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# Mid-Late Pleistocene Neanderthal landscapes in southern Italy: paleoecological contributions of the avian assemblage from Grotta del Cavallo, Apulia, southern Italy

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## Abstract

We present a detailed paleoecologic analysis of avian assemblages from the Mousterian layers of the Middle Paleolithic Grotta del Cavallo site in southern Italy. Findings improve knowledge of the landscape that was exploited by Neanderthals. During the MIS 7, 6 and 3, the cave was surrounded by extensive grasslands and shrublands, locally interspersed by open woodland and rocky outcrops, whereas the coastal plain (currently underwater) hosted wetlands. Water bird taxa show an increase in population size during the cool-temperate climatic interval attributed to MIS 3, possibly linked to more humid conditions or a shorter distance between the wetland settings and the cave, compared to the previous glacial phase (MIS 6). In addition, coverage-based rarefied richness suggests higher avian diversity during MIS 3, which may reflect greater landscape heterogeneity due to the presence of wetland habitats. The tentative discovery of *Branta leucopsis*, together with several bird species currently found at higher altitudes, reinforces geochemically-derived palaeoclimate inferences of cooler than the present conditions. These assemblages also include the first fossil occurrence of *Larus genei* worldwide, the first Italian occurrence of *Emberiza calandra*, the oldest Italian occurrence of



*Podiceps nigricollis*, and the occurrence of the rarely reported *Sylvia* cf. *communis*. Taphonomic analyses indicate that bone modifications are mainly due to physical syn- and post-depositional processes, and that the assemblage mainly accumulated through short-range physical transport and the feeding activities of nocturnal raptors.

## **Keywords**

Fossil bird; Paleoenvironment reconstruction; Paleoclimate; Taphonomy; Late Quaternary

### **1. Introduction**

Birds' ecological needs are currently well known, thanks to hundreds of years of ornithological observations. Most species have narrow environmental and dietary requirements and a high degree of ecological specialization. The avian fossil record shows that most of the extant bird species originated approximately in the Early Pleistocene of Europe (Mourer Chauviré, 1993; Tyrberg, 1998, 2008; Finlayson, 2011; Bedetti and Pavia, 2013). Molecular data partially support the inferences provided by the fossil record, suggesting also some rather young divergences linked to glacial-interglacial dynamics in the Pleistocene and others dating back to Pliocene or even Miocene (Voelker and Light, 2011; Drovetski et al., 2013; Pellegrino et al., 2017; Ghorbani et al., 2020). These aspects, together with the evolutionary stability of bird species and the ability to fly, which eases the spatial tracking of suboptimal ecological conditions (Michailidis et al., 2018), make the Pleistocene avian remains an excellent tool to reconstruct past ecological scenarios and climate dynamics. Past avifaunal assemblages can reveal the paleo-landscapes and ecological interactions (Eastham, 1997; Gál, 2006; Serjeantson, 2009; Bedetti and Pavia, 2013), as exhaustively as mammal remains, and may compensate for each other's weakness. Furthermore, bird species turnover through time can be used to infer the response of the terrestrial ecosystems to past climate-driven changes (Tomek and Bocheński, 2005; Tomek et al., 2012; Prassack, 2014; Carrera et al., 2018a; Prassack et al., 2018). For instance, during the late Quaternary glacial periods, the Balkans, Iberia, Italian peninsula and Transcaucasia became refugial areas, as the northern latitudes became unsuitable for the survival of Palearctic species (Tyrberg, 1991; Sanchez Marco, 2004; Pellegrino et al., 2014; Drovetski et al., 2018; Raković et al., 2019). Lastly, fossil birds from archaeological sites could also provide insights on subsistence strategies and

technological skills of archaic human populations and detail the characteristics of the landscape that they exploited (Blasco and Peresani, 2016). Despite the great potential of this field, paleornithology is quite neglected, probably because of the paucity of paleobiologists specialised in the identification of bird bones and due to the limited diffusion of bird skeletal reference collections.

