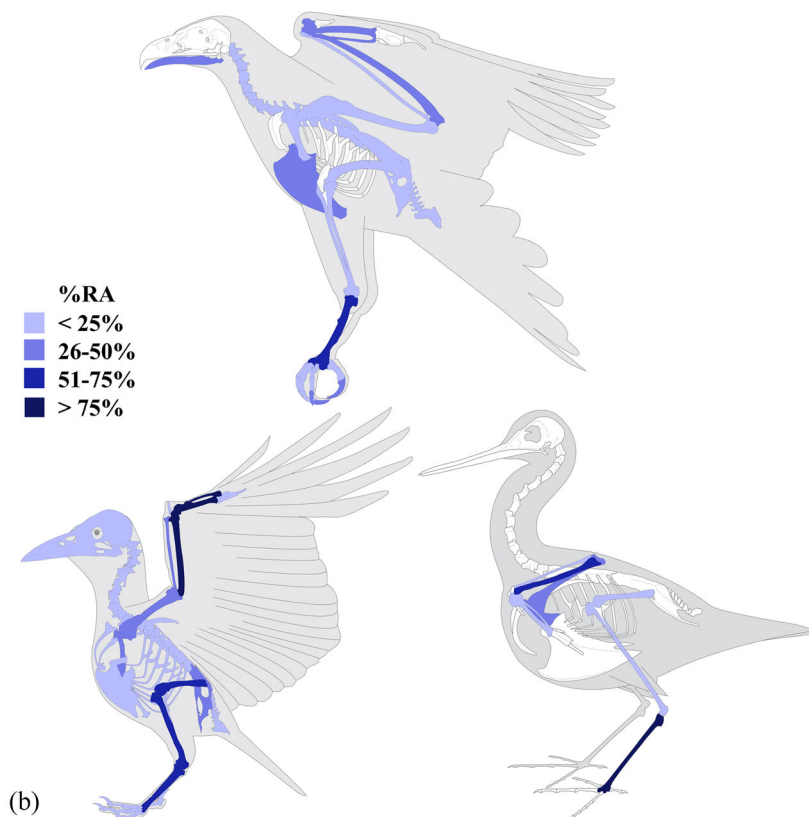
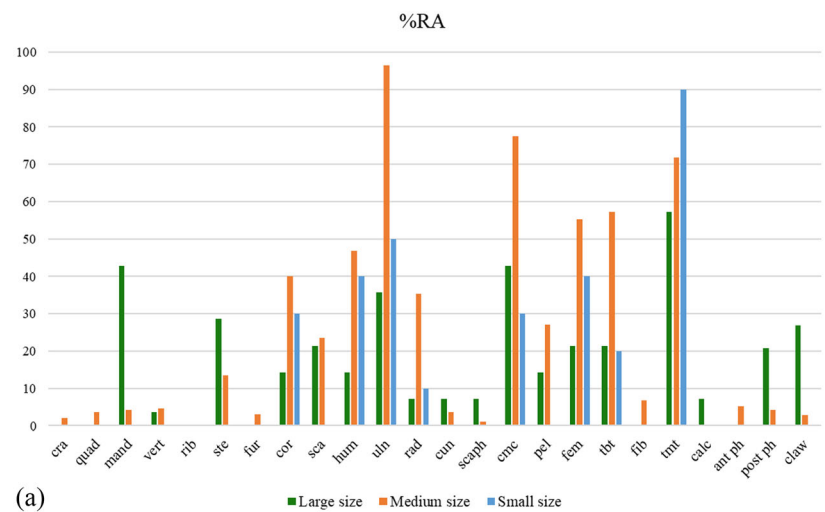


FIGURE 2 %RA estimation of every skeletal element in relation with weight sizes. (a) Column chart %RA representation. (b) Representation of %RA on skeletal models for each weight size [Colour figure can be viewed at wileyonlinelibrary.com]

111 remains from large birds have been identified, compared to the 1725 medium-sized remains. The %RA values have been calculated according to weight size categories. It can be observed how the general value of the %RA in the group of large birds (10.8%) is close to that in the group of medium-sized birds (13%). The representation values are markedly low. The small-sized group has a slightly lower conservation rate than the other sizes (6.1%). This could be associated with the fragility of bird bones of all sizes, as well as the accumulation processes of the deposit itself.

The %RA results show how elements from the medium-sized group are the best represented in the sample. The ulna is the most well-represented element with a total of 96.4%. The results for wings and legs are very similar, but wings are slightly better represented.

For large birds, the tarsometatarsus is the best-represented element with a RA of 57%. The legs, including the posterior phalanges (RA 21%) and claws (26.8%), are better represented than the wings in this size group. Finally, the small bird group has high values for the tarsometatarsus (90%). In this size group there are no elements of the axial or cranial skeleton, except for the coracoid.

Skeletal ratios show similar values for all size categories; however, there are minor differences in the wing/leg ratios (Table 3). Among

large and small birds, legs predominate over wings (48.1% and 44.4%, respectively), while for medium-sized birds there is a slightly higher value of wing elements than leg elements (54.5%). The core/limb ratio reveals a significant tendency for all three sizes: the high presence of limbs outweighs the representation of core bones. The small group shows the lowest proportion of core elements (10.7%), with only three coracoids. This is comprehensible if the great fragility of core elements such as pelvis, sternum or scapulae of small birds is considered. The proximal/distal ratio is very similar for the three size groups with distal elements predominating. In the TE9d level, some remains of all bird size groups have been recovered anatomically connected. These connections are mainly in the wing and leg extremities.

4.3 | Fragmentation

The study of the fragmentation of the remains is not conclusive in the analysis of this assemblage due to the high modern fragmentation (66.5%) during the excavation process. However, we have obtained percentages on the complete remains (20.5%) and those with ancient fractures (13.1%) by considering only the sample that has not been altered by modern fracturing in the excavation (Table 4).

4.4 | Bone surface modifications

No evidence of anthropogenic or mammalian carnivore modification has been found in the analyzed sample. However, damage produced by raptors, such as digestion and beak/talon marks has been identified.

TABLE 3 Skeletal ratios by weight sizes categories

| | Wing/Leg | Core/Limb | Proximal/Distal |
|---------------------|-------------|-------------|-----------------|
| Large size | 48.1 | 22.2 | 39.4 |
| Medium size | 54.5 | 16 | 44.2 |
| Small size | 44.4 | 10.7 | 41.9 |
| Whole sample | 58.3 | 17.8 | 45.5 |

| | Large size | Medium size | Small size |
|---------------------------------|----------------|---------------|-----------------|
| NISP | 111 | 1725 | 37 |
| MNE | 91 | 1278 | 33 |
| MNI | 8 | 96 | 5 |
| % Immature | 0.1 | 0.9 | 0.1 |
| Main elements | tmt, cmc, mand | uln, cmc, tmt | tmt, uln, fe/hu |
| Wing/Leg | Leg | Wing | Leg |
| Core/Limb | Limb | Limb | Limb |
| Proximal/Distal | Distal | Distal | Distal |
| % Complete elements | 6.5 | 53.1 | 1.4 |
| % Old fractures | 2.8 | 34.5 | 1.3 |
| % Digested bones | 2 | 2 | 29.7 |
| % Total beak/talon marks | 6.3 | 11.7 | 21.6 |
| % Depressions | 0.6 | 14.7 | 0.8 |
| % Perforations | 1.1 | 34.2 | 1.9 |
| % Pecking | 0.8 | 20.8 | 0.3 |
| % Scratches | 0 | 16.7 | 0.8 |
| % Chipping | 0 | 6.4 | 0.3 |

Note: The percentages in italics are calculated from the total number of remains with beaks/talon marks identified (NISP = 360). This table includes the remains that could be classified anatomically and by weight size (NISP = 1873), excluding a total of four indeterminate remains.

TABLE 4 Main data from avifaunal assemblage of level TE9d of Sima del Elefante. NISP, MNE, MNI, anatomical representation, percentages of immature remains, complete elements, ancient fractures and modifications on the surface of the bones

Digestion damage is present in 2.7% of the sample (52 remains). Light digestion is the most abundant, accounting for 82.7%, followed by moderate (13.5%) and heavy (2%) digestion of elements.

Very few large taxa remains show digestion damage (2%), and this is only light. Both of these remains are the first digits of the posterior phalanges. Medium-sized digested remains (2%) display a greater variety of digestion degrees (light-moderate-heavy) however, light digestion is predominant. This group shows modifications by digestion mainly in the long bones that compose the limbs and the coracoid

(Figure 3). Specimens from the small bird group have the highest digestion percentage (29.7%) as well as variety in intensity (light-moderate).

