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The fossil avian assemblage from Cova Foradada (Calafell, Spain) during the Late Pleistocene to Holocene transition

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ABSTRACT

The end of the Pleistocene to the Holocene is a moment of particular interest, as several environmental changes coincided with some significant culture shifts: the Middle-to-Upper Palaeolithic and the Palaeolithic to Neolithic transitions. Here we present the analysis of the environmental conditions during this period in the Northeast Iberian Peninsula, based on the bird remains from Cova Foradada (Calafell, Tarragona), a site known for its archaeological record, including the symbolic use of imperial eagle phalanges. The stratigraphic sequence of the site is divided into five units, spanning from the Late Pleistocene (Units V to III) to the Northgrippian (Units II and I). A total of 1310 avian remains from these five units have been analysed, revealing the presence of at least 25 bird taxa. This suggests a landscape dominated by open areas with forest or scattered trees. The presence of four species, currently absent around the site, could be related to habitat expansions during colder periods, or to sporadic visits to the area. The layers in Unit IV show a trend towards a reduction in woodlands and an increase of open areas, which may be related to the Heinrich 4 event (ca. 40Ka). The layers in Unit III show the lowest proportion of woodlands and the highest proportions of rocky areas in the sequence. In the Holocene units the presence of water bodies is indicated by the presence of aquatic taxa. Diurnal birds of prey appear to be the main contributors to the bird accumulation, and probably also contributed to the accumulation of leporids. The impact of humans on birds at the site has been documented in several remains, confirming the mixed origin of the avian accumulation and contributing to increasing cases of interaction between humans and large diurnal raptors during Iberian prehistory.

1. Introduction

The Late Pleistocene and the Early Holocene are characterized by significant climatic and landscape variability (Naughton et al., 2009; González-Sampériz et al., 2017). Climate variations generally impacted ecosystems, which is detected in the size of mammal populations and their distribution, with extirpations and appearances of species adapted to changing environments (Ersmark et al., 2019; Gamboa et al., 2024). These landscape variations, associated with cyclic climatic changes,

shaped the transition between the Middle and Upper Palaeolithic, with the demise of Neanderthal populations, the emergence of anatomically modern humans, the development and geographic distribution of the Upper Palaeolithic cultures, and the late arrival of the Neolithic (Benazzi et al., 2011; López-García et al., 2012; Timmermann, 2020). This strong climatic variability also affected the distribution of the birds, leading to changes in the distribution of avian taxa, and variations in the populations diversity (Holm and Svenning, 2014; Carrera et al., 2022). The analysis of the Pleistocene and Holocene assemblages has proven that

birds are useful climatic and palaeoenvironmental indicators (Sánchez-Marco, 2004; Núñez-Lahuerta et al., 2018), which can shed light on the landscapes and the past relationships between birds, human and carnivores in the past.

This work aims to analyse the avian assemblage from the Late Pleistocene to Holocene sequence of Cova Foradada in order to:

1) Characterize the origin of the bird accumulation across the different units;
2) To perform a palaeoecological analysis;
3) This approach is expected to shed light on the Mediterranean environment and landscape during the Late Pleistocene to Holocene, and the effects of the climatic oscillations in the past ecosystems.

1.1. Cova Foradada site

The Cova Foradada site is a small cave located in the town of Calafell, in Tarragona (NE of the Iberian Peninsula) (Fig. 1A), at 1.8 km from the Mediterranean coastline. It opens at 110 m.a.s.l., at the top of L'Escarnosa hill. The archaeological record of the cave was accidentally discovered in 1997, with the finding of several Late Neolithic human remains.

The cave is developed in Miocene (Serravalian-Tortonian) calcarenites, in discordant contact with Lower Cretaceous (Valanginian-Barremian) limestones and dolomites. Cova Foradada has a circular entrance (Fig. 1B) that gives access to a 14 m^2 chamber, where the excavation was conducted. A travertine formation forms a 7 m long ascending ramp, which reaches an upper, smaller entrance (Morales et al., 2019).

The stratigraphic sequence described for the main chamber includes Upper Pleistocene to Northgrippian units. Major Units V, IV and III are Pleistocene in age, and Units II and I are Holocene (Fig. 1C, D).

Unit V is the lower unit of the infilling, and it is comprised of a breccia with travertine cobbles and boulders, infilled with calcareous muddy sands. Unit IV is a stratified breccia of boulder-size travertine slabs with calcareous muddy sands infilling the space between the boulders. It is also subdivided in three layers IV, IV.1 and IV.2, due to the
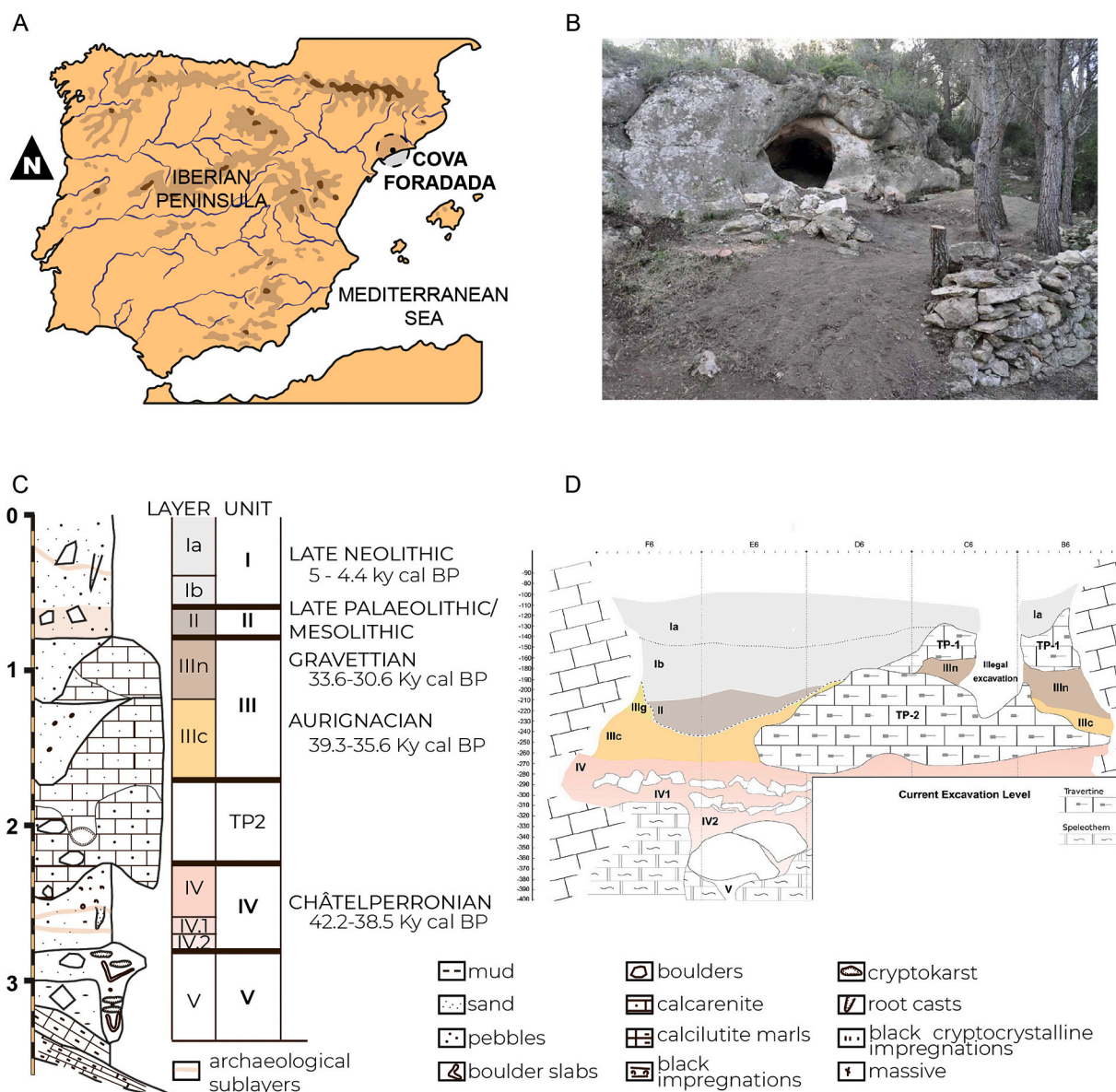

Fig. 1. Cova Foradada context. A: Location of the site; B: Entrance of the cave; C: Lithostratigraphic column; D: Stratigraphic reconstruction of the cave infilling. Modified from Morales et al. (2019).

presence of two tabular travertine strata.

Unit III is the most complex unit, and it is subdivided in the archaeological layers IIIn, IIIg and IIIc. Due to the erosive processes, Unit III is unevenly distributed along the main chamber. Layer IIIn is comprised by a breccia with calcarenite fragments, yellow sands and charcoal remains. Layer IIIg is composed of yellow calcareous sands, and is almost sterile in archaeological remains. Layer IIIc is the first continuous Pleistocene layer and it is composed of massive pale brown calcareous sands, with calcarenite slabs. It also contains charcoal and combustion structures (Morales et al., 2019).

Unit II is a small lenticular stratum comprised by brown sandy clays with calcarenite rocks from the cave roof. This unit is also affected by bioturbation, trampling, and the funerary activities related to Unit I.

Unit I is composed of calcarenite breccias with dusty organic sand, pebbles and charcoal and tabular ashes. It is thoroughly affected by bioturbation, including burrowing, root growth an anthropic activity.