We present here a paleoecologic analysis of the avian fossil assemblage coming from the Pleistocene Mousterian layers of Grotta del Cavallo (Southern Italy, Nardò, Fig. 1a). This archaeological site represents, with its thick sedimentary succession, a reference for Mousterian lithic industries of Southern Italy and one of the most important Italian Paleolithic sites (Sarti et al., 1998-2000 2002, 2017; Benazzi et al., 2011; Romagnoli et al., 2015; Moroni et al., 2018). The sedimentary succession of Grotta del Cavallo covers a wide time span, from Marine Isotope Stage (MIS) 7 to 1 (Holocene Fabbri et al., 2016; Martini, 2016; Martini and Sarti, 2017; Sarti et al., 2017; Zanchetta et al., 2018; Sarti and Martini, in press). Except for a small fossil assemblage from the Uluzzian layers (i.e., MIS 3; Pavia, 2000), the bird remains from Grotta del Cavallo have never been studied in detail (the Mousterian fossil birds have only preliminarily been described in Carrera, in press). The investigation of the avian assemblages coming from the Apulia region during glacial-interglacial cycles, results pivotal also from a paleobiogeographic perspective to elucidate the processes that led to the current avifaunal distribution and current genetic diversity (Boano et al., 2015; Newton, 2003; Pellegrino et al., 2014 2015a, 2015b, 2017; Tietze, 2018).

In sum, this work aims to add new evidence of the effects of the Pleistocene interglacial-glacial transitions on the Apulia environmental scenario based on the data provided by avian remains from Grotta del Cavallo. It will also detail the main habitat types available to Neanderthal hunter-gatherer groups in the surroundings of the cave and in the Salento area and explore the dynamics of the avian biodiversity in this area that acted as a refugial during glacial periods.

## **2. Grotta del Cavallo**

Grotta del Cavallo (40° 9' 18.85" N, 17° 57' 37.27" E) is a karstic cave which opens at approximately 15 m asl on the coastal rocky cliff of the Bay of Uluzzo, near the town of Nardò (Lecce province, Apulia), facing the Ionian Sea (Fig. 1a, 1b). The cave is a single roughly circular chamber, approximately 9 m in diameter. Above the cave extends a wide undulating limestone plateau that does not exceed 60 m asl, which

is retained to represent one of the Neanderthal hunting areas. However, during the last glacial phases, the drop in the sea level allowed the subaerial exposure of great part of the Italian continental shelf (Benjamin et al., 2017), and the present-day shallow marine setting of Italian continental shelf turned into wide coastal plains (Vai et al., 2004; Azzarone et al., 2020).

## POSITION OF THE FIGURE 1

The first archaeological excavations in the cave took place during the 1960s under the direction of Arturo Palma di Cesnola. In 1986, the cave was subjected to new excavations under the direction of Lucia Sarti with the collaboration of the Florence University (Italy). The Middle Paleolithic deposits were excavated in the following years on a surface area of approximately 12 m<sup>2</sup> (Sarti et al. 1998-2000, 2002, 2017). The thick sedimentary succession (Fig. 1c) lies on two beach deposits: the layer R, the most ancient beach, and the layer O, the latest one, separated by the layer Q (a terrestrial deposit with scattered archaeological material). The layer P is mainly composed by boulders. The beach deposits, previously attributed to MIS 5e, are currently referred to MIS 7 after a chronological revision of the lower portion of the stratigraphic succession (Sala and Berto, in press). Above the beach deposit O, the sequence is composed by four chrono-cultural units: the Mousterian (layers N-F) here examined; the Uluzzian (layers E-D); the Final Upper Paleolithic and Mesolithic (layer B); and the Neolithic (layer A). In the 4 m thick Mousterian sequence (layers N to F) (Fig. 1c) multiple sub-units (horizons) have been distinguished, with hearths and local concentrations of faunal remains and anthropic artifacts on flint, limestone, and shells (Romagnoli et al., 2015; Sarti et al., 2017; Sarti, in press; Martini and Sarti, in press). All N-F layers contain more or less abundant archaeological material, except for the tephra layer G (Fig. 1c), which has been recently dated to  $108.7 \pm 0.9$  kyr B.P. (Zanchetta et al., 2018) and is separated from the layer F by an erosion phase. Indeed, layer F is referred to MIS 3 (57 - 29 kyr B.P.), as suggested by the recent dating of tephra level Fa (located at the top of the studied succession) and by previous radiocarbon datings (Fabbri et al., 2016; Zanchetta et al., 2018). Thus, layer F represents a key stratigraphic unit as it records the upper boundary of Neanderthal occupation of Grotta del Cavallo (Sarti et al., 1998-2000) and approximates Neanderthal-Sapiens turnover in southern Europe (Benazzi et al., 2011; Higham et al., 2014; Staubwasser et al. 2018). The layers N and M are

attributed, on the basis of a recent chronological revision, to MIS 7 (291 - 193 kyr B.P.), whereas the layers L-IIc are referred to MIS 6 (191 - 130 kyr B.P.) (Sala and Berto, in press).