Across the entire sample, modification by raptor beaks or talons is documented in 39.6% of the remains (Figure 4). Perforations (37.2%), pecking (21.9%), and scratching (17.5%) are the most abundant types of modification. Remains from the large bird group show few beak/talon modifications, only 6.3% of the remains of this size show any alterations of this type, with perforation (1.1%) being the

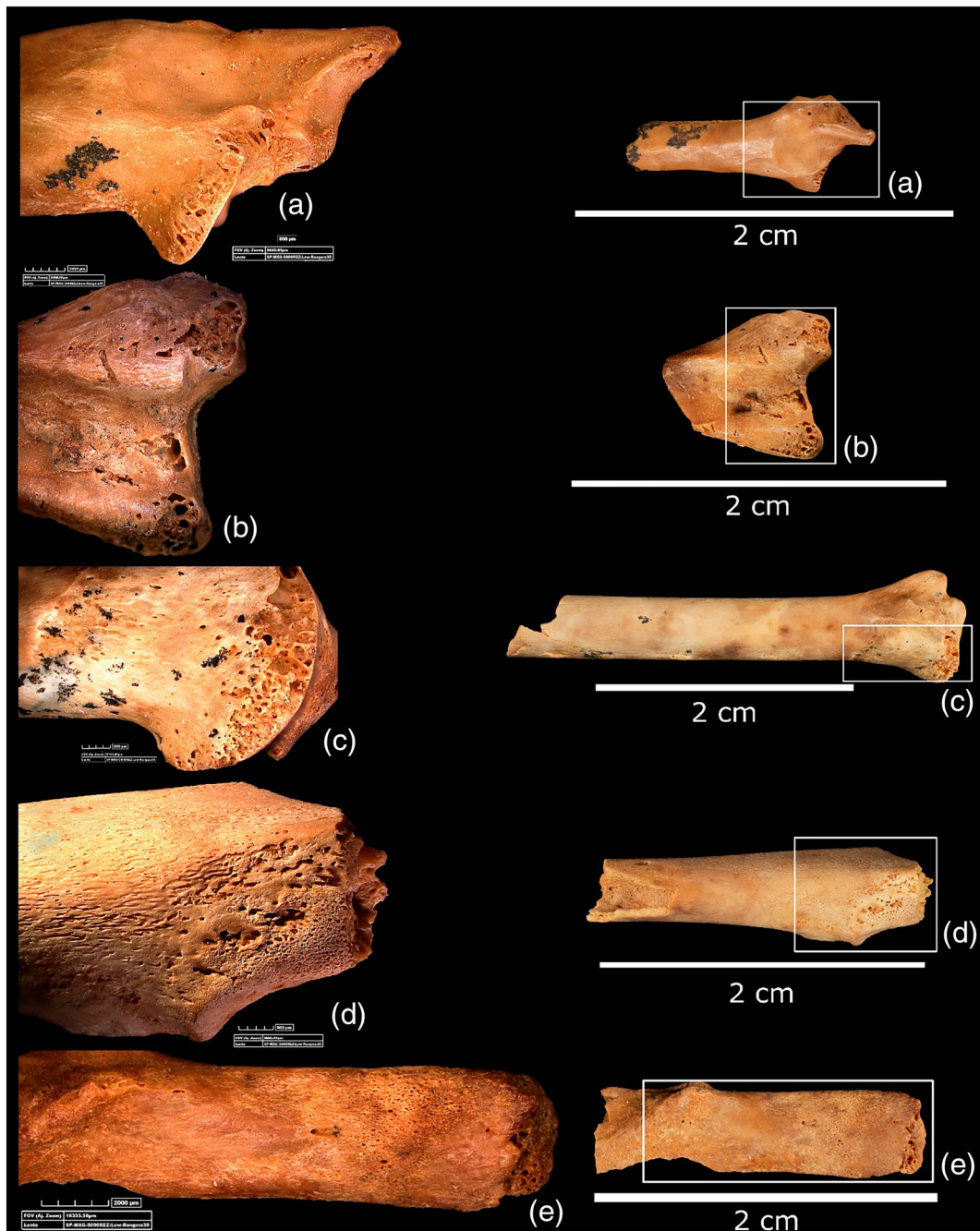
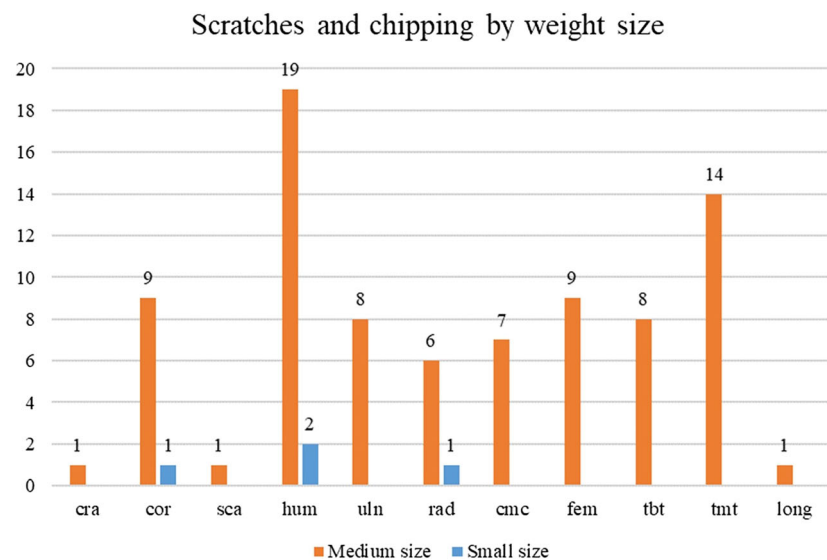
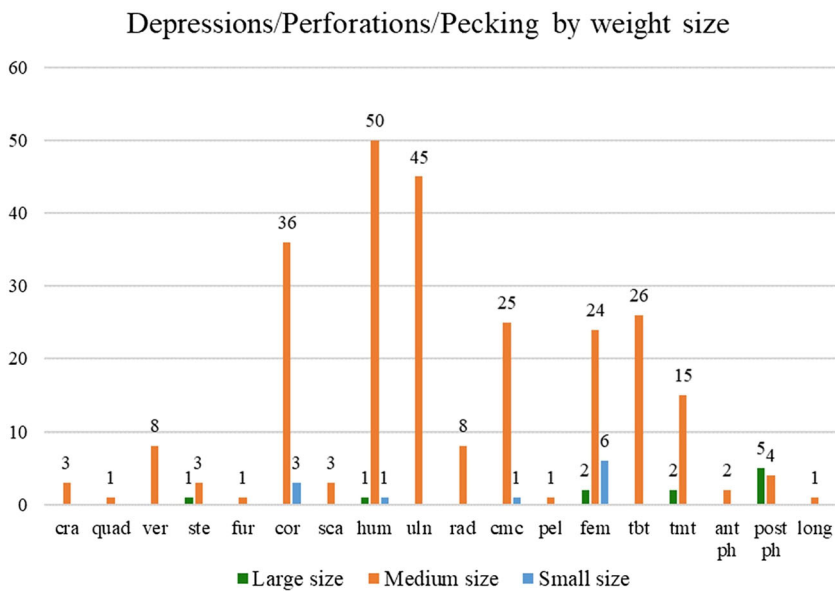


FIGURE 3 Bones with digestion damage. (a) Light degree in proximal epiphysis of small-sized bird ulna; (b) moderate degree in distal epiphysis of small-sized bird femur; (c) moderate degree in distal epiphysis of small-sized bird ulna; (d) moderate degree in proximal metaphysis of medium-sized bird coracoid; (e) heavy degree in medium-sized bird mandible [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3185)]



most common modification, followed by pecking (0.8%), and depressions (0.6%).

The remains from the medium-sized group present beak/talon marks on a total of 11.7%. The most common alteration is perforation (34.2%), mainly focused on the humerus and the ulna and being exclusively unilateral. Pecking is also widely represented (20.6%). These damage types are focused on the wing (humerus, ulna and carpometacarpus) and axial (coracoid) elements, followed by the legs (femur, tibiotarsus, and tarsometatarsus) (Figure 5). Medium-sized bird remains show the highest number of scratches (16.7%) and chipping marks (6.4%). These modifications are mainly located on the limbs, especially on long bones such as the humerus (19) and tarsometatarsus (14) (Figure 6). Scratches and chipping are more prevalent in the medium-sized group, followed by the small bird group. These alterations seem to be focused on the long bones, in a similar way to perforations, depressions, and pecking. The humerus is again the most modified element. It is also remarkable that these modifications are

mainly located on the proximal epiphyses and diaphysis. Some of the scratching/chipping marks have been found in association with other raptor beak/talon modifications on skeletal remains. Although they are currently under study and we cannot yet associate them with a particular species, in this work we have considered them a raptor signature.