The Pleistocene sequence, comprising Units V to III, is characterized by continuous use of the cave by carnivores, with short and sporadic human occupations leaving scarce archaeological evidence. The taxonomic representation, skeletal, and mortality profiles from the faunal assemblage is similar across the Pleistocene sequence. Middle-sized birds and leporids are the most abundant groups in Units V to III. The next group in abundance are the carnivores, with *Lynx pardinus, Ursus arctos, Panthera pardus* and *Crocuta crocuta*. Other carnivore mammals appear occasionally in the assemblage, as is it the case of *Vulpes vulpes, Canis/Cuon* sp. and *Panthera leo*, represented mostly by isolated elements. The Iberian lynx *Lynx pardinus* is the species with the highest representation across Units V to III. A few specimens of ungulates such as *Cervus elaphus, Bos/Bison* sp. and *Equus* sp., have been also identified in the assemblage, together with some remains of cf. *Testudo hermanni* remains documented in Layer IIIc. Large avian raptors are also recorded in the assemblage, highlighting the presence of several species in Unit IV (Morales et al., 2019; Rodríguez-Hidalgo et al., 2019).

1.1.1. The archaeological record

The Cova Foradada sequence includes the southernmost European record for the Middle-to-Upper Palaeolithic transition. Unit IV is characterized by the presence of Châtelperronian technology. A pedal phalanx of an Imperial Eagle *Aquila [heliaca] adalberti* with cut-marks was recovered from layer IV.1, representing the first evidence in the Iberian Peninsula for the symbolic use of eagle talons (Rodríguez-Hidalgo et al., 2019).

Within the Unit III, Layer IIIn dates back to the Early Gravettian and is characterized by the abundance of pierced shell ornaments, and a small stone-tool assemblage containing Gravettian points and microgravettes. Layer IIIc belongs to the Early Aurignacian and is characterized by the presence of Dufour bladelets and bone and antler artefacts, along with combustion features.

Unit II shows relics of a Late Upper Palaeolithic occupation, totally disturbed by subsequent funerary dynamics (Morales et al., 2016).The Holocene deposits of Unit I have been interpreted as a sepulchral accumulation, with over 2500 human remains, dating back to the Late Neolithic-Chalcolithic and the Early Cardial Neolithic (Oms et al., 2014; Moreno-Ibáñez et al., 2021, 2022).

1.1.2. Taphonomy of the Cova Foradada

Concerning the taphonomic analyses of the Cova Foradada assemblages, previous preliminary analysis have shown that the bone assemblages of the Pleistocene levels of Cova Foradada presented a mixture of accumulations generated by natural processes, such as small carnivorous mammals, large raptors, large carnivorous mammals and small but significant activity of humans (Morales et al., 2019; Rodríguez-Hidalgo et al., 2019). Based on actualistic studies (Rodríguez-Hidalgo et al., 2013; Rodríguez-Hidalgo et al., 2016), the presence of abundant leporid remains with high percentages of complete foot bones and significant levels of long-bone breakage, among other factors, suggests that the cave

primarily served as an Iberian lynx den. In the same preliminary analysis, we pointed out that large raptors probably also contributed to the accumulation of leporid bones. The presence of heavily digested complete long limb bones is one of the main arguments supporting this hypothesis (Lloveras et al., 2018) as well as the relative abundance of bones of large birds of prey in various units.

Hyenas and leopards also used the cave, leaving taphonomic signatures such as large tooth marks (furrowing in the epiphysis of long bones from large-sized ungulates), breakage of large mammals' bones and coprolites, but their influence on the accumulation of birds is unlikely. Despite the non-anthropogenic origin of most of the faunal assemblage, almost every layer at Cova Foradada has yielded anthropogenically modified bones, suggesting that hominins contributed to the formation of the assemblage, mainly through the consumption of small game such as rabbits. The presence of abundant midshaft bone cylinders with notches from what are possibly human bite marks, burned rabbit bones and some cut marks are the main elements that enable the interpretation of part of the rabbit remains as being of anthropogenic origin (Morales et al., 2019; Rodríguez-Hidalgo et al., 2019).

The Cova Foradada site was occupied ephemerally but recurrently by Palaeolithic foragers from around Heinrich Event 4 (40,000 to 39,000 years BP) until the Late Glacial-Early Holocene period. Later during the middle Holocene, Neolithic and Chalcolithic groups used the cave as place for a collective burial (Cebrià et al., 2011; Morales et al., 2016; Moreno-Ibáñez et al., 2022). One of the most significant characteristics of the Palaeolithic use of Cova Foradada is the brief nature of the occupations. This transitory use is further evidenced by the almost insignificant anthropogenic impact on the faunal assemblages of every stratigraphic unit (Morales et al., 2019). Despite this minimal evidence of human habitation in the cave based on taphonomic outcomes and the sparse presence of cultural remains, nearly all layers of the Cova Foradada have produced bones showing taphonomic modifications generated by human activity.

2. Material and methods

A total of 1310 avian remains from the fieldwork campaigns 2006 to 2016 and corresponding to the Units V to I have been analysed. The sample include the materials recorded during the systematic excavations and those recovered during the sediment washing and sieving process. The remains have been photographed with a Sony α58 and measured using a digital-calliper and the software ImageJ (Schneider et al., 2012).

Both osteological keys (Erbesdobler, 1968; Kraft, 1972; Fick, 1974; Jánossy, 1983; Gilbert et al., 1985; Solti, 1996; Tomek and Bochenski, 2000; Wójcik, 2002; Kessler, 2015, 2016; Bochenski et al., 2022) and comparative anatomy collections (Laboratorio de Arqueociências in Lisbon and Muséum National d'Histoire Naturelle in Paris) have been used to assign the remains. The taxonomy follows the work of Billerman et al. (2022), which also has been used as the main reference for the current distribution and habitat preferences analysis of the taxa identified. For their past distribution, the syntheses works of Tyrberg (2008) and Hernández-Carrasquilla (1993) have been used as main references.

For the taphonomic remarks of the site, the state of conservation of the bird remains have been analysed. The proportion between complete and incomplete bones has been calculated for each layer, allowing to distinguish between three main groups of raptor birds: group 1 (complete bones <30%) includes the pellets of diurnal birds of prey; group 2 (30–60% complete bones) includes owl pellets; and group 3 (complete bones >60%) includes uneaten remains of diurnal birds of prey (Bochenski, 2005).

To distinguish whether the assemblage is composed of pellets or uneaten remains, the ratio between wing elements (total number of humeri, ulnae and carpometacarpi) and leg elements (total number of femora, tibiotarsi and tarsometatarsi) (Ericson, 1987) has been applied. A 1:1 ratio suggests pellet remains, while a predominance of wing elements suggests uneaten remains. An overrepresentation of leg remains

could indicate human consumption of the preys, but the results of this ratio must be interpreted carefully as it has been shown that the predominance of wing elements can also be related to human action (Livingston, 1989; Laroulandie, 2010; Finlayson et al., 2012). To shed light on this issue, the presence of other bone modifications such as cut-marks have been analysed, as human processing has already been identified in large-sized diurnal raptor remains from the assemblage (Rodríguez-Hidalgo et al., 2019).

The ratio between proximal (total number of scapulae, coracoids, humeri, femora, and tibiotarsi) and distal elements (total number of ulnae, radii, carpometacarpi and tarsometatarsi) has been calculated (Bochenski and Nekrasov, 2001) to distinguish between three different groups: group 1, which includes pellets of diurnal birds of prey (1:1 ratio); group 2, which includes the pellets of nocturnal birds of prey and uneaten remains of diurnal birds of prey (proximal elements slightly predominant); and group 3, which includes uneaten remains from eagle (proximal elements clearly predominant). The predominance of proximal elements could also suggests human activity over the preys (Laroulandie, 2010).

The Habitat Weighting method has been applied to perform a palaeoenvironmental approach (Evans et al., 1981; Andrews, 2006). For this, the habitat preferences of the taxa have been described based on five habitat types: woodlands (WO), open humid areas (OH), water (WA), open dry areas (OD) and rocky areas (RO). The data base of Birds of the World has been used as a basis for the taxa habitat scores (Billerman et al., 2022) (Table 1).

3. Results

3.1. Avian assemblage

At least 25 different taxa have been identified in the assemblage (including the data from Rodríguez-Hidalgo et al., 2019) (Table 1): Anseriformes indet., *Tetrao urogallus* (Fig. 2A), *Alectoris rufa* (Fig. 2B), *Alectoris* sp., Galliformes indet., *Columba livia* (Fig. 2C), *Columba livia/oenas,* Columbidae indet., Charadriiformes indet., *Gyps fulvus, Aquila [heliaca] adalberti, Aquila* sp., cf. *Aquila* sp., cf. *Accipiter* sp., *Milvus milvus, Haliaeetus albicilla* (Fig. 2Q), Accipitridae indet., *Athene noctua* (Fig. 2D), *Dendrocopos* sp. (Fig. 2E), *Falco naumanni* (Fig. 2F), *Falco tinnunculus* (Fig. 2G), *Falco* sp., *Lanius meridionalis, Pica pica* (Fig. 2H), *Pyrrhocorax pyrrhocorax* (Fig. 2I,J,K), *Pyrrhocorax graculus* (Fig. 2L), *Pyrrhocorax* sp., *Corvus monedula* (Fig. 2M), *Corvus frugilegus* (Fig. 2N), *Corvus* sp., Corvidae indet. 1 (middle sized), Corvidae indet. 2 (small sized), Corvidae indet., *Hirundo rustica, Sturnus* sp., *Turdus viscivorus, Turdus torquatus* (Fig. 2O), *Turdus* sp., *Montifringilla nivalis* (Fig. 2P), Motacillidae indet., Passeriformes indet., and Aves indet (Table 1).