The mammal remains and the pollen sequence of the Middle Paleolithic sequence provided some hints about the environmental and climatic framework that characterized the surroundings of the cave at the time of the Neanderthal occupation. Macromammal remains, whose presence in the cave is mainly due to Neanderthal hunting activity, testify to periodic reductions and expansions of the woodland cover likely related to moisture and temperature oscillations (Palma di Cesnola, 1966; Sarti et al., 1998-2000, 2002; Boscato et al., 2013; Sala and Berto, in press). The pollen sequence, that reports the prevalence of herbaceous taxa, reveals the presence of a steppe landscape with a variable wood cover. The trees are represented by conifers and by some mesophilous taxa (Ricciard , 2005). The micromammal assemblages from the Mousterian sequence, due to the activity of nocturnal raptors in the cave, revealed a scarce species biodiversity and points to the predominance of open environments in the whole sequence (Dalla Valle, 2008; Petruso et al., 2011; Berto, in press).

### **3. Material and methods**

The avian bone material consists of 1050 remains coming from the Mousterian layers (F, H, I, L, M, N) plus layer Q (Sarti excavations, 1986-2005). These bones have been collected after sediment wet sieving (mesh size: 1 - 1.5 mm). Each specimen was given a provisional catalogue code, formed by a progressive number preceded by the letter “C” that refers to “Cavallo”, the name of the cave. The bones have been analysed on both taphonomical (Tab. 1) and taxonomical perspectives (Tab. 2). The bone material object of the present study is housed at the Dipartimento di Scienze storiche e dei Beni culturali of the University of Siena.

The taxonomic identification of the remains relied on specimens from several bird skeletal collections, that are listed in the Supplementary Material (SM-Modern osteological comparative collections). For taxonomic identifications, we also used handbooks devoted to the osteology of several bird families or orders. For osteological terminology, we used as reference Baumel and Witmer 1993, whereas for systematics we followed Del Hoyo et al. (2014, 2016). Number of Identified Specimens (NISP) has been calculated for each taxon and layer, whereas Minimal Number of Individuals (MNI, see Howard, 1930;

Lyman 1994, 2008) has been calculated for each taxon (from the species to the family level) in each layer, as reported in Tab. 2. Taxonomic characterizations at the species level (grouped by family) are reported in the Supplementary Material (SM-Diagnostic features and taxonomic inferences).

As for environmental reconstructions, most of the species identified were assigned to one of the following four environmental macro-categories, based on their environmental requirement: open (O), rocky (R), water/wet (Wa), and woodland (Wo) habitats (Tab. 2). Open habitats include a variety of treeless landscapes such as grasslands, shrublands, and steppe. Rocky habitats are characterized by the presence of rocky cliffs, crags, or exposures. Water/wet environments include wetlands, wet meadows, rivers, lakes and coastal marine settings, whereas woodland is defined by evergreen or deciduous forests and also open woodlands. Finally, for taxa in open nomenclature and those species having a eurytopic distribution (Cramp, 1998), environmental labels were not assigned (NA in Tab. 2). Those layers containing the remains of at least eight species considered as “environmental markers”, have been considered representative from a paleoenvironmental point of view, allowing us to define the changes in the landscape across the studied interval of the sedimentary sequence (Tomek and Bocheński, 2005; Tomek et al., 2012; Carrera et al., 2018a; Izvarin et al., 2020).

Single sample rarefaction analysis on species level taxa recovered in the studied succession was conducted on investigated layers to evaluate any change in standardized diversity of avian assemblages to complement paleoenvironmental inferences. The sampled layers vary substantially in terms of the MNI per sample (Tab. S1), so rarefaction was employed to correct for the unbalanced sampling structure. Rarefaction strategies include a series of methods commonly used in paleontology for different purposes (e.g., Scarponi and Kowalewski, 2007; Randle and Sansom, 2019). Here iNEXT R-package was employed for rarefaction specimens and coverage-based analyses (see Hsieh et al., 2016 and references therein for further information).