The remains of small birds have the highest percentage (21.6%) of raptor beak/talon damage. Perforations are once again the most abundant marks (1.9%), mostly found on the femur (6). Scratches and chipping have only been found on a total of 4 remains, all from anterior limbs: two humeri, one coracoid, and one radius.

5 | DISCUSSION

In the lower levels of Sima del Elefante, including TE9d, the presence of bird remains is very prominent. Analyzing them allows us to

FIGURE 4 Number of remains with bone surface modifications: Depressions, perforations, pecking, scratches, and chipping by weight sizes [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3185)]

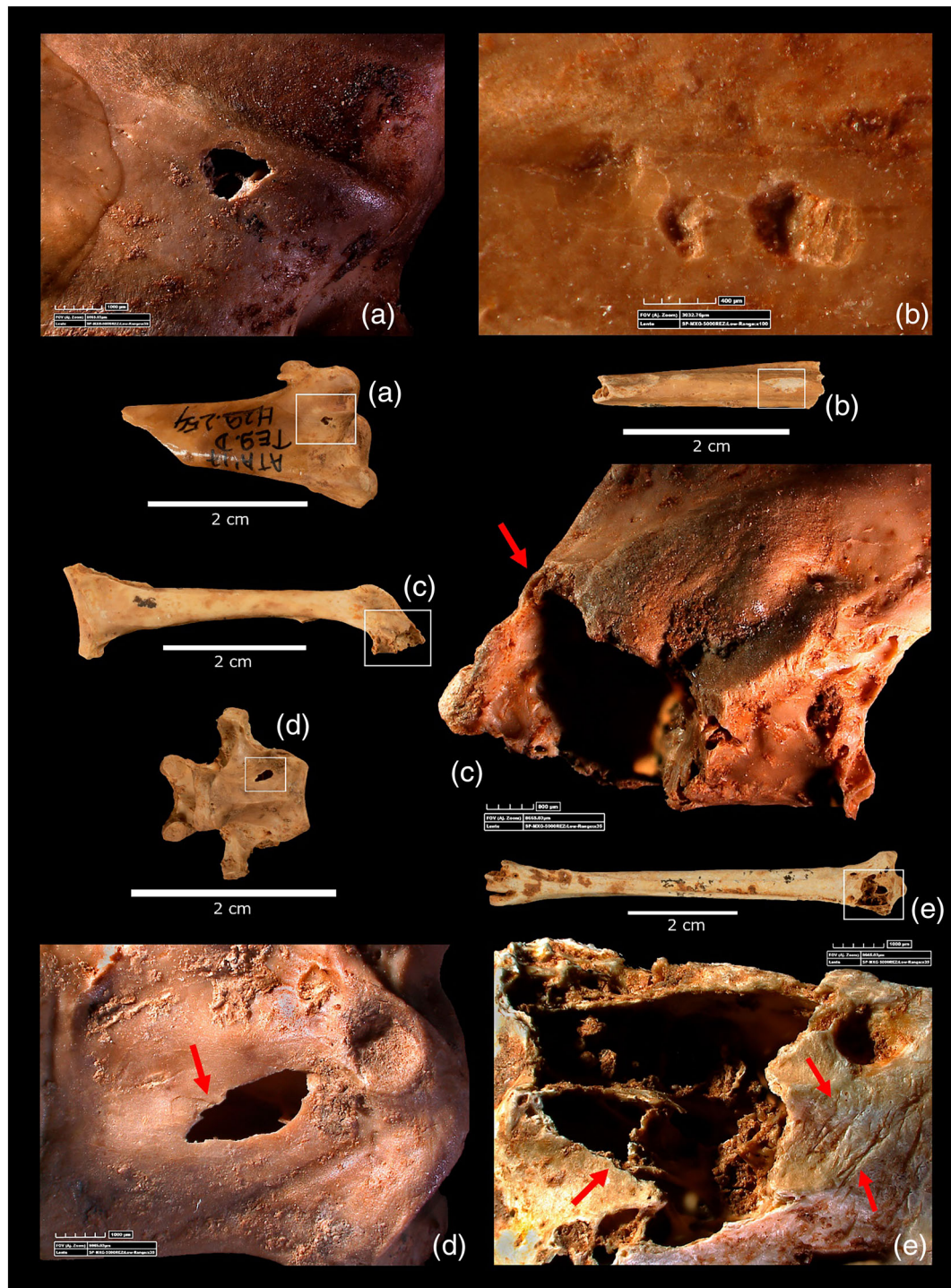


FIGURE 5 Beak/talon modifications on medium-sized birds. (a) perforation on humerus distal epiphysis; (b) depressions on tibiotarsus diaphysis; (c) pecking on coracoid proximal epiphysis; (d) perforation on vertebrae; (e) pecking with associated scratches on tarsometatarsus proximal epiphysis [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3185)]

reconstruct the habitat in which the first hominins lived, as well as identify the role hominins or other agents played in their accumulation inside the cavity.

Corvidae is the most widely represented group in level TE9d. Most of the remains in this study could be associated to the extinct species *Corvus pliccaenus* identified in other levels of this site (Núñez-

Lahuerta et al., 2021). The lack of palaeoecological data for this species complicates its association with a specific ecosystem, considering that several corvid species are ubiquitous (Boarman & Heinrich, 2020). In any case, the high presence of corvid remains in Pleistocene karst sites suggest that this species, like modern corvids, prefers to inhabit rocky areas.

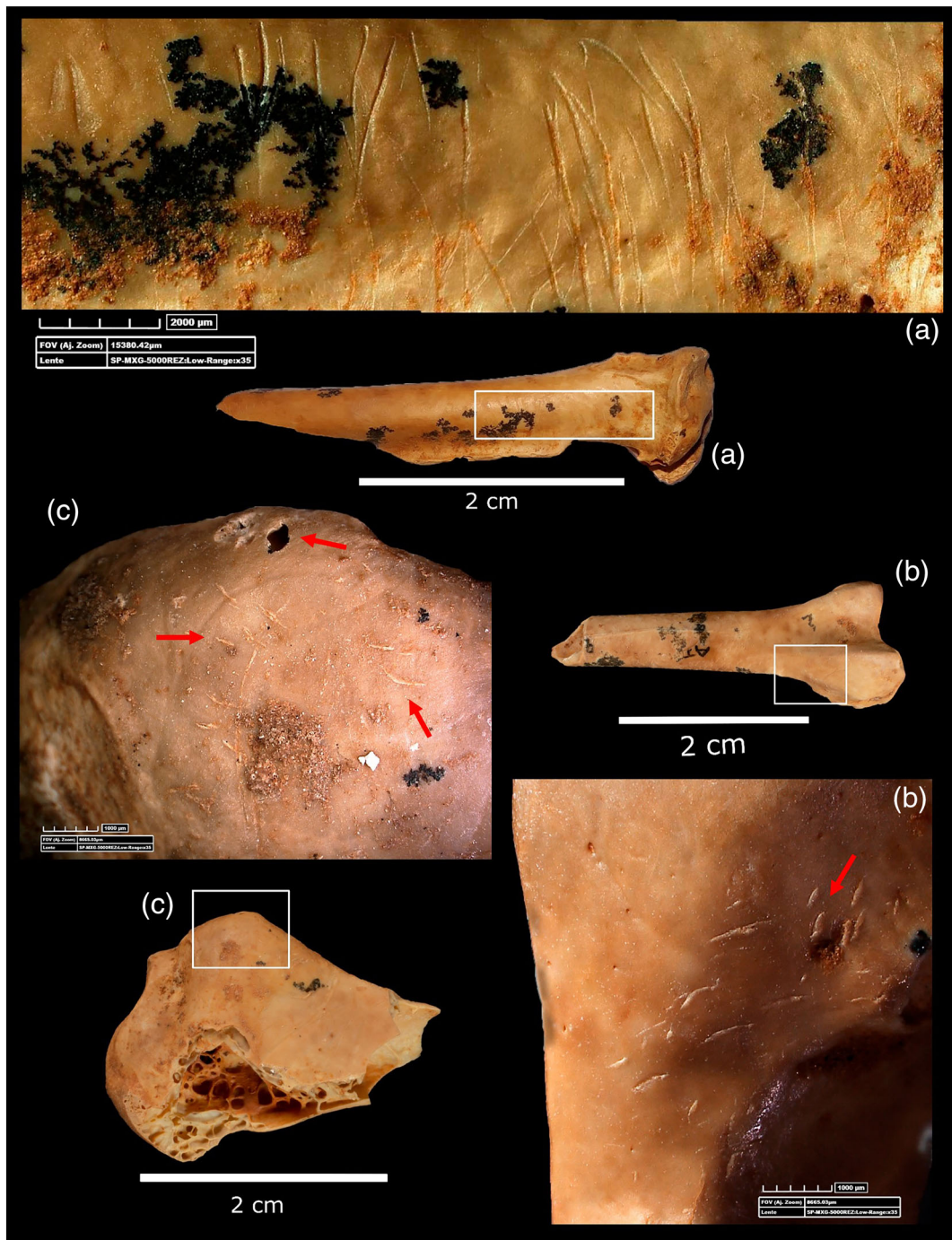


FIGURE 6 Scatching and chipping on different medium-sized elements. (a) Scatching on a tibiotarsus metaphysis; (b) Chipping on femur distal metaphysis; (c) Chipping and beak perforation on humerus proximal epiphysis [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3185)]