3.1.1. Unit V

Unit V is characterized by a low number of remains and low diversity (Fig. 3). Corvidae is the most abundant group in the assemblage, led by the presence of *P. pyrrhocorax*. The proportion represented by small-sized Passeriformes is the lowest of all the sequence.

Table 1

Bird remains from the Late Pleistocene to middle Holocene site of Cova Foradada. NISP: number of identified specimens. MNI: minimum number of individuals. WO: woodland. OH: open humid. WA: water bodies. OD: open dry. RO: rocky areas. The colour code of the first column corresponds to Fig. 3.

| TAXA	I NISP	I MNI	II NISP	II MNI	IIIn NISP	IIIn MNI	IIIc NISP	IIIc MNI	IV NISP	IV MNI	IV.1 NISP	IV.1 MNI	IV.2 NISP	IV.2 MNI	V NISP	V MNI	WO	OH	WA	OD	RO
Anseriformes indet.													1				0	0.6	0.4	0	0
Tetrao urogallus	1																1	0	0	0	0
Alectoris rufa									3	1			1				0	0	0	0	0
Alectoris sp.	1		1						1		2	1	1								
Galliformes indet.	6	1	1		1				1		2										
Columba livia									1								0	0	0	0.2	0.8
Columba livia/oenas			1						1				3	1	1						
Columbidae indet.	1																				
Charadriiformes indet.	1																				
Gyps fulvus									1								0	0	0	0.8	0.2
Aquila [heliaca] adalberti									3	1	3	1					0.5	0	0	0.5	0
Aquila sp.									1												
cf. *Aquila* sp.											1										
cf. *Accipiter* sp.									1								1	0	0	0	0
Milvus milvus									1				1				0.5	0.2	0	0.3	0
Halieetus albicilla			2	1													0.4	0	0.4	0	0.2
Accipitridae indet.			1				1		2		1										
Athene noctua									1								0	0.5	0	0.5	0
Dendrocopos sp.													1				1	0	0	0	0
Falco naumanni													3	1			0	0	0	1	0
Falco tinnunculus	2						1				2	1	1				0.3	0.2	0	0.5	0
Falco sp.	3						2	1	6	2			6	1	1						
Lanius meridionalis	1																0.1	0	0	0.9	0
Pica pica			1						1		1		3	1			0.1	0.5	0	0.4	0
Pyrrhocorax pyrrhocorax	10	1			22	3	32	4	36	6	46	5	33	4	7	1	0	0.3	0	0	0.7
Pyrrhocorax graculus	1				1		1		3	2	1		1		1		0	0.3	0	0	0.7
Pyrrhocorax sp.			1		3	2	5	1	7	2	5	2	3	2			0	0.3	0	0	0.7
Corvus monedula	1										1						0.1	0.4	0	0.4	0.1
Corvus frugilegus													2				0.1	0	0	0.9	0
Corvus sp.			1				1		2	1	1		3	2							
Corvidae indet. (ms)	16		2		33		14		44		46		45		3						
Corvidae indet. (ss)							5														
Corvidae indet.					6		5		5		2				5						
Hirundo rustica	1																0	0.4	0.1	0.4	0.1
Sturnus sp.	1																				
Turdus viscivorus											1						0.5	0.2	0	0.3	0
Turdus torquatus											1		2	1			0.5	0	0	0.5	0
Turdus sp.	4	1	2		2	1	3	2	13	3	11	3	13	4	2	1					
Turdidae indet.							1														
Montifringilla nivalis									1								0	0	0	0.5	0.5
Motacillidae indet.	1																				
Passeriformes indet.	39	1			37		14		110		81		56		1						
Aves indet.	39	1			32		15		113		84		72		7						
Total	**129**		**13**		**139**		**90**		**363**		**295**		**253**		**28**						
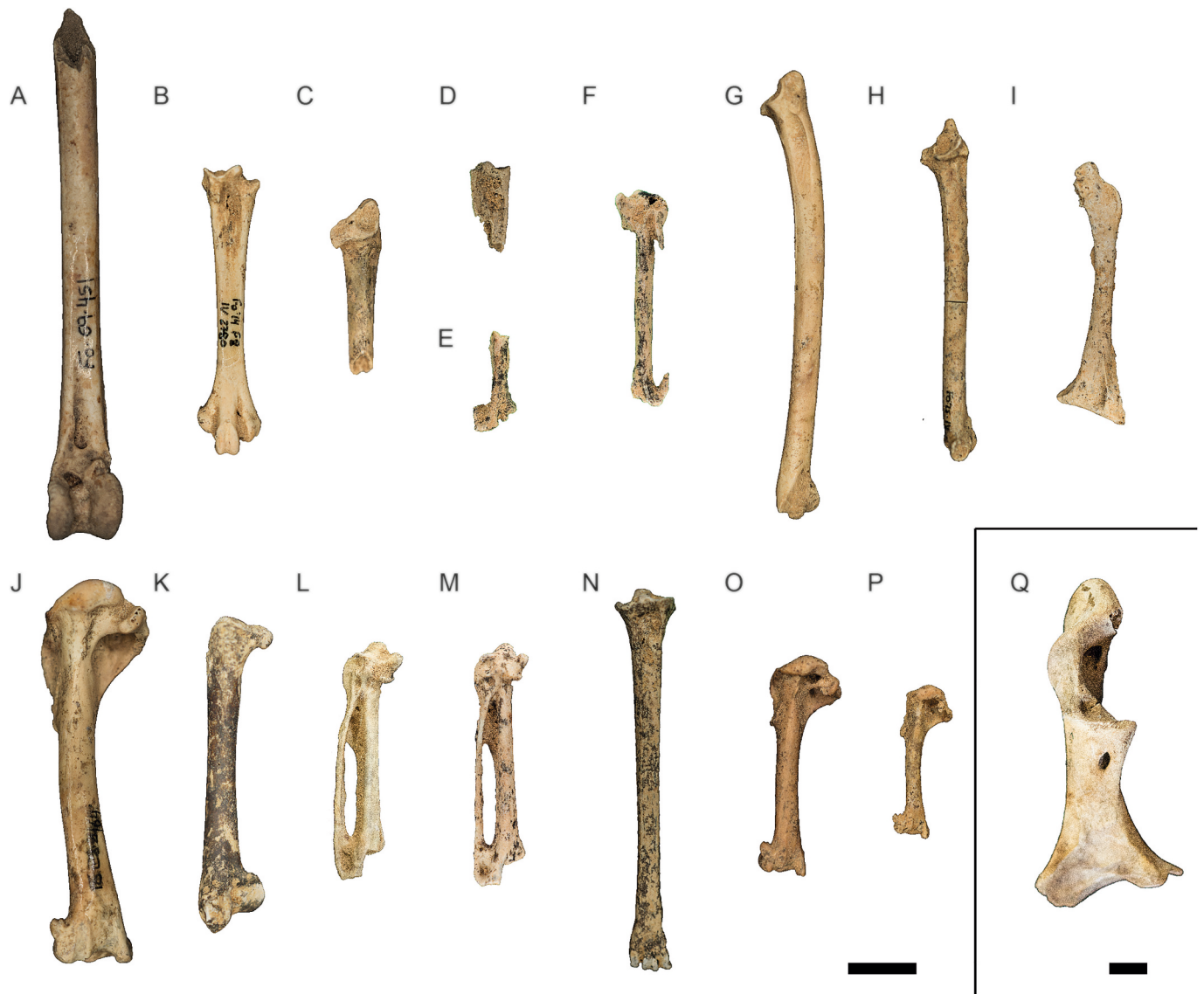
Fig. 2. Bird remains from the Late Pleistocene to middle Holocene site of Cova Foradada. A: *Tetrao urogallus*, distal left tibiotarsus, cranial view (Unit I G9 451); B: *Alectoris rufa*, left tarsometatarsus, dorsal view (Layer IV F8 2780); C: *Columba livia*, proximal left ulna, cranial view (Layer IV D8 1056); D: *Athene noctua*, proximal left tarsometatarsus, dorsal view (Layer IV F8 3200); E: *Dendrocopos* sp., distal right carpometacarpus, dorsal view (Layer IV.2 D7 305–310); F: *Falco naumanni*, right carpometacarpus, ventral view (Layer IV.2 D7 305–310); G: *Falco tinnunculus*, right ulna, ventral view (Layer IV.1 E8 3229); H: *Pica pica*, right ulna, ventral view (Layer IV.1 D6 888); I: *Pyrrhocorax pyrrhocorax*, left coracoid, ventral view (Layer IV.2 E6 280–300); J: *Pyrrhocorax pyrrhocorax*, left humerus, caudal view (Layer IIIc E8 2464); K: *Pyrrhocorax pyrrhocorax*, left femur, caudal view (Layer IV.2 F8 340–350); L: *Pyrrhocorax graculus*, left carpometacarpus, ventral view (Layer IV E8 2820); M: *Corvus monedula*, left carpometacarpus, ventral view (Layer IV.1 D6 290–300); N) *Corvus frugilegus*, right tarsometatarsus, dorsal view (Layer IV.2 F8 340–350); O: *Turdus torquatus*, left humerus, caudal view (Layer IV.2 F8 300–305); P: *Montifringilla nivalis*, left humerus, caudal view (Layer IV D8 1263); Q: *Haliaeetus albicilla*, left coracoid, dorsal view (Layer II E8 2300). Scale bars = 1 cm.