Lastly, the taphonomic analysis to evaluate degradation patterns and infer dominant processes of sample accumulation within studied sedimentary units, was achieved by examining all avian remains recovered using a 30x magnifying glass, in raking or reflected artificial light, and detected marks have been additionally observed with a 0.75-70x Leica S6D Greenough stereomicroscope. Remains from each paleosurface were merged and analysed at sub-unit scale (as defined in Martini and Sarti, in press), only sub-

units that reported more than 10 bones were considered for the analysis. A total of 16 sub-units yielded sufficient material for taphonomic investigations (Tab. S3a, S3b). For each remain, twelve variables were recorded and scored following the protocol defined in Tab. 1. Pictures of the main categories of taphonomic damages retrieved in the bird assemblage from Grotta del Cavallo are provided in Fig. S1. Fragments/bones varied in dimension from 3 mm to 58 mm. The prevalence of each taphonomic modification has been calculated for each sub-unit. The pairwise distances between samples were based on multivariate Euclidean distances using log-transformed relative abundances of selected variables (Tab. S3b). Then, for sub-units yielding  $\geq 18$  items, non-metric multidimensional scaling (NMDS) was employed to visualize relative similarities of all samples in terms of their taphonomic signatures (see Scarponi et al., 2017 and references therein for detailed information on the ordination technique).

POSITION OF THE TABLE 1

## **4. Results**

### ***4.1. Taxonomy, paleoenvironmental and diversity inferences***

The taxonomic analysis allowed the identification of 77% (n=809) of the bird bones, represented by 70 taxa and 35 identified species (Tab. 2). 48 taxa have been considered environmental key-species and have been used to infer changes in the landscape across the Mousterian sequence (Fig. 3).

POSITION OF THE TABLE 2

As for compositional diversity, rarefaction analyses standardized by sample-size and coverage-based (Hsieh et al., 2016) were conducted on layers F, I, N and M. Sample-size rarefaction considering specimen abundance (see Tab. S2) returned a substantial homogeneity with strong overlaps of rarefied richness values among layers (even if layer F tended to show higher standardized richness; Fig. 2; Tab. S2). Whereas, when sample richness is standardized to the same sample coverage (i.e., estimated degree of sample completeness with respect to the expected species richness of the sampled assemblage), layer F at standardized cover of

70% shows the highest and significantly different values of all three analysed descriptors of diversity (i.e., species richness, Shannon and Simpson index; Fig. 2, Tab. S2).

The bird species identified in this work all belong to the extant Italian avifauna (Brichetti and Fracasso, 2015). Some taxonomic, environmental, and paleobiogeographic remarks of the identified species, presented by families, are reported here. Further details on the osteological features that support the taxonomic identifications are described in the Supplementary Material (SM-Diagnostic features and taxonomic inferences).

POSITION OF THE FIGURE 2

POSITION OF THE FIGURE 3

**Galliformes - Phasianidae.** Eight bone remains have been attributed to *Coturnix coturnix*. This migratory species prefers wide open spaces with low vegetation up to 1000 m (Cramp, 1998). Three bones have been identified as *Alectoris graeca*, a sedentary species that lives in dry, rocky mountains between the treeline and snowline (Cramp, 1998). Twelve bones have been assigned to *Perdix perdix*, a sedentary species living in grasslands and shrublands (Cramp, 1998). *C. coturnix*, *A. graeca* and *P. perdix* are known in the fossil record since the Early Pleistocene (Tyrberg, 1998, 2008; Núñez-Lahuerta et al., 2016).

**Anseriformes - Anatidae.** One proximal left ulna is dubitatively referred to *Branta leucopsis*. *B. leucopsis* is a cold-adapted migratory species spread in the northern latitudes and breeding mainly in the arctic regions (Cramp, 1998). It is a rare migratory and wintering species in Italy, mostly observed in Northern and Central Italy (Brichetti and Fracasso, 2003). During winter, it frequents coastal lowlands and floodlands and wet meadows (Cramp, 1998). One distal right carpometacarpus has been dubitatively assigned to *Aythya nyroca*, a migratory species which lives in shallow or coastal water and large lagoons (Cramp, 1998). Another distal right carpometacarpus has been referred to *Aythya fuligula*, which is a migratory species living in open and often deep fresh waters or coastal sheltered areas (Cramp, 1998). One distal left humerus has been attributed to *Spatula querquedula*, a migratory species that lives in shallow standing freshwaters (Cramp, 1998). Two remains have been identified as *Anas crecca*, a migrant that

frequents wetlands and lakes (Cramp, 1998). *B. leucopsis* is known since the Middle Pleistocene, whereas *A. nyroca*, *A. fuligula*, *S. querquedula* and *A. crecca* are known in the fossil record since the Early Pleistocene (Tyrberg, 1998, 2008; Pavia et al., 2018).