The white-tailed eagle (*H. albicilla*) is one of the most remarkable species found at the site. This raptor is a clear indicator for the presence of large water masses near the cave (Orta et al., 2020). This interpretation is reinforced by the presence in the studied assemblage of some small taxa from the Scolopacidae and Rallidae families. Previous studies have documented species that fit with these small taxa, including the Common Rail (*Rallus aquaticus*) or the Common Moorhen (*Gallinula chloropus*) (Núñez-Lahuerta et al., 2021).

The presence of other diurnal raptors in TE9d has been documented. Although we have not been able to identify all of these to species

level, some remains could be assigned to *Aquila* cf. *heliaca/adalberti*. Both species are found in forested areas, but in the case of *A. heliaca* this includes wetland areas (Meyburg et al., 2020). All these taxonomic associations fit with those obtained in previous studies at Sima del Elefante (Núñez-Lahuerta et al., 2021).

The presence of medullary bone tissue in a corvid ulna provides data on its seasonality. This feature indicates that the female died shortly before egg-laying (Whitehead, 2004). Some corvids tend to lay eggs during the spring, between February and May (Boarman & Heinrich, 2020). However, this varies depending on

the climate and species involved. In terms of age, adult individuals predominate.

The analysis of the material in this study was carried out considering all potential bird-accumulating agents: humans, mammalian carnivores and raptors. This is mainly since evidence of all these agents had already been found at different levels of the Sima del Elefante fossil record.

The absence of anthropogenic modifications such as cut marks and human tooth marks or anthropic breakage (Blasco et al., 2014, 2019; Blasco & Fernández Peris, 2009; Finlayson et al., 2012; Laroulandie, 2005; Laroulandie et al., 2016; Morin & Laroulandie, 2012; Peresani et al., 2011; Rodríguez-Hidalgo et al., 2019; Romandini et al., 2014) suggests that hominins were not involved in the accumulation of avifaunal remains from TE9d level.

On the other hand, no carnivorous mammal activity has been identified neither in terms of depressions, perforations, or gnawing. Not only works on bird remains from archeological sites have been considered (Rufà & Laroulandie, 2021; Rufà et al., 2016, 2017; Laroulandie, 2000; Lloveras, García, et al., 2018; Lloveras et al., 2020), but also neo-taphonomic studies of bird-accumulating mammalian carnivores (Arilla et al., 2020; Krajcarz & Krajcarz, 2014; Laroulandie, 2000; Rodríguez-Hidalgo et al., 2016; Rufà & Laroulandie, 2020).

The presence of raptor activity indicates that these agents were indeed involved in the avifaunal accumulation at TE9d level of Sima del Elefante. The signature of these predators has been observed mainly from digestion damage, anatomical representation and beak or claw modifications that are usually isolated on bones, unilaterally disposed (Table S1 and Figure S2). Beak/talon modifications are usually found in the epiphyses of both the anterior and posterior elements, and are also very small, considering the sizes of the taxa identified. Their morphologies are usually oval-circular or arc-shaped (Alonso et al., 2020; Bochenski et al., 1993, 1997, 2009; Bochenski & Nekrasov, 2001; Bochenski & Tomek, 1997; Laroulandie, 2000, 2002; Lloveras, Nadal, et al., 2014; Mlíkovský, 1996; Rufà & Laroulandie, 2019).

The anatomical representation reveals that long bones, specifically the tarsometatarsus, ulna, and carpometacarpus are the most abundant in all the weight size groups. Meanwhile, the axial (except the coracoid) and cranial skeleton are poorly represented. The results of this ratio provide no additional information on predators. The proximal/distal ratio is the only one that sheds more light on the accumulating agents in this case. The predominance of distal elements in all size groups coincides with the patterns observed for some diurnal raptors such as the Gyrfalcon (*Falco rusticolus*), Spanish Imperial Eagle (*Aquila adalberti*), and Bonelli's eagle (Bochenski et al., 1997, 1998; Lloveras, Nadal, et al., 2014). The greater representation of limb compared to core elements reflects the dietary patterns of most diurnal and nocturnal raptors studied (Bochenski & Tomek, 1997; Lloveras, Nadal, et al., 2014). However, the proportions of wing and leg elements are very close to 50% for all size groups, which does not help us to discriminate a specific accumulation agent.

The percentages of beak/talon modifications are 6.3% for the large bird group and 11.7% and 21.6% for the medium-sized and small groups, respectively. Among the weight sizes, the small bird group

seems to be the most susceptible to beak/talon modification. In general terms, perforations are the most abundant damage typology, followed by pecking and depressions. In all size groups, limb bones focus the beak/talon modifications. Meat-rich elements such as the humerus and femur seem to be the most heavily damaged among the three size groups. The morphology and locations of these marks are coincident with those observed on the bird remains consumed by modern raptors, such as the Spanish Imperial Eagle (Bochenski et al., 1997), White-tailed Eagle (Bochenski et al., 2009; Mlíkovský, 1996), Bonelli's eagle (Lloveras, Nadal, et al., 2014), or Eagle-Owl (Alonso et al., 2020; Bochenski et al., 1993; Bochenski & Nekrasov, 2001; Bochenski & Tomek, 1997; Laroulandie, 2000, 2002; Rufà & Laroulandie, 2019).

The digestion damage provides further evidence of raptor action on the assemblage. Light, followed by moderate damage, is the most abundant in the whole sample. Only one element from the medium-sized group was found with heavy damage. The small bird group accounts for the highest number of digested remains (29.7%). The medium-sized individuals present a greater variety of bone elements with digestion damage, although these remains represent just 2% of the total number of remains for this group. The case of the large-sized bird group is peculiar since only two posterior phalanges show digestion damage. These elements are particularly meat-poor parts, so it is unusual for a raptor to have ingested them.

Neo-taphonomic studies (Alonso et al., 2020; Bochenski et al., 2009; Laroulandie, 2002; Lloveras, Nadal, et al., 2014; Rufà & Laroulandie, 2019) suggest that when the size of the prey does not allow the predator to fully ingest it, wing elements tend to be less frequently ingested, while leg elements are ingested more often. In addition, it is also reported that meat-rich bones (humerus and femur) tend to be ingested more than meat-poor bones (ulna, radius, carpometacarpus, and tarsometatarsus). As stated above, this discrimination does not apply to small-sized individuals. In the studied sample, it is surprisingly the meat-poor elements that show the most digestion-related alteration. The ulnae, tarsometatarsi, posterior phalanges, radii and tibiotarsi are the most digested in the sample and, according to the literature, these would be the least likely to be consumed.

In terms of digestion damage, nocturnal raptors are likely to have played a greater role in the avifaunal accumulation of all size groups, as light-moderate degrees are mainly associated with the action of these predators. Species such as the Eagle-Owl (*Bubo bubo*) and Tawny-Owl (*Strix aluco*) could be potential accumulating agents. The identification of heavy damage on a medium-sized mandible may indicate the occasional contribution by a diurnal raptor. Considering the location of the damage, it could match the patterns made by the Spanish Imperial Eagle (Bochenski et al., 1997).

Some of the raptor species proposed as potential accumulating agents, have also been identified among the fossil remains in the assemblage. This is the case of *H. albicilla* and *Aquila cf. heliaca/adalberti*. In addition, species such as *B. bubo* and *S. aluco* have also been proposed as potential accumulating agents in the taphonomic study carried out on micromammals from the TE9 unit (Bennàsar et al., 2016).