3.1.2. Unit IV

Unit IV is the richest unit of the sequence in terms of both number of specimens and diversity, although this latter aspect could be related to the differences in the number of identified specimens (Fig. 3). This Unit is divided in three archaeological layers (Layer IV, Layer IV.1 and Layer IV.2) which show similar proportions for the main avifaunal groups (Fig. 3), including high proportions of Corvidae and non-Corvidae Passeriformes.

Layer IV presents the assemblage with the lowest proportion of corvids in the Pleistocene sequence, and a higher proportion of non-corvid taxa than in Layers IV.1 and IV.2, including Columbiformes, four different large-sized Accipitridae, *Athene noctua,* and *Montifringilla nivalis*.

Layers IV.1 and IV.2 are more similar to each other, presenting a very similar composition of the main groups (Fig. 3) including the presence of *Alectoris, Falco tinnunculus*, large-sized Corvidae, and different species of *Turdus* (Table 1). Layer IV.2 is slightly more diverse, and also includes the presence of an undetermined Anseriformes, *Columba livia/oenas, Dendrocopos* sp., and *Falco naumanni*.

3.1.3. Unit III

Unit III (layers IIIn and IIIc), is richer than Units I and II. Corvidae remains dominates, especially in Layer IIIc, followed by small-sized Passeriformes (including *Turdus* sp.) (Table 1, Fig. 3). *P. pyrrhocorax* is the most abundant species in Unit III, while its sister species *P. graculus* has also been recorded. Some subtle differences have been observed in the taxa composition. Apart from Corvidae and small passerines, Galliformes and *Columba livia/oenas* appear in Layer IIIn while undetermined
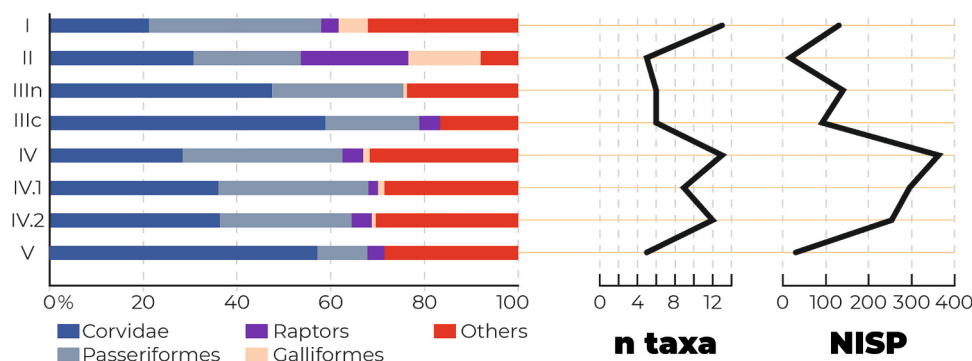
Fig. 3. Proportion between the five main avifaunal groups in each layer. Passeriformes does not include the Corvidae remains. Raptors include both diurnal and nocturnal birds of prey (colour code in Table 1). n taxa: number of taxa, NISP: number of identified specimens.

Accipitridae, and kestrels (*Falco tinnunculus* and *Falco* sp.) are recorded in Layer IIIc.

3.1.4. Unit II

Unit II yielded the poorest avian assemblage in terms of number of specimens, (**Table 1**), yet it shows a relatively high diversity (Fig. 3). It is dominated by the Corvidae family, including one large-sized corvid (*Corvus* sp.), as well as *Alectoris* sp., *Turdus* sp., and *Haliaeetus albicilla*. It presents the highest proportion of Galliformes from all the sequence.

3.1.5. Unit I

The assemblage from Unit I is dominated by the presence of non-Corvidae Passeriformes (Fig. 3), including *Lanius meridionalis*, *Hirundo rustica*, *Sturnus* sp., *Turdus* sp., and an indeterminate Motacillidae, Corvidae (including *P. pyrrhocorax*), while the presence of *Tetrao urogallus* can be also highlighted. Undetermined Columbidae, Charadriiformes and *Falco tinnunculus* remains have also been identified in Unit I.

3.2. Taphonomic remarks

Most of the bones are incomplete, and no great differences have been identified between the percentage of complete and incomplete bones across the different levels (Fig. 4A). Likewise, no major differences have been observed between the different groups from each layer, with the percentage of complete and incomplete bones varying between 83% and 89%. Although these results could align with the action of diurnal birds of prey (Bochenski, 2005), the trampling effect related with the occupation dynamics (Morales et al., 2019) could have had also led to bone breakage.

Ulnae are the most common elements in Units IV and II, while Layer IIIn and Unit I are dominated by carpometacarpi, and Layer IIIc by humeri. Beyond the cut-marks already described for an imperial eagle *Aquila [heliacal] adalberti* pedal phalange from layer IV.1 (Rodríguez-Hidalgo et al., 2019), one cut mark on a coracoid of a white-tailed eagle (*Haliaeetus albicilla*) form the Unit II have been observed. The mark is located in the subcoracoscapularis and/or scapulohumeralis cranialis muscle insertion (Fig. 5). Punctures have been identified in a *Tetrao urogallus* distal tibiotarsus from Unit I (Fig. 4B).

Wing vs. Leg and Proximal vs. Distal ratios have been calculated exclusively for the different layers of Unit IV and Unit III. Unit I is strongly affected by bioturbation and intense sepulchral activity (Oms et al., 2014; Moreno-Ibáñez et al., 2022), and the low number of remains from Units V and II hampers the possibility of a deep taphonomic analysis (**Table 1**). Both ratios have been calculated for the dominant Corvidae and non-Corvidae Passeriformes groups from each layer. The rest of the avian groups have not been included in this analysis as the number of remains is low and the results would not be representative.

3.2.1. Unit IV

The avian assemblages from Unit IV layers are dominated by the presence of wing elements, while the proportion between proximal and distal elements varies across layers and groups.

Corvids and non-Corvidae Passeriformes from layer IV show a predominance of wing elements (Fig. 4C), and a very slight predominance of distal elements (Fig. 4D). The results are similar for Layer IV.1, with both groups showing the same proportions. Wing elements predominate in the assemblage (Fig. 4C), and the proportion of proximal vs distal is balanced (Fig. 4D). In Layer IV.2, there are differences in the results for small passerines and corvids. The proportion of wing elements in passerines reaches the 80% (Fig. 4C). There is also a slight predominance of proximal elements (Fig. 4D). In corvids, the wing elements are also dominant, but in a lesser proportion than in the passerine birds (Fig. 4C). Finally, there is also a slight predominance of distal elements.

3.2.2. Unit III

Unit III is dominated by the presence of wing and proximal elements in both corvids and small passerines both in Layers IIIn and IIIc, although some differences can be highlighted. The small passerines from Layer IIIn show a clear dominance of proximal and wing elements (Fig. 4C). The results fit with a group II raptor (Fig. 4D). The proportion between wing and legs elements in corvids show a slight predominance of wing elements (Fig. 4C). The proportion of proximal and distal elements is also close to 50% (Fig. 4D).

The assemblage from Layer IIIc is also dominated by wing and proximal elements, and the differences between small passerines and corvids are smaller than in Layer IIIn. Wing elements are clearly more abundant than leg ones in non-corvid (Fig. 4C). The proportion between proximal and distal elements passerines is close to 50% (Fig. 4B). Wing elements are most abundant in Corvidae too, but not as dominant as in passerines (Fig. 4C),. Proximal elements are more abundant than distal ones.

3.3. Palaeoenvironmental reconstruction

The results of the Habitat Weighting method point to a relatively stable landscape, dominated by open areas with forests or scattered trees (Fig. 6). Units V and II yielded the most distinct results, but the low number of remains recovered in both units must be considered when interpreting these results. In general terms, the avian assemblage is dominated by the presence of middle-sized corvids, Galliformes, Passeriformes resembling what has been defined from other Upper Pleistocene assemblages from the north of the Iberian Peninsula (Sánchez-Marco, 2005; Tyrberg, 2007; Núñez-Lahuerta et al., 2016, 2021).