**Podicipediformes - Podicipedidae.** Two remains have been identified as *Podiceps cristatus*. This partly migratory species prefers cold standing fresh or brackish waters on deltas and tidal channels or lagoons (Cramp, 1998). One proximal right tarsometatarsus has been ascribed to *P. nigricollis*, a small migratory grebe that frequents shallow productive waters during breeding and shifts to open standing waters or sheltered estuaries in other periods (Cramp, 1998). *P. cristatus* is known in the fossil record since the Early Pleistocene. *P. nigricollis* fossil records are mostly of Late Pleistocene age, with only one Upper Pliocene record (Tyrberg, 1998, 2008; Sánchez Marco, 2005). In Italy, it has been previously identified only in 3 Late Pleistocene (late glacial) deposits (Tyrberg, 2008; Gala and Tagliacozzo, 2010; Gala et al., 2018), and therefore the fossil remain from Grotta del Cavallo (layer F) stands out as the oldest Italian fossil occurrence of this species, testifying its presence in Italy at least since MIS 3.

**Columbiformes - Columbidae.** Four remains have been ascribed to *Columba livia*. The natural habitat of this sedentary species is linked to nest-sites on rock faces (Cramp, 1998). Two humeri have been assigned to *Streptopelia turtur*, a migratory species living in borders of woodland or wetland, open woodland and heaths with clumps of trees (Cramp, 1998). *C. livia* is known in the fossil record since the Early Pleistocene, whereas *S. turtur* is reported since the Middle Pleistocene (Tyrberg, 1998, 2008).

**Caprimulgiformes - Apodidae.** One right coracoid has been referred to *Tachymarptis melba* and one right tarsometatarsus has been identified as *Apus apus*. Both species are migrant, strongly aerial, and linked to nest sites in cliffs and crags (Cramp, 1998). Both species are also known in the fossil record since the Middle Pleistocene (Boev, 1998, 2001; Tyrberg, 1998, 2008).

**Gruiformes - Rallidae.** One right quadratum is referred to *Fulica atra*, a partly migratory species living in standing waters like lakes, lagoons, and wetlands (Cramp, 1998). *F. atra* is known in the fossil record since the Early Pleistocene (Tyrberg, 1998, 2008).

**Otidiformes - Otididae.** Eight remains have been assigned to *Tetrax tetrax*, a species that prefers steppe grasslands and scrublands, and is migratory in the eastern part of its range (Cramp, 1998). *T. tetrax* is reported in the fossil record since the Early Pleistocene (Tyrberg 1998, 2008; Bedetti and Pavia, 2013).



**Pelecaniformes - Threskiornithidae.** One proximal radius has been identified as *Plegadis falcinellus*, a migratory species that lives in shallow water environments in lakes or lagoons (Cramp, 1998). *P. falcinellus* is reported in the fossil record since the Middle Pleistocene (Tyrberg 1998, 2008), with one older Upper Pliocene record (Sánchez Marco, 2005). The oldest Italian occurrence of this species is from the Middle Pleistocene deposits of Casal Selce (Pavia et al., 2018).

**Charadriiformes - Charadriidae.** One distal left tibiotarsus has been attributed to *Pluvialis squatarola*, a migratory species breeding in the lowland tundra of the high Arctic and frequenting, outside the breeding season, mudflats, pools, or grassy fields (Cramp, 1998). One right coracoid has been identified as *Eudromias morinellus*, a migratory species breeding in the arctic tundra and alpine zones, below snowline, favouring bare ground treeless areas or heathland during migration and steppe and semi-desert areas in winter (Cramp, 1998). *P. squatarola* is known in the fossil record since the Middle Pleistocene (Tyrberg, 1998, 2008), whereas *E. morinellus* is reported since the Early Pleistocene (Tyrberg, 1998, 2008).

**Charadriiformes - Laridae.** One distal right ulna has been attributed to *Larus genei*, a migratory colonial species breeding along sheltered coasts or in meadows and frequenting coastal and marine areas outside the breeding season (Cramp, 1998). This fossil remain, which comes from layer F of the Grotta del Cavallo, is remarkably interesting from a paleontological perspective, since *Larus genei* has never been reported as a fossil in any other known deposit. Therefore, this ulna represents the first fossil occurrence ever of this species (Mlíkovský, 2002; Tyrberg, 1998, 2008), confirming the presence of this species in the Mediterranean basin at least since the Late Pleistocene.

#### POSITION OF THE FIGURE 4

**Strigiformes - Strigidae.** Nineteen bone remains have been assigned to *Athene noctua*. This sedentary species needs open hunting ground, hunting perches, and nest holes (mainly in trees or walls) (Cramp, 1998). A portion of the rostrum mandibulae is referred to *Strix aluco*, a sedentary species living in deciduous or conifer woodlands that