There is little literature on the differentiation between diurnal and nocturnal raptor contribution, partly due to a lack of neotaphonomic studies. Raptor activity tends to be represented in most bird assemblages. Some of the sites where the activity of these predators has been documented are: Arbreda Cave, Mandrin Cave, Les Fieux, Arago, Lazaret, and Gran Dolina TD10.1 (Desclaux, 1992; Laroulandie et al., 2016; Lloveras et al., 2020; Lloveras, Garcia, et al., 2018; Rodríguez-Hidalgo et al., 2015). Our results are similar to those from sites such as Arbreda Cave and Les Fieux. In these two avifaunal assemblages nocturnal birds of prey played a greater role in the accumulation, specifically species such as *B. bubo* and *Bubo scandiacus*, while the diurnal raptor activity was scarce.

The studied assemblage shows some evidence, such as anatomical connections, the presence of immature individuals (1%) and one element with medullary tissue, that could be related to natural death accumulation (Laroulandie, 2010). For this reason, we cannot rule out the possibility that some of the remains could have been accumulated by natural death, as previous studies have already considered, particularly in terms of species such as *Corvus pliccaenus* (Núñez-Lahuerta et al., 2021).

In the southern part of the site, being close to the entrance fissure, we find the strongest sedimentary packages (≈ 2 m), which is precisely where the greatest number of bird remains accumulate. This could be caused by the fact that rock-dwelling birds could have nested in this part of the cavity, as well as in the trees that would be found at the limits of the fissure.

Regarding the interpretation of this assemblage, the results coincide with those obtained previously at the site (Bennàsar et al., 2016; Núñez-Lahuerta et al., 2021). On the other hand, as no in-depth taphonomic analysis related to the bird accumulating agents at Sima del Elefante had been carried out so far, the results and interpretations presented here complement the general interpretation of the site (Huguet et al., 2013, 2017; Rosas et al., 2006).

6 | CONCLUSIONS

Bird remains are very frequently found at archeological sites. Characterizing them and determining the origin of their accumulation is key to understanding the processes of formation of the assemblage as well as the interaction between different agents.

The zooarchaeological and taphonomic analyzes of the avifaunal assemblage from TE9d level at Sima del Elefante has allowed us to establish a series of inferences about its origin of accumulation, the agents that acted there and the landscape exist around the site:

1. At Sima del Elefante, the abundance of birds is higher than at most other sites with a similar chronology in the Iberian Peninsula, such as Quibas (Sánchez-Marco, 2005), Huéscar (Sánchez-Marco, 2005), Cueva Victoria (Gibert & Ferràndez-Cañadell, 2015; Sánchez-Marco, 2012), Cal Guardiola (Meijer et al., 2016), and Barranc de la Boella (Pineda et al., 2017). At level TE9d, adult corvids are the most widely represented taxa.

2. Individuals associated with *Aquila cf. heliaca/adalberti*, *Aquila/Hieraaetus* and two different groups of eagles (*Aquila* sp. 1 and *Aquila* sp. 2) have also been documented. The White-tailed Eagle (*H. albicilla*) is one of the most prominent. Together with the small individuals identified as Rallidae and Scolopacidae, these are clear indicators of aquatic environments.
3. Raptors were the main accumulating agents at the TE9d avifaunal assemblage. Nocturnal raptors would have been the principal predator, with a lesser contribution by diurnal raptors. Considering the patterns observed in neo-taphonomic studies, raptors such as the White-tailed Eagle (*H. albicilla*), Spanish Imperial Eagle (*A. adalberti*), Golden Eagle (*Aquila chrysaetos*), Gyrfalcon (*F. rusticolus*), or Peregrine Falcon (*Falco peregrinus*) could have been potential accumulating agents. In terms of nocturnal raptors, the Eagle-Owl (*B. bubo*), Long-eared Owl (*Asio otus*), or Tawny-Owl (*S. aluco*) could have participated in accumulating the bird assemblage. Some of these species (*Bubo* and *S. aluco*) have already been proposed as accumulating agents in taphonomic studies of microfauna from the same site.
4. No anthropogenic or mammalian carnivore evidence has been documented. However, the natural death of some individuals who nested on the rocky walls cannot be ruled out.

In summary, this work reveals the accumulation processes of bird remains in level TE9d of Sima del Elefante. Diurnal and nocturnal birds of prey, as well as the natural deaths of the individuals themselves, have probably been the main causes of the accumulation of the remains. These results contribute to a better understanding of the palaeoecological and paleoenvironmental niche of both the fauna identified, as well as the humans that frequented the Sierra de Atapuerca 1.2 MA.

ACKNOWLEDGMENTS

We would like to thank the organizers of the ICAZ Bird Working Group in Bergen 2022 for the invitation to participate in the congress volume and the Atapuerca research team and the participants in the fieldwork for that project. The authors thank Maria Dolors Guillén for the photos of the material and Javier Quesada for allowing us access to the osteological collection at the *Museu de Ciències Naturals de Barcelona*. This research was conducted as part of competitive projects PGC2018-093925-B-C32 (MICINN-FEDER); AGAUR SGR 2017-1040; URV 2014, 2015, and 2016 PFR-URV-B2-17; [100576, 2014], C.N.-L. is the recipient of a Juan de la Cierva-Formación contract (FJC2020-044561-I), supported by the MCIN and co-financed by the NextGenerationEU/PRTR. The research technical support of Maria Dolors Guillén was supported by the Spanish Ministry of Science and Innovation through the “María de Maeztu” excellence accreditation (CEX2019-000945-M).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Mario Marqueta  <https://orcid.org/0000-0002-2442-8832>