Unit V,along to Unit II, is the poorest in terms of diversity and number of remains (Fig. 3). The results of the Habitat Weighting method point to an open landscape (Fig. 6) reflecting the preference of the representatives of the *Pyrrhocorax* genus, which dominate in the unit
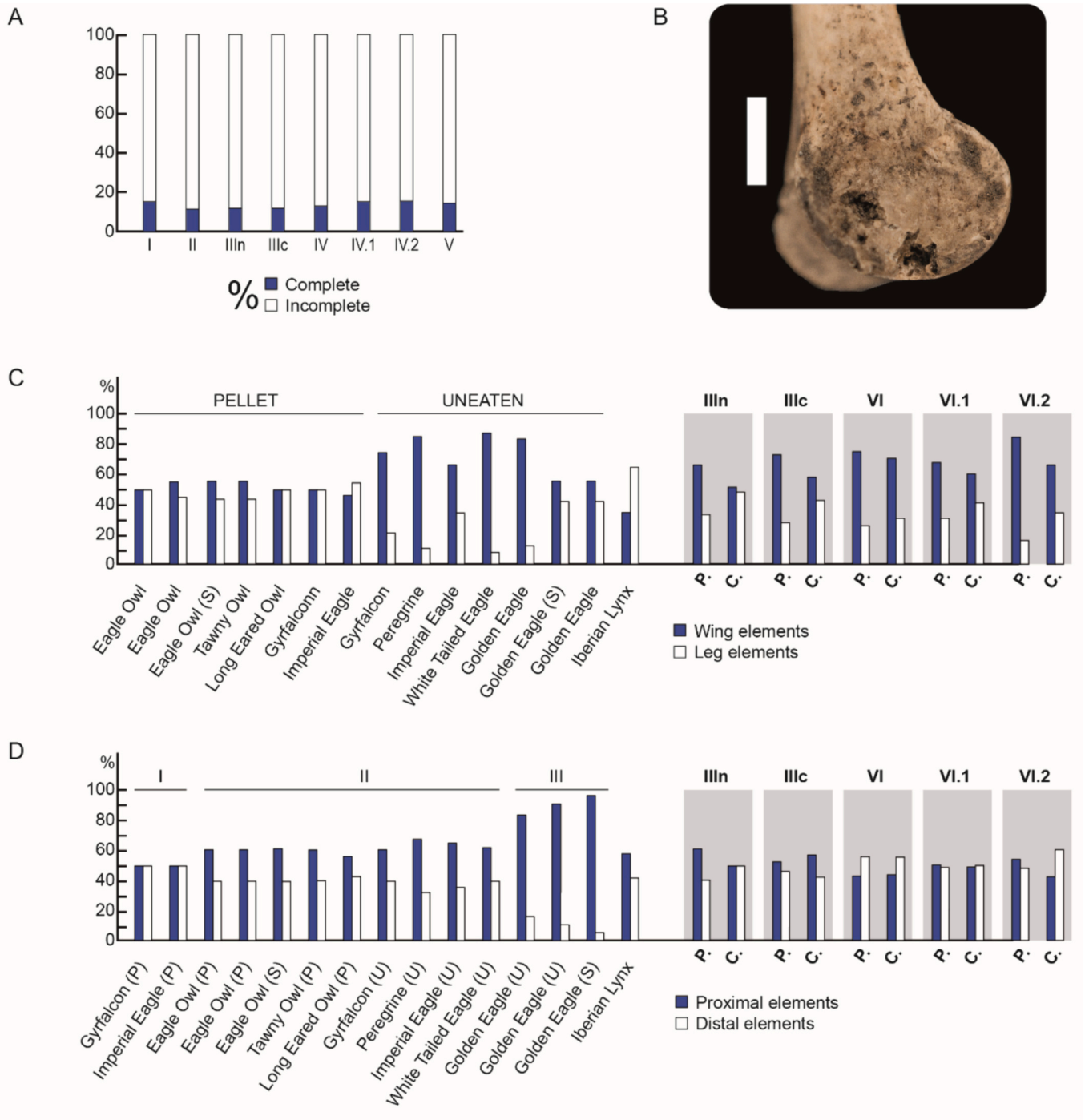
Fig. 4. Taphonomic remarks of the Cova Foradada bird assemblage A: Proportion between complete and incomplete elements in each layer; B: Punctures in a distal tibiotarsus of *Tetrao urogallus* from Unit I (Scale bar 0.5 mm); C: Wing versus leg elements proportion, D: Proximal versus distal elements proportion. (P: non-Corvidae Passeriformes; C: Corvidae; P: Pellet; U: Uneaten; S: Subfossil).C and D published data (left part of the graphic) from: Bramwell et al., 1987; Bochenski et al., 1993, 1997, 1998, 1999; Bochenski and Tomek, 1994; Mlikovsky, 1996; Laroulandie, 2000, 2002; Bochenski and Nekrasov, 2001; Bochenski and Tornberg, 2003; Rodríguez-Hidalgo et al., 2019.

(Madge, 2020). Unit IV is divided in three layers. The three yielded similar results in the Habitat Weighting analysis (Fig. 6), with a landscape dominated by the presence of open areas, and presence of woodlands of scattered trees. A tendency towards the reduction of woodlands and an increase of rocky areas is observed towards the top of the Unit IV. The presence of the white-winged Snowfinch *Montifringilla nivalis* can be highlighted for Layer IV. Nowadays its presence in the Iberian Peninsula is limited to the central parts of the Pyrenees (Summers-Smith and Bonan, 2020).

The avian assemblages from the layers IIIn and IIIc yielded results with the lowest proportion of woodlands, and highest proportion of rocky areas (Fig. 6), reflecting the high dominance of *Pyrrhocorax* representatives in both layers. The diversity in the layers from Unit III is low, but this seems to be more related with the low number of remains recovered in both layers. Also, the composition of the assemblage is similar to the other units.

The results of Unit II point to the highest proportion of water bodies in the entire sequence (Fig. 6), but the results of the Habitat Weighting
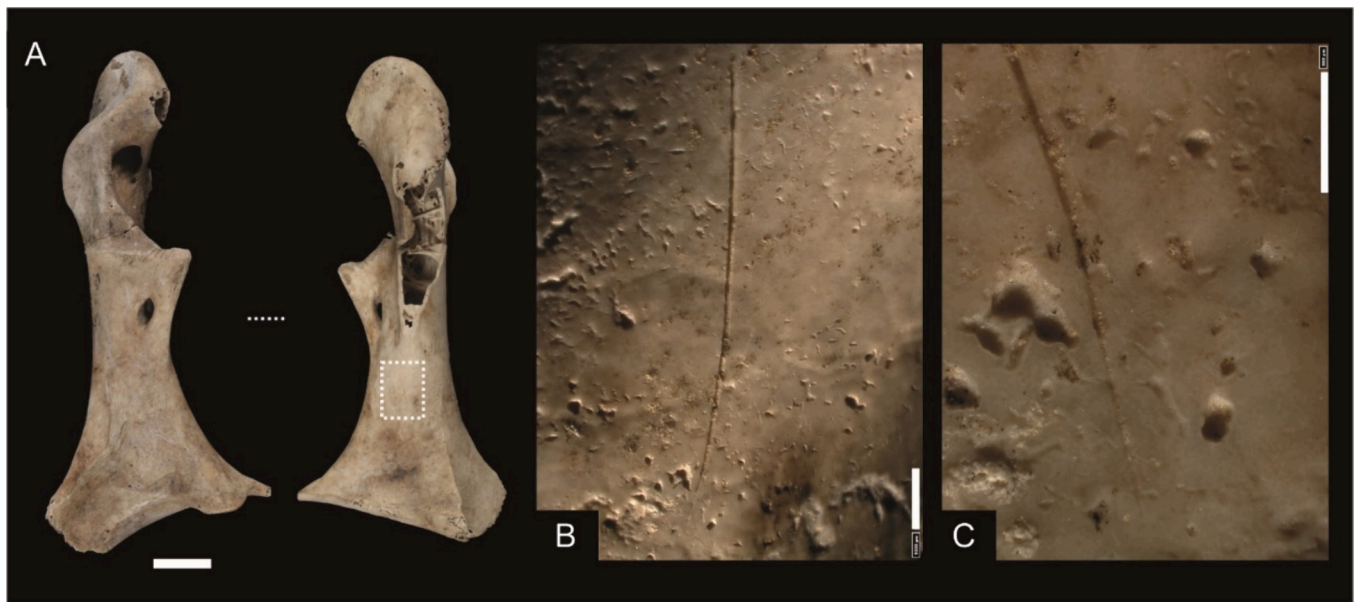
Fig. 5. Coracoid of *Haliaeetus albicilla* (Unit II E7 2300) showing an oblique cut mark in the central area of the ventral view a); detail at different magnifications observed using 3D digital microscope HIROX KH-8700 b) & c) (scale bar 1 cm in a, 1 mm in b & c).
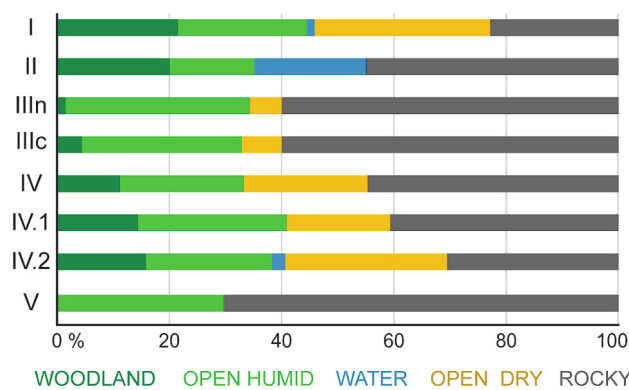

Fig. 6. Results of the Habitat Weighting analysis in the different layers of the Cova Foradada Sequence.

method in this level may not reflect the landscape, as it yielded the poorest avian assemblage of the sequence both in terms of diversity and number of remains (Fig. 3). The high proportion of water bodies is due to the presence of *Haliaeetus albicilla*, which appears in various aquatic environments in northern Europe and is sporadic in the Iberian Peninsula (Orta et al., 2020).

The landscape reconstruction from Unit I reflects a similar proportion of woodlands, open humid, open dry and rocky areas, plus a small proportion of water bodies (Fig. 6). It yielded the most diverse assemblage from the sequence, despite not having the highest number of remains. Here the presence of the western capercaillie must be highlighted.