Rosa Huguet  <https://orcid.org/0000-0002-1750-6249>

Carmen Núñez-Lahuerta  <https://orcid.org/0000-0002-2882-6061>

REFERENCES

- Alonso, G., Rufà, A., Arilla, M., & Blasco, R. (2020). Taphonomic signature of the Eurasian eagle-owl (*Bubo bubo*) on the avian accumulation of Cau del Duc (Lleida, Spain). *Historical Biology*, 32(10), 1320–1333. <https://doi.org/10.1080/08912963.2019.1587614>
- Andrews, P., & Cook, J. (1990). *Owls, caves and fossils: Predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset*. University of Chicago Press.
- Arilla, M., Rufà, A., Rosell, J., & Blasco, R. (2020). Small carnivores' cave-dwelling: Neo-taphonomic study of a badger (*Meles meles*) sett and its archaeological implications. *Historical Biology*, 32(7), 951–965. <https://doi.org/10.1080/08912963.2018.1558449>
- Arnold, L., & Demuro, M. (2015). Insights into TT-OSL signal stability from single-grain analyses of known-age deposits at Atapuerca, Spain. *Quaternary Geochronology*, 30, 472–478. <https://doi.org/10.1016/j.quageo.2015.02.005>
- Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E., & Berge, J. C. V. (1993). *Handbook of avian anatomy: Nomina Anatomica Avium*. Nuttall Ornithological Club.
- Bennàsar, M., Cáceres, I., & Cuenca-Bescós, G. (2016). Palaecological and microenvironmental aspects of the first European hominids inferred from the taphonomy of small mammals (Sima del Elefante, Sierra de Atapuerca, Spain). *Comptes Rendus Palevol*, 15(6), 635–646. <https://doi.org/10.1016/j.crpv.2015.07.006>
- Bermúdez de Castro, J. M., Martínón-Torres, M., Gómez-Robles, A., Prado-Simón, L., Martín-Francés, L., Lapresa, M., Olejniczak, A., & Carbonell, E. (2011). Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A comparative morphological study. *Journal of Human Evolution*, 61(1), 12–25. <https://doi.org/10.1016/j.jhevol.2011.03.005>
- Binford, L. R. (1978). *Nunamiut ethnoarchaeology*. Academic Press.
- Blasco, R., & Fernández Peris, J. (2009). Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *Journal of Archaeological Science*, 36, 2213–2223. <https://doi.org/10.1016/j.jas.2009.06.006>
- Blasco, R., Finlayson, C., Rosell, J., Marco, A. S., Finlayson, S., Finlayson, G., Negro, J. J., Pacheco, F. G., & Vidal, J. R. (2014). The earliest pigeon fanciers. *Scientific Reports*, 4(1), 1–7. <https://doi.org/10.1038/srep05971>
- Blasco, R., Rosell, J., Sánchez-Marco, A., Gopher, A., & Barkai, R. (2019). Feathers and food: Human-bird interactions at Middle Pleistocene Qesem Cave, Israel. *Journal of Human Evolution*, 136, 102653. <https://doi.org/10.1016/j.jhevol.2019.102653>
- Boarman, W. I., & Heinrich, B. (2020). Common Raven (*Corvus corax*), version 1.0. In S. M. Billerman (Ed.), *Birds of the world*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.comrav.01>
- Bochenski, Z. M. (2005). Owls, diurnal raptors and humans: signatures on avian bones. In T. O'Connor (Ed.), *Biosphere to lithosphere. New studies in vertebrate taphonomy* (pp. 31–45). OxbowBooks.
- Bochenski, Z. M., Huhtala, K., Jussila, P., Pulliainen, E., Tornberg, R., & Tunkkari, P. S. (1998). Damage to bird bones in pellets of gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science*, 25(5), 425–433. <https://doi.org/10.1006/jasc.1997.0213>
- Bochenski, Z. M., Korovin, V. A., Nekrasov, A. E., & Tomek, T. (1997). Fragmentation of bird bones in food remains of Imperial Eagles (*Aquila heliaca*). *International Journal of Osteoarchaeology*, 7, 165–171. [https://doi.org/10.1002/\(SICI\)1099-1212\(199703\)7:2<165::AID-OA332>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1099-1212(199703)7:2<165::AID-OA332>3.0.CO;2-4)
- Bochenski, Z. M., & Nekrasov, A. E. (2001). The taphonomy of sub-Atlantic bird remains from Bazhukovo III, Ural Mountains, Russia. *Acta Zoologica Cracoviensia*, 44(2), 93–106.
- Bochenski, Z. M., & Tomek, T. (1997). Preservation of bird bones: Erosion versus digestion by owls. *International Journal of Osteoarchaeology*, 7(4), 372–387. [https://doi.org/10.1002/\(SICI\)1099-1212\(199707\)08:7:4<372::AID-OA355>3.0.CO;2-W](https://doi.org/10.1002/(SICI)1099-1212(199707)08:7:4<372::AID-OA355>3.0.CO;2-W)
- Bochenski, Z. M., Tomek, T., Boev, Z., & Mitev, I. (1993). Patterns of bird bone fragmentation in pellets of the Tawny Owl (*Strix aluco*) and the Eagle Owl (*Bubo bubo*) and their taphonomic implications. *Acta Zoologica Cracoviensia*, 36(2), 313–328.
- Bochenski, Z. M., Tomek, T., Tornberg, R., & Wertz, K. (2009). Distinguishing nonhuman predation on birds: Pattern of damage done by the white-tailed eagle *Haliaeetus albicilla*, with comments on the punctures made by the golden eagle *Aquila chrysaetos*. *Journal of Archaeological Science*, 36(1), 122–129. <https://doi.org/10.1016/j.jas.2008.07.018>
- Bochenski, Z. M., & Tornberg, R. (2003). Fragmentation and preservation of bird bones in uneaten food remains of the Gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science*, 30(12), 1665–1671. [https://doi.org/10.1016/S0305-4403\(03\)00069-4](https://doi.org/10.1016/S0305-4403(03)00069-4)
- Bramwell, D., Yalden, D. W., & Yalden, P. E. (1987). Black grouse as the prey of the golden eagle at an archaeological site. *Journal of Archaeological Science*, 14(2), 195–200. [https://doi.org/10.1016/0305-4403\(87\)90006-9](https://doi.org/10.1016/0305-4403(87)90006-9)
- Carbonell, E., Bermúdez de Castro, J. M., Parés, J. M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., Van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D. J., Martínón-Torres, M., Rodríguez, X. P., Stock, G. M., Vergès, J. M., Allué, E., ... Arsuaga, J. L. (2008). The first hominin of Europe. *Nature*, 452, 465–469. <https://doi.org/10.1038/nature06815>
- Cohen, A., & Serjeantson, D. (1996). *A manual for the identification of Bird Bones from archaeological sites* (Revised ed.). A. P. Ltd.
- Cuenca-Bescós, G., Blain, H. A., Rofes, J., Lozano-Fernández, I., López-García, J. M., Duval, M., Galán, J., & Núñez-Lahuerta, C. (2015). Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): Biochronological implications and significance of the Jaramillo subchron. *Quaternary International*, 389, 148–158. <https://doi.org/10.1016/j.quaint.2014.12.059>
- Cuenca-Bescós, G., & García, N. (2007). Biostratigraphic succession of the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). In Late neogene and quaternary biodiversity and evolution (regional developments and interregional correlations: proceedings of the 18th International Senckenberg Conference. Volume II). 259, 99–110.
- de Lombera-Hermida, A., Bargalló, A., Terradillos-Bernal, M., Huguet, R., Vallverdú, J., García-Antón, M. D., Mosquera, M., Ollé, A., Sala, R., Carbonell, E., & Rodríguez-Álvarez, X. P. (2015). The lithic industry of Sima del Elefante (Atapuerca, Burgos, Spain) in the context of Early and Middle Pleistocene technology in Europe. *Journal of Human Evolution*, 82, 95–106. <https://doi.org/10.1016/j.jhevol.2015.03.002>
- Desclaux, E. (1992). Les petits vertèbres de la Caune de l'Arago à Tautavel. *Bulletin du Musée d'Anthropologie préhistorique de Monaco*, 35, 35–64.
- Driesch, A., & Boessneck, J. (1976). Castro do Zambujal Die Fauna. *Studien über frühe Tierknochenfunde von der Iberischen Halbinsel*, 5, 4–142.
- Ericson, P. G. P. (1987). Interpretations of archaeological bird remains: A taphonomic approach. *Journal of Archaeological Science*, 14(1), 65–75. [https://doi.org/10.1016/S0305-4403\(87\)80006-7](https://doi.org/10.1016/S0305-4403(87)80006-7)
- Fernández-Jalvo, Y., & Andrews, P. (2016). *Atlas of taphonomic identifications: 1001+ images of fossil and recent mammal bone modification*. Springer. <https://doi.org/10.1007/978-94-017-7432-1>
- Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., Bortolotti, G. R., Finlayson, G., Sánchez-Marco, A., Giles Pacheco, F., Rodríguez Vidal, J., Carrión, J. S., & Rodríguez Llanes, J. M. (2012). Birds of a feather:

- Neanderthal exploitation of raptors and corvids. *PLoS ONE*, 7(9), e45927. <https://doi.org/10.1371/journal.pone.0045927>
- Fiore, I., Gala, M., & Tagliacozzo, A. (2004). Ecology and subsistence strategies in the eastern Italian Alps during the middle Palaeolithic. *International Journal of Osteoarchaeology*, 14(3–4), 273–286. <https://doi.org/10.1002/oa.761>
- García, E., & Menéndez, M. (1998). Instrumentos musicales paleolíticos: la flauta magdaleniense de la Cueva de la Güelga (Asturias). *Espacio Tiempo Y Forma. Serie I, Prehistoria Y Arqueología*, 11). <https://doi.org/10.5944/etfi.11.1998.4671>
- Gaudzinski-Windheuser, S., & Niven, L. (2009). Hominin subsistence patterns during the Middle and Late Paleolithic in northwestern Europe. In J. J. Hublin & M. P. Richards (Eds.), *The evolution of Hominin diets* (pp. 99–111). Springer. https://doi.org/10.1007/978-1-4020-9699-0_7
- Gibert, L., & Ferrández-Cañadell, C. (2015). Geología y paleontología de Cueva Victoria. *Mastia: Revista del Museo Arqueológico Municipal de Cartagena*, 11–13.
- Huguet, R., Saladié, P., Cáceres, I., Díez, C., Rosell, J., Bennàsar, M., Blasco, R., Esteban-Nadal, M., Gabucio, M. J., Rodríguez-Hidalgo, A., & Carbonell, E. (2013). Successful subsistence strategies of the first humans in South-Western Europe. *Quaternary International*, 295, 168–182. <https://doi.org/10.1016/j.quaint.2012.11.015>
- Huguet, R., Vallverdú, J., Rodríguez-Álvarez, X. P., Terradillos-Bernal, M., Bargalló, A., Lombera-Hermida, A., Menéndez, L., Modesto-Mata, M., Van der Made, J., Soto, M., Blain, H. A., García, N., Cuenca-Bescós, G., Gómez-Merino, G., Pérez-Martínez, R., Expósito, I., Allué, E., Rofes, J., Burjachs, F., ... Carbonell, E. (2017). Level TE9c of Sima del Elefante (Sierra de Atapuerca, Spain): A comprehensive approach. *Quaternary International*, 433, 278–295. <https://doi.org/10.1016/j.quaint.2015.11.030>
- Krajcarz, M., & Krajcarz, M. T. (2014). The red fox (*Vulpes vulpes*) as an accumulator of bones in cave like environments. *International Journal of Osteoarchaeology*, 24(4), 459–475. <https://doi.org/10.1002/oa.2233>
- Laroulandie, V. (2000). Taphonomie et archéozoologie des Oiseaux en grotte: applications aux sites paléolithiques du Bois-Ragot (Vienne), de Combe Saunière (Dordogne) et de La Vache (Ariège) Ph.D. Université Sciences et Technologies-Bordeaux I, Bordeaux.
- Laroulandie, V. (2001). Les traces liées à la boucherie, à la cuisson et à la consommation d'oiseaux: apport de l'expérimentation. In L. Bourguignon, I. Ortega, & M. C. Frère Sautot (Eds.), *Préhistoire et Approche Expérimentale* (pp. 97–108).
- Laroulandie, V. (2002). Damage to Pigeon long bones in pellets of the Eagle Owl *Bubo* and food remains of Peregrine Falcon, *Falco peregrinus*: Zooarchaeological implications. *Acta Zoologica Cracoviensia*, 45, 331–339.
- Laroulandie, V. (2005). *Bird exploitation pattern: The case of ptarmigan *Lagopus* sp. in the upper Magdalenian site of La Vache (Ariège, France)*. *Documenta Archaeobiologiae* (Vol. 3) (pp. 165–178). Verlag Marie Leidorf.
- Laroulandie, V. (2010). Alpine chough *Pyrrhocorax graculus* from Pleistocene sites between Pyrenees and Alps: natural versus. In Groningen Archaeological Studies, W. Prummel, D. Brinkhuizen, & J. Zeiler (Eds.), *Birds in archaeology: Proceedings of the 6th meeting of the ICAZ bird working Group in Groningen (23.8-27.8. 2008)* (Vol. 12). 219.
- Laroulandie, V., Faivre, J. P., Gerbe, M., & Murre, V. (2016). Who brought the bird remains to the Middle Palaeolithic site of Les Fieux (Southwestern, France)? Direct evidence of a complex taphonomic story. *Quaternary International*, 421, 116–133. <https://doi.org/10.1016/j.quaint.2015.06.042>
- Lentacker, A., & Van Neer, W. (1996). Bird remains from two sites on the Red Sea coast and some observations on medullary bone. *International Journal of Osteoarchaeology*, 6, 488–496. [https://doi.org/10.1002/\(SICI\)1099-1212\(199612\)6:5<488::AID-OA301>3.0.CO;2-W](https://doi.org/10.1002/(SICI)1099-1212(199612)6:5<488::AID-OA301>3.0.CO;2-W)
- Lloveras, L., Cosso, A., Solé, J., Claramunt-López, B., & Nadal, J. (2018). Taphonomic signature of golden eagles (*Aquila chrysaetos*) on bone prey remains. *Historical Biology*, 30(6), 835–854. <https://doi.org/10.1080/08912963.2017.1319830>
- Lloveras, L., García, L., Maroto, J., Soler, J., & Soler, N. (2018). The bird assemblage from the Middle Palaeolithic level I of Arbreda Cave: A taphonomic story. *Journal of Archaeological Science: Reports*, 21, 758–770. <https://doi.org/10.1016/j.jasrep.2018.08.040>
- Lloveras, L., García, L., Marqueta, M., Maroto, J., Soler, J., & Soler, N. (2020). The role of birds in Upper Palaeolithic sites: Zooarchaeological and taphonomic analysis of the avian remains from Arbreda Cave (Serinyà, Northeast Iberia). *Quaternary International*, 626–627, 22–32. <https://doi.org/10.1016/j.quaint.2020.10.022>
- Lloveras, L., Moreno-García, M., Nadal, J., & Thomas, R. (2014). Blind test evaluation of accuracy in the identification and quantification of digestion corrosion damage on leporid bones. *Quaternary International*, 330, 150–155. <https://doi.org/10.1016/j.quaint.2013.07.033>
- Lloveras, L., Nadal, J., Moreno-García, M., Thomas, R., Anglada, J., Baucells, J., Martorell, C., & Vilasis, D. (2014). The role of the Egyptian vulture (*Neophron percnopterus*) as a bone accumulator in cliff rock shelters: An analysis of modern bone nest assemblages from North-Eastern Iberia. *Journal of Archaeological Science*, 44, 76–90. <https://doi.org/10.1016/j.jas.2014.01.018>
- Lloveras, L., Thomas, R., Lourenço, R., Caro, J., & Dias, A. (2014). Understanding the taphonomic signature of Bonelli's Eagle (*Aquila fasciata*). *Journal of Archaeological Science*, 49, 455–471. <https://doi.org/10.1016/j.jas.2014.06.005>
- López-García, J. M., Blain, H. A., de Marfà, R., García, A., Martinell, J., Bennàsar, M. L., & Cuenca-Bescós, G. (2011). Small mammals from the Middle Pleistocene layers of the Sima del Elefante (Sierra de Atapuerca, Burgos, northwestern Spain). *Geologica Acta*, 9(1), 29–43. <https://doi.org/10.1344/105.000001644>
- Louchart, A., Bedetti, C. P., & Pavia, M. (2005). A new species of eagle (Aves: Accipitridae) close to the steppe eagle, from the Pleistocene of Corsica and Sardinia, France and Italy. *Health or Wealth: Reassessment of an Old Dilemma*, 272(5–6), 121–148. <https://doi.org/10.1127/pala/272/2005/121>
- Louchart, A., Mourer-Chauviré, C., Güleç, E., Howell, F. C., & White, T. D. (1998). L'avifaune de Dursunlu, Turquie, Pléistocène inférieur: climat, environnement et biogéographie. *Comptes Rendus de l'Académie Des Sciences - Series IIA - Earth and Planetary Science*, 327(5), 341–346. [https://doi.org/10.1016/S1251-8050\(98\)80053-0](https://doi.org/10.1016/S1251-8050(98)80053-0)
- Lyman, R. L. (1994a). Quantitative units and terminology in zooarchaeology. *American Antiquity*, 59(1), 36–71. <https://doi.org/10.2307/3085500>
- Lyman, R. L. (1994b). *Vertebrate taphonomy*. Cambridge University Press. <https://doi.org/10.1017/CBO9781139878302>
- Mannermaa, K., & Rainio, R. (2020). Needle case, sound instrument or something else? A worked and ornamented swan (*Cygnus* sp.) ulna from a Late Mesolithic male burial, Yuzhnyi Oleniy Ostrov, Northwest Russia. *Quaternary International*, 543, 34–42. <https://doi.org/10.1016/j.quaint.2020.02.032>
- Meijer, H. J. M., Pavia, M., Madurell-Malapeira, J., & Alba, D. M. (2016). A revision of fossil eagle owls (Aves: Strigiformes: *Bubo*) from Europe and the description of a new species, *Bubo ibericus*, from Cal Guardiola (NE Iberian Peninsula). *Historical Biology*, 29(6), 822–832. <https://doi.org/10.1080/08912963.2016.1247836>
- Meyburg, B. U., Kirwan, G. M., & de Juana, E. (2020). Spanish Imperial Eagle (*Aquila adalberti*), version 1.0. In J. del Hoyo, A. Elliot, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Birds of the world*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.spaeag1.01>
- Mlíkovský, J. (1996). New data on the food of the White-tailed Sea Eagle (*Haliaeetus albicilla*) in the Svjatoj Nos wetlands, Lake Baikal. *Buteo*, 8, 115–118.