4. Discussion

4.1. Taphonomy of the site

During the analysis carried out in this work we have been able to identify a new evidence of human manipulation of bird remains. A cut mark on a coracoid of a white-tailed eagle (*Haliaeetus albicilla*) form the Unit II was found. The location of the mark, which cuts the sub-coracoscapularis and/or scapulohumeralis cranialis muscle, is common

in other birds from archaeological assemblages and has been interpreted as a defleshing cut and also as a consequence of wing disarticulation (Díez Fernandez-Lomana et al., 1995; Laroulandie, 2002; Blasco and Fernández Peris, 2009; Lloveras and Nadal, 2020). Human processing of birds has already been proven at the site (Rodríguez-Hidalgo et al., 2019). The use of birds of prey as food and for their symbolic value, such as for their feathers, wings, talons or secondary products, has been widely discussed and abundant evidence has been presented since the Middle Palaeolithic/Middle Stone age, being a recurring behavior during the European Upper Palaeolithic (Serjeantson, 2009; Rodríguez-Hidalgo et al., 2019).

In light of the stratigraphic complications arising from various post-depositional processes, such as trampling, bioturbation, and sediment removal in Unit II it is prudent to refrain from establishing hypotheses concerning this bone. However, it is undoubtedly one more piece of evidence of anthropogenic manipulation of large birds of prey during the prehistory of the Iberian Peninsula.

Regarding the anthropogenic role, all the assemblages are dominated by the presence of wing elements. According to Ericson (1987), this should allow us to discard the human processing of the birds in the formation of the assemblage. Nevertheless, this ratio has been criticised (Livingston, 1989), and even a predominance of wing elements has been interpreted as a reflection of the use of feathers in Neanderthal contexts (Finlayson et al., 2012). This fact, along with the presence of cut-marks in the large-sized diurnal raptors in the Units IV and II points to an influence of humans as an accumulation agent.

The results of the taphonomic analysis from Unit IV varies across layers. Layers IV and IV.1 show a similar proportion for both small passerines and corvids, pointing to the same predator acting over both groups, likely an eagle (Bochenski and Nekrasov, 2001; Bochenski, 2005). The results from Layer IV.2 are different, and point also to the action of hawks. Layers IV and IV.1 show the higher proportion and diversity of diurnal birds of prey, including taxa such as *Aquila [heliaca] adalberti*, *Accipiter* and *Milvus*, while *Falco* appears in a lower proportion. The presence of these taxa is compatible with the taphonomic results for Layers IV and IV.1. Accordingly, Layer IV.2 shows the higher proportion of *Falco* spp. remains, fitting with the similarities found in the proportions. The possible influence of the humans accumulating raptors must be considered when understanding the high diversity of raptors in Unit IV, as it has been already documented (Rodríguez-Hidalgo et al.,

2019).

In Unit III the results point to different predators affecting the small passerines and the corvids. Small passerines show proportions compatible with the action of Imperial eagles and hawks, and the corvid proportions are compatible with the action of large-sized Accipitridae or Strigiformes (Bochenski and Nekrasov, 2001; Bochenski, 2005). No bird of prey has been identified in Layer IIIn, but an indeterminate Accipitridae and *Falco tinnunculus* and *Falco* sp. appear in Layer IIIc.

Lynx dens have been identified along most of the Pleistocene sequence, with a high number of lynx remains recovered. The high number of leporid may be related with the action of the lynxes, but also with the action of large raptors (Morales et al., 2019). The taphonomic results of the avian assemblage also fit with the action of raptorial birds, which is compatible with the presence of dens (of lynxes or other carnivores) in the cave, although contribution of these carnivores in the avian accumulation seems to be sporadic.

To sum up, the results point to the mixed origin of the avian assemblages found along the sequence from Cova Foradada, with birds of prey as main accumulators, but with lynxes and humans acting over the birds occasionally. These results are compatible with the activity of taxa such as imperial eagles and hawks (Bochenski and Nekrasov, 2001: Bochenski, 2005). This, along with the continued presence of birds of prey along the sequence, suggest the presence of a cache or nest site in the surroundings of the cave. The future systematic and taphonomic analysis of the avian eggshell remains recovered from these layers will shed light on this issue.

4.2. Palaeoenvironmental inferences

The results of palaeoenvironmental reconstruction point to a landscape dominated by open areas with forests or scattered trees (Fig. 6). Some of the taxa identified in the assemblages are nowadays absent, or have a sporadic presence in this region, as it is the case of *Montifringilla nivalis* from the Layer IV, *Pyrrhocorax graculus* from Units I, III, IV and V, *Haliaeetus albicilla* from Unit II, *and Tetrao urogallus* from Unit I.

4.2.1. Unit V

Unit V is along to Unit II the poorest in terms of diversity and number of remains (Fig. 3). The results of the Habitat Weighting method reflect the open landscape preferences of *Pyrrhocorax*, which dominate the unit assemblage (Fig. 6). The presence of *P. graculus* in the area of the site is currently limited to sporadic sightings. Nevertheless, during the Late Pleistocene its distribution was broader (Carrera et al., 2022), and it has been identified in many sites of the north of the Iberian Peninsula (Elorza, 1990; Moreno-García, 2017; Núñez-Lahuerta et al., 2018, 2021; Suárez-Bilbao et al., 2020, among others).

4.2.2. Unit IV

The progressive change in the landscape observed in Unit IV (reduction of woodlands, increase of rocky areas) could be reflecting the two phases observed in the Iberian Peninsula of the Heinrich 4 event (ca. 40Ka), with a first cold humid moment (reflected by the presence of Anseriformes) and a subsequent main cold drier phase (Naughton et al., 2009). This moment of climatic deterioration has been detected in other sites of the north of the Iberian Peninsula, with different responses depending on their geographic location: in Terrasses de la Riera dels Canyars in the Mediterranean coast, the proxies point a dry open, steppe-dominated landscape with scattered trees (Daura et al., 2013; López-García et al., 2013), while in the Cueva del Conde in the Cantabrian coast, the small vertebrates point to open humid meadowlands (López-García et al., 2011). The presence of the white-winged snowfinch *Montifringilla nivalis* can be highlighted for Layer IV. Nowadays its presence in the Iberian Peninsula is limited to the central parts of the Pyrenees (Summers-Smith and Bonan, 2020). This expansion to the southern lower altitudes can reflect the cooling related to Heinrich 4 event, although *M. nivalis* sporadically occurs in the area nowadays

(Summers-Smith and Bonan, 2020), and its presence during the Late Pleistocene and Holocene in the Balearic archipelago has been confirmed (Guerra, 2015 and references therein). In the Iberian Peninsula, *M. nivalis* has been identified in the MIS3 levels from Cueto de la Mina, in Asturias (Sánchez-Marco, 2005).

4.2.3. Unit III

According to its age, Layer IIIc could correlate with the Greenland Interstadial 8, a moment characterized by an increasing tendency towards woodland, which is not reflected in the obtained results (Sánchez-Goñi et al., 2009; Morales et al., 2019). The diversity in the layers from Unit III is low, but this seems to be more related with the low number of remains recovered in both layers. Also, the composition of the assemblage is similar to the other units. Thus, the avian assemblage of Unit III does not provide enough arguments to establish or discard its relationship with GI-8.

4.2.4. Unit II

The high proportion of water bodies observed in Unit II is due to the presence of, *Haliaeetus albicilla*, which appears in various aquatic environments in northern Europe and is sporadic in the Iberian Peninsula (Orta et al., 2020). Its presence at Unit II at Cova Foradada represents the last known fossil record on the Mediterranean coast of the Iberian Peninsula. The fossil record of the white-tailed eagle is common in the European Pleistocene (Tyrberg, 2007); however, its presence decreases during the Late Pleistocene and Holocene periods. Its presence near the Mediterranean coast in this chronology may be related with the cooling pulses that occurred in the Late Pleistocene-Holocene transition (Björk et al., 1998).

4.2.5. Unit I

Unit I is characterized by similar proportions of woodlands, open humid, open dry and rocky areas, and a small proportion of water bodies. *T. urogallus* has been identified in this assemblage, and it is absent from this region. Also, its distribution in the Iberian Peninsula is scarce and limited to the Pyrenees and Picos de Europa (de Juana and Kirwan, 2020). It has only been recorded at the site of Laminak II from the Basque Country (Hernández-Carrasquilla, 1993). According to the chronology of Unit I (5–4.4 ky cal BP), the presence of *T. urogallus* in the Unit I assemblage of Cova Foradada could be related to the cooling episode which affected the Iberian Peninsula prior to the 4.2 ky event, during the Neoglaciation (Kumar, 2011; Moreno-Ibáñez et al., 2022). The sporadic movement for feeding requirements, or for searching new logged areas cannot be ruled out (Borchtchevski and Moss, 2014).

5. Conclusions

The analysis of the bird remains (NISP = 1310) revealed the presence in the assemblages from Cova Foradada of at least 25 different taxa, with a notable presence of eight different raptorial taxa. The general composition of the bird assemblage is similar to the current one in the area, and those from other Upper Pleistocene sites of the Iberian northeast. The landscape reflected by the assemblages is stable throughout the sequence and is dominated by open landscapes with the presence of forests or scattered trees. Four species appearing in the avian assemblage are currently absent in the area of the site: *T. urogallus*, *H. albicilla*, *P. graculus* and *M. nivalis*. Their record in the site could be related to expansions of the habitat during colder moments, or to sporadic visits to the area. The Pleistocene Units IV and III yielded the highest number of remains and show slight differences in the landscape reconstruction results. Unit IV layers shows a tendency towards a reduction in woodlands and an increase of open areas, which may be related to the Heinrich 4 event (ca. 40Ka). Unit III layers show the lowest proportion of woodlands and the highest proportions or rocky areas in the sequence. In the Holocene units, presence of water bodies is indicated by the presence of aquatic taxa such as Anseriformes and

H. albicilla.

Concerning the origin of the avian accumulation, the diurnal birds of prey seem to be the main actors in the bird accumulation. These birds of prey probably also contributed to the abundant accumulation of leporid fossils remains throughout the sequence. Additionally, the action of human on birds at the site has been documented, contributing to increasing cases of interaction between humans and large diurnal raptors during Iberian prehistory.

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CRediT authorship contribution statement

Carmen Núñez-Lahuerta: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Antonio Rodríguez-Hidalgo:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Formal analysis. **Sandra Bañuls-Cardona:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Juan Ignacio Morales:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Formal analysis.

Declaration of competing interest

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

Data availability

Data will be made available on request.

References

Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixture. Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 572–589.

Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011. Early dispersal of modern humans in Europe and implications for Neanderthal Behaviour. Nature 479, 525–528. https://doi.org/10.1038/ nature10617.

Billerman, M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S., 2022. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/ bow/home.

Björk, S., Walker, M.J.C., Cwynar, L.C., Johnsen, S., Knudsen, K.L., Lowe, J.J., Wohlfarth, B., 1998. An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. J. Quat. Sci. 13 (4), 283–292.

Blasco, R., Fernández Peris, J., 2009. Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). J. Archaeol. Sci. 36, 2213–2223.

Bochenski, Z.M., 2005. Owls, diurnal raptors and humans: Signatures on avian bones. In: O'Connor, T. (Ed.), Biosphere to Lithosphere. 9th ICAZ Conference, Durham, pp. 31–45.

Bochenski, Z.M., Nekrasov, A.E., 2001. The taphonomy of sub-Atlantic bird remains from Bazhukovo III, Ural Mountains, Russia. Acta Zool. Cracov. 44 (2), 93–106.

Bochenski, Z.M., Tomek, T., 1994. Pattern of bird bone fragmentation in pellets of the Long-eared Owl *Asio otus* and their taphonomic interpretations. Acta Zool. Cracov. 37 (1), 177e190.

Bochenski, Z.M., Tornberg, R., 2003. Fragmentation and preservation of bird bones in uneaten food remains of the Gyrfalcon *Falco rusticolus*. J. Archaeol. Sci. 30 (12) https://doi.org/10.1016/S0305-4403(03)00069-4, 1665e1671.

Bochenski, Z.M., Boev, Z., Mitev, I., Tomek, T., 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 Zool. Cracov. 36 (2), 313–328.

Bochenski, Z.M., Korovin, V.A., Nekrasov, A.E., Tomek, T., 1997. Fragmentation of bird bones in food remains of Imperial Eagles, *Aquila heliaca*. Int. J. Osteoarchael. 7 (2), 165e171. https://doi.org/10.1002/(SICI)1099-1212(199703)7:2<165:: AIDOA332>3.0.CO;2-4.

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*. J. Archaeol. Sci. 25, 425–433. https://doi.org/10.1006/jasc.1997.0213.

Bochenski, Z.M., Huhtala, K., Sulkava, S., Tornberg, R., 1999. Fragmentation and preservation of bird bones in food remains of the Golden Eagle *Aquila chrysaetos*. ARCHAEOFAUNA 8, 31–39.

Bochenski, Z.M., Tomek, T., Wertz, K., 2022. Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey. Int. J. Osteoarchaeol. https://doi.org/10.1002/oa3165.

Borchtchevski, V., Moss, R., 2014. Age structure of Capercaillie males (*Tetrao urogallus*) in NW Russia may reflect two-way movements - a hypothesis. Ornis Fennica 91 (1), 14–28l.

Bramwell, D., Yalden, D.W., Yalden, P.E., 1987. Black grouse as the prey of the Golden Eagle at an archaeological site. J. Archaeol. Sci. 14 (2), 195–200. https://doi.org/ 10.1016/0305-4403(87)90006-9.

Carrera, L., Pavia, M., Varela, S., 2022. Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds. Sci. Rep. 12, 10813. https://doi.org/10.1038/s41598-022-14972-.

Cebrià, A., Morales, J.I., Oms, F.X., Pedro, M., Solé, A., Subirà, M.E., 2011. La Cova Foradada (Calafell, Baix Penedès), la problemàtica de la convivència en el registre d'inhumacions i cremacions durant la prehistòria recent. In: Blasco, A., Edo, M., Villalba, M.J. (Eds.), La Cova de Can Sadurní i la prehistòria de Garraf. Edar. Arqueología y Patrimonio, Milano, pp. 411–420.

Daura, J., Sanz, M., García, N., Allué, E., Vaquero, M., Fierro, E., Carrión, J.S., López-García, J.M., Blain, H.-A., Sánchez-Marco, A., Valls, C., Albert, R.M., Fornós, J.J., Julià, R., Fullola, J.M., Zilhão, J., 2013. Terrases de la Riera dels Canyars (Gavà, Barcelona): the landscape of Heinrich Stadial 4 north of the "Ebro Frontier" and implications for modern human dispersal into Iberia. Quat. Sci. Rev. 60, 26–48. https://doi.org/10.1016/j.quatscirev.2012.10.042.

de Juana, E., Kirwan, G.M., 2020. Western Capercaillie (*Tetrao urogallus*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow. wescap1.01.

Díez Fernandez-Lomana, C., Sánchez Marco, A., Moreno Lara, V., 1995. Grupos avicaptores del Tardiglaciar: las aves de Berroberria. Munibe 47, 3–22.

Elorza, M., 1990. Restos de aves en los yacimientos prehistóricos vascos. Estudios realizados. Munibe 42, 263–267.

Erbesdobler, K., 1968. Vergleichend morphologische Untersuchungen en Einselknochen des postcranialen Skeletta in Mitteleropa vorkommender mittelgroßer Hühnervögel. Unpublished PhD Dissertation,. Universität Munchen.

Ericson, P.G.P., 1987. Interpretation of archaeological bird remains: a taphonomical approach. J. Archaeol. Sci. 14 (65–75), 80006–80007.

Ersmark, E., Baryshnikov, G., Higham, T., Argant, A., Castaños, P., Döppes, D., Gasparik, M., Germonpré, M., Lidén, K., Lipecki, G., Marciszak, A., Miller, Moreno-García, M., Pacher, M., Robu, M., Rodríguez-Varela, R., Rojo Guerra, M., Sabol, M., Spassov, N., Storå, J., Valdiosera, C., Villaluenga, A., Stewart, J.R., Dalén, L., 2019. Genetic turnovers and northern survival during the last glacial maximum in European brown bears. Ecol. Evol. 9 (10), 5891–5905. https://doi.org/10.1002/ ece3.5172.

Evans, E.M.N., Van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in western Kenya. J. Hum. Evol. 10, 99–116.

Fick, O.K.M., 1974. Vergleichend Morphologische Untersuchungen an Einzelknochen Europäischer Taubernarten. Unpublished PhD Dissertation,. Universität Munchen.

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., Fa, D.A., Rodríguez-Llanes, J.M., 2012. Birds of a Feather: Neanderthal Exploitation of Raptors and Corvids. PLoS One 7 (9), e45927.

Gamboa, S., Galván, S., Varela, S., 2024. Vrba was right: Historical climate fragmentation, and not current climate, explains mammal biogeography. Glob. Chang. Biol. 30 (5), e17339 https://doi.org/10.1111/gcb.17339.

Gilbert, B.M., Martin, L.D., Savage, H.G., 1985. Avian Osteology. Modern Printing Co, Laramie, Wyoming.

González-Sampériz, P., Aranbarri, J., Pérez-Sanz, A., Gil-Romera, G., Moreno, A., Leunda, M., Sevilla-Callejo, M., Corella, J.P., Morellón, M., Oliva, B., Valero-Garcés, B., 2017. Environmental and climate change in the southern Central Pyrenees since the last Glacial Maximum: a view from the lake records. Catena 149, 668–688. https://doi.org/10.1016/j.catena.2016.07.041.

Guerra, C., 2015. Avifauna del Pleistoceno Superior-Holoceno de las Pitiusas: Passeriformes y sus depredadores. PhD Dissertation.. Universidad de Salamanca.

Hernández-Carrasquilla, F., 1993. Catálogo provisional de los yacimientos con aves del Cuaternario de la península ibérica. Archaeofauna 2, 231–375.

Holm, S.R., Svenning, J.C., 2014. 180,000 years of climate change in Europe: Avifaunal responses and Vegetation Implications. PLoS One 9 (4), e94021. https://doi.org/10.1371/journal.pone.0094021.

Jánossy, D., 1983. Humeri of the central European smaller Passeriformes. Fragment Mineral. Paleontol. 11, 85–112.

Kessler, E., 2015. Osteological guide of songbirds from Central Europe. Ornis Hungarica 23 (2), 62–155.

Kessler, E., 2016. Picidae in the European fossil, subfossil and recent bird faunas and their osteological characteristcis. Ornis Hungarica 24 (1), 96–114.

Kraft, E., 1972. Vergleichend morphologische Untersuchungen an Einzelknochen Nord- und Mitteleuropäischer kleinerer Jühnervögel. Unpublished PhD Dissertation,. Universität Munchen.

Kumar, R., 2011. Neoglaciation. Encyclopaedia of Snow, Ice and Glaciers. Springer, USA.

Laroulandie, V., 2000. Taphonomie et Archéozoologie des Oiseaux en Grotte: Applications aux sites Paléolithiques du Bois-Ragot (Vienne), de Combe Sauniére (Dordogne) et de La Vache (Ariége). PhD Dissertation.. Université de Bordeaux, Bordeaux, p. 396.