- Morin, E., & Laroulandie, V. (2012). Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE*, 7(3), e32856. <https://doi.org/10.1371/journal.pone.0032856>
- Mourer-Chauviré, C. (1989). Les oiseaux. In M. Campy, J. Chaline, & M. Vuillemeij (Eds.), *La Baume de Gigny (Jura)*. *Gallia Préhistoire (supplement)* (pp. 121–129).
- Mourer-Chauviré, C., & Bonifay, M. F. (2018). The birds from the Early Pleistocene of Ceysaguet (Lavoûte-sur-Loire, Haute-Loire, France): description of a new species of the genus *aquila*. *Quaternaire. Revue de l'Association française Pour l'étude du Quaternaire*, 29(3), 183–194. <https://doi.org/10.4000/quaternaire.9957>
- Núñez-Lahuerta, C., Cuenca-Bescós, G., & Hugué, R. (2016). First report on the birds (Aves) from level TE7 of Sima del Elefante (Early Pleistocene) of Atapuerca (Spain). *Quaternary International*, 421, 12–22. <https://doi.org/10.1016/j.quaint.2015.08.016>
- Núñez-Lahuerta, C., Galán, J., Cuenca-Bescós, G., & Hugué, R. (2021). Birds from Sima del Elefante, Atapuerca, Spain: Palaeoecological implications in the oldest human bearing levels of the Iberian Peninsula. *Rivista Italiana di Paleontologia e Stratigrafia*, 127(2). <https://doi.org/10.13130/2039-4942/16027>
- Ollé, A., Mosquera, M., Rodríguez, X. P., de Lombera-Hermida, A., García-Antón, M. D., García-Medrano, P., Peña, L., Menéndez, L., Navazo, M., Terradillos, M., Bargalló, A., Márquez, B., Sala, R., & Carbonell, E. (2013). The Early and Middle Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). *Quaternary International*, 295, 138–167. <https://doi.org/10.1016/j.quaint.2011.11.009>
- Orta, J., Kirwan, G. M., Christie, D. A., Boesman, P. F. D., & Marks, J. S. (2020). White-tailed Eagle (*Haliaeetus albicilla*), version 1.0. In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Birds of the world*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.whteag.01>
- Parés, J. M., Pérez-González, A., Rosas, A., Benito, A., Bermúdez de Castro, J. M., Carbonell, E., & Hugué, R. (2006). Matuyama-age lithic tools from the Sima del Elefante site, Atapuerca (northern Spain). *Journal of Human Evolution*, 50(2), 163–169. <https://doi.org/10.1016/j.jhevol.2005.08.011>
- Peresani, M., Fiore, I., Gala, M., Romandini, M., & Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky BP, Italy. *Proceedings of the National Academy of Sciences*, 108(10), 3888–3893. <https://doi.org/10.1073/pnas.1016212108>
- Pineda, A., Saladié, P., Hugué, R., Cáceres, I., Rosas, A., Estalrich, A., García-Taberner, A., & Vallverdú, J. (2017). Changing competition dynamics among predators at the late Early Pleistocene site Barranc de la Boella (Tarragona, Spain). *Palaeogeography Palaeoclimatology Palaeoecology*, 477, 10–26. <https://doi.org/10.1016/j.palaeo.2017.03.030>
- Rodríguez-Hidalgo, A., Morales, J. I., Cebrià, A., Courtenay, L. A., Fernández-Marchena, J. L., García-Argudo, G., Marín, J., Saladié, P., Soto, M., Tejero, J. M., & Fullola, J. M. (2019). The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. *Science Advances*, 5(11), eaax1984. <https://doi.org/10.1126/sciadv.aax1984>
- Rodríguez-Hidalgo, A., Saladié, P., Marín, J., & Canals, A. (2016). Bird-bone modifications by Iberian lynx: A taphonomic analysis of non-ingested red-legged partridge remains. *Quaternary International*, 421, 228–238. <https://doi.org/10.1016/j.quaint.2015.11.078>
- Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., & Carbonell, E. (2015). Hominin subsistence and site function of TD10. 1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. *Journal of Quaternary Science*, 30(7), 679–701. <https://doi.org/10.1002/jqs.2815>
- Romandini, M., Peresani, M., Laroulandie, V., Metz, L., Pastoors, A., Vaquero, M., & Slimak, L. (2014). Convergent evidence of eagle talons used by late Neanderthals in Europe: A further assessment on symbolism. *PLoS ONE*, 9(7), e101278. <https://doi.org/10.1371/journal.pone.0101278>
- Rosas, A., Hugué, R., Pérez-González, A., Carbonell, E., Bermúdez de Castro, J. M., Vallverdú, J., van der Made, J., Allué, E., García, N., Martínez-Pérez, R., Rodríguez, J., Sala, R., Saladié, P., Benito, A., Martínez Maza, C., Bastir, M., Sánchez, A., & Parés, J. M. (2006). The “sima del Elefante” cave site at Atapuerca (Spain). *Estudios Geológicos*, 62(1), 327–348.
- Rosas, A., Pérez-González, A., Carbonell, E., van der Made, J., Sánchez, A., Laplana, C., Cuenca-Bescós, G., Parés, J. M., & Hugué, R. (2001). Le gisement pléistocène de la “Sima del Elefante” (Sierra de Atapuerca, Espagne). *L'Anthropologie*, 105(2), 301–312. [https://doi.org/10.1016/S0003-5521\(01\)80018-2](https://doi.org/10.1016/S0003-5521(01)80018-2)
- Rufá, A., Blasco, R., Roger, T., & Moncel, M. H. (2016). 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). *Quaternary International*, 421, 46–61. <https://doi.org/10.1016/j.quaint.2015.05.016>
- Rufá, A., Blasco, R., Roger, T., Rué, M., & Daujeard, C. (2017). A rallying point for different predators: the avian record from a Late Pleistocene sequence of Grotte des Barasses II (Balazuc, Ardèche, France). *Archaeological and Anthropological Sciences*, 10(6), 1459–1476. <https://doi.org/10.1007/s12520-017-0469-6>
- Rufá, A., & Laroulandie, V. (2019). Prey size as a critical factor for bird bone taphonomy in Eagle Owl (*Bubo bubo*) pellets. *Scientific Reports*, 9(1), 1–13. <https://doi.org/10.1038/s41598-019-55721-7>
- Rufá, A., & Laroulandie, V. (2020). Carnívoros y carroñeros. Una nueva visión sobre la depredación de los lobos sobre las aves carroñeras y su implicación en el registro arqueológico. *ArkeoGazte*, 10, 127–140.
- Rufá, A., & Laroulandie, V. (2021). Unravelling the Taphonomic stories of bird bones from the middle Pleistocene layer VIII of Grotte Vaufray, France. *Quaternary*, 4(4), 30. <https://doi.org/10.3390/quat4040030>
- Sánchez-Marco, A. (2004). Avian zoogeographical patterns during the Quaternary in the Mediterranean region and paleoclimatic interpretation. *Ardeola*, 51(1), 91–132.
- Sánchez-Marco, A. (2005). Avifaunas cuaternarias de la península ibérica: sistemática, paleoecología y paleozoogeografía. Tesis doctoral, Universidad Autónoma de Madrid, 559 pp.
- Sánchez-Marco, A. (2012). Aves del Pleistoceno inferior de Cueva Victoria (costa sudoriental mediterránea de la Península Ibérica). *Mastia: Revista del Museo Arqueológico Municipal de Cartagena*, 11, 253–267.
- Sánchez-Marco, A. (2018). Aves fósiles de la Península Ibérica, Canarias y Baleares: balance de los estudios realizados. *PH: Boletín del Instituto Andaluz del Patrimonio Histórico*, 26(94), 154–181.
- Serjeantson, D. (2002). Goose husbandry in medieval England, and the problem of ageing goose bones. *Acta Zoologica Cracoviensia*, 45, 39–54.
- Serjeantson, D. (2009). *Birds*. Cambridge University Press.
- Soressi, M., Rendu, W., Texier, J. P., Claud, E., Daulny, L., D'Errico, F., Laroulandie, V., Maureille, B., Niclot, M., Schwartz, S., & Tillier, A. M. (2008). Pech-de-l'Azé I (Dordogne, France): Nouveau regard sur un gisement moustérien de tradition acheuléenne connu depuis le XIX siècle. In J. Jaubert, J.-G. Bordes, & I. Ortega (Eds.), *Les Sociétés Paléolithiques d'un Grand Sud-Ouest: Nouveaux Gisements, Nouvelles Méthodes, Nouveaux Résultats* (pp. 95–132). Société Préhistorique Française.
- Steadman, D. W., Plourde, A., & Burley, D. V. (2002). Prehistoric butchery and consumption of birds in the Kingdom of Tonga, South Pacific. *Journal of Archaeological Science*, 29(6), 571–584. <https://doi.org/10.1006/jasc.2001.0739>
- Tomek, T., & Bochenki, Z. M. (2000). *The comparative osteology of European corvids (Aves: Corvidae), with a key to the identification of their skeletal elements*. Instytutu Systematyki i Ewolucji Zwierząt PAN.

- Van der Made, J. (2001). Les ongulés d'Atapuerca. Stratigraphie et biogéographie. *L'Anthropologie*, 105(1), 95–113. [https://doi.org/10.1016/S0003-5521\(01\)80008-X](https://doi.org/10.1016/S0003-5521(01)80008-X)
- Vilette, P. (1983). Avifaunes du Pléistocène final et de l'Holocène dans le Sud de la France et en Catalogne. *Atacina Carcassonne*, 11, 1–90.
- Vilette, P. (1999). Bilan provisoire sur la chasse aux oiseaux pendant le leptolithique dans le sud de la France. *Les Faciès leptolithiques du nord-ouest méditerranéen: milieux naturels et culturels*, actes du XXIVe congrès préhistorique de France, septembre 1994. Carcassonne, Paris, Éditions Société préhistorique française, 267–276.
- Whitehead, C. C. (2004). Overview of bone biology in the egg-laying hen. *Poultry Science*, 83(2), 193–199. <https://doi.org/10.1093/ps/83.2.193>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Marqueta, M., Huguet, R., & Núñez-Lahuerta, C. (2022). Accumulation agents and bird assemblages: The case of the TE9d level at Sima del Elefante (Sierra de Atapuerca, Spain). *International Journal of Osteoarchaeology*, 1–16. <https://doi.org/10.1002/oa.3185>