Laroulandie, V., 2002. Damage to pigeon long bones in pellets of the eagle owl *Bubo bubo* and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological. In: Bochenski, Z.M., Bochenski, Z., Stewart, J.R. (Eds.), Proceedings of the 4th Meeting of the ICAZ Bird Working Group, Krakow, vol. 45. Acta Zoologica Cracoviensia, pp. 331–339.

Laroulandie, V., 2010. Alpine chough *Pyrrhocorax graculus* from Pleistocene sites between Pyrenees and Alps: natural versus cultural assemblages. In: Prummel, W., Zeiler, J.T., Brinkhuizen, D.C. (Eds.), Birds in Archaeology, Proceedings of the 6th Meeting of the ICAZ Bird Group in Groningen. Groningen University Library, pp. 219–232.

Livingston, S.D., 1989. The taphonomic interpretation of Avian Skeletal Part Frequencies. J. Archaeol. Sci. 16, 537–547.

Lloveras, L., Cosso, A., Solé, J., Claramunt-López, B., Nadal, J., 2018. Taphonomic signature of golden eagles (*Aquila chrysaetos*) on bone prey remains. Hist. Biol. 30 (6), 835–854. https://doi.org/10.1080/08912963.2017.1319830.

López-García, J.M., Cuenca-Bescós, G., Blain, H.-A., Álvarez-Lao, S., Uzquiano, P., Adán, G., Arbizu, M., Arsuaga, J.L., 2011. Palaeoenvironmental and palaeoclimate of the Mousterian-Aurignacian transition in northern Iberia: the small-vertebrate assemblage from Cueva del Conde (Santo Adriano, Asturias, Spain). J. Hum. Evol. 61, 108–116.

López-García, J.M., Blain, H.-A., Burjachs, F., Ballesteros, A., Allué, E., Cuevas-Ruiz, G.E., Rivals, F., Blasco, R., Morales, J.I., Rodríguez-Hidalgo, A., Carbonell, E., Serrat, D., Rosell, J., 2012. A multidisciplinary approach to reconstructing the chronology and environment of southwestern European Neanderthals: the contribution of Teixoneres cave (Moià, Barcelona, Spain). Quat. Sci. Rev. 43, 33–44. https://doi.org/10.1016/j.quascirev.2012.04.008.

Lloveras, L., Nadal, J., 2020. Estudio experimental del procesado de carcasas de aves. Interpretándo el consumo de anátidas en contextos paleolíticos. Sagvntum Extra 21, 49-49.

López-García, J.M., Blain, H.-A., Bennàsar, M., Sanz, M., Daura, J., 2013. Heinrich event 4 characterized by terrestrial procies in southwestern Europe. Clim. Past 9, 1053–1064. https://doi.org/10.5194/cp-9-1053-2013.

Madge, S., 2020. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Red-Billed Chough (*Pyrrhocorax pyrrhocorax*), Version 1.0. In Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rebcho1.01.

Mlikovsky, J., 1996. New data on the food of the white-tailed eagle (*Haliaeetus albicilla*) in the Svjatoj Nos wetlands. Lake Baikal. Buteo 8, 115–118.

Morales, J.I., Tejero, J.M., Cebrià, A., Pedro, M., Rodríguez-Hidalgo, A., Oms, X., Soto, M., Vallverdú, J., Allué, E., Saladié, P., Fernández-García, M., García-Argudo, G., Fernández-Marchena, J.L., López-García, J.M., Bañuls-Cardona, S., Burguet-Coca, A., Fullola, J.M., 2016. Expanding the geography of the Middle to Upper Paleolithic transition: Foradada Cave (Calafell, Spain), a new site on the Iberian Mediterranean Coastline. Antiquity Project Gallery 90 (351).

Morales, J.I., Cebrià, A., Burguet-Coca, A., Fernández-Marchena, J.L., García-Argudo, G., Rodríguez-Hidalgo, A., Soto, M., Talamo, S., Tejero, J.M., Vallverdú, J., Fullola, J.M., 2019. The Middle-to-Upper Paleolithic transition occupations from Cova Foradada (Calafell, NE Iberia). PLoS One 14 (5), e0215832.

Moreno-García, M., 2017. Estudio de la avifauna de la cueva de Praileaitz I (Deba, Gipuzkoa). Munibe Monogr. Anthropol. Archaeol. Ser. 1, 287–325.

Moreno-Ibáñez, M.Á., Saladié, P., Morales, J.I., Cebrià, A., Fullola, J.M., 2021. Was it an axe or an adze? A cranial trauma case study from the late Neolithic – Chalcolithic site of Cova Foradada (Calafell, Spain). Int. J. Paleopathol. 32, 23–30.

Moreno-Ibáñez, M.A., Saladié, P., Morales, J.I., Cebriá, A., Fullola, J.M., 2022. Inhumation and cremation: identifying funerary practices and reuse of space through forensic taphonomy at Cova Foradada (Calafell, Spain). Archaeol. Anthropol. Sci. 14, 57.

Naughton, F., Sánchez-Goñi, M.F., Kageyama, M., Bard, E., Duprat, J., Cortijo, E., Desprat, S., Malaizé, B., Joly, C., Rostek, F., Turon, J.-L., 2009. Wet to dry climatic trend in North-Western Iberia within Heinrich events. Earth Planet. Sci. Lett. 284, 329–342. https://doi.org/10.1016/j.epsl.2009.05.001.

Núñez-Lahuerta, C., Cuenca-Bescós, G., Sauqué, V., Galán, J., 2016. Avian remains from the Upper Pleistocene (MIS3) site of Aguilón P-7, south of the Ebro River, Spain. Hist. Biol. 28 (6), 774–786. https://doi.org/10.1080/08912963.2015.1028928.

Núñez-Lahuerta, C., Galán, J., Sauqué, V., Cuenca-Bescós, G., 2018. The role of birds in Late Pleistocene Eurosiberian-Mediterranean boundary reconstructions in Western Europe. Quat. Int. 481, 113–122. https://doi.org/10.1016/j.quaint.2018.01.023.

Núñez-Lahuerta, C., Sauqué, V., Sanchís, A., Duarte, E., de la Rasilla, M., 2021. Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain). Comptes Rendus Palevol. 20 (30), 627–640. https://doi.org/10.5852/cr-palevol2021v20a30.

Oms, F.X., Esteve, X., Mestres, J., Martín, P., Martins, H., 2014. La neolitización del nordeste de la Península Ibérica: datos radiocarbónicos y culturales de los asentamientos al aire libre del Penedès. Trab. Prehist. 71 (1), 42–55.

Orta, J., Kirwan, G.M., Christie, D.A., Boesman, P.F.D., Marks, J.D., 2020. White-tailed Eagle (*Haliaeetus albicilla*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whteag.01.

Rodríguez-Hidalgo, A., Lloveras, A., Moreno-García, M., Saladié, P., Canals, A., Nadal, J., 2013. Feeding behaviour and taphonomic characterization of non-digested rabbit remains produced by the Iberian lynx (*Lynx pardinus*). J. Archaeol. Sci. 40 (7), 3031–3045. https://doi.org/10.1016/j.jas.2013.03.006.

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. Quat. Int. 421 (9), 228–238. https://doi.org/10.1016/j.quaint.2025.11.078.

Rodríguez-Hidalgo, A., Morales, J.I., Cebría, A., Courtenay, L., 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. Sci. Adv. 5, eaax1984.

Sánchez-Goñi, M.F., Landais, A., Cacho, I., Duprat, J., Rossignol, L., 2009. Contrasting intrainterstadial climatic evolution between high and middle North Atlantic latitudes: A close-up of Greenland interstadials 8 and 12. Geochem. Geophys. Geosystems 10 (4). https://doi.org/10.1029/2008GC002369.

Sánchez-Marco, A., 2004. Avian zoogeographical patterns during the Quaternary in the Mediterranean region and paleoclimatic interpretation. Ardeola 51 (1), 91–132.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Serjeantson, D., 2009. Birds. Cambridge University Press, Cambridge.

Solti, B., 1996. The Comparative Osteomorphological Study of the European Small-statured Falcons (Aves: Falconidae). Folia Historico Naturalia Musei Matraensis 21, 1–282.

Suárez-Bilbao, A., Elorza, M., Castaños, J., Arrizabalaga, A., Iriarte-Chiapusso, M.J., Murélaga, X., 2020. The Late Pleistocene avifauna from Artazu VII (Basque Country, northern Iberian Peninsula). Hist. Biol. 32 (3), 307–320. https://doi.org/10.1080/08912963.2018.1491566.

Summers-Smith, D., Bonan, A., 2020. White-winged Snowfinch (*Montifringilla nivalis*), versión 1.0 in. In: del Hoyo, J., Elliot, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whwsno1.01.

Timmermann, A., 2020. Quantifying the potential causes of Neanderthal extinction: abrupt climate change versus competition and interbreeding. Quat. Sci. Rev. 238, 106331 https://doi.org/10.1016/j.quascirev.2020.106331.

Tomek, T., Bochenski, Z.M., 2000. The Comparative Osteology of European Corvids (Aves: Corvidae), with a Key to the Identification of their Skeletal Elements. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow.

Tyrberg, T., 2008. Pleistocene Birds of the Palearctic: A Catalogue, vol. 27. Publications of the Nutall Ornithological Club.

Wójcik, J.D., 2002. The comparative osteology of the humerus in European thrushes (Aves, *Turdus*) including a comparison with other similarly sized genera of passerine birds e preliminary results. Acta Zool. Cracov. 45 (Special Issue), 369–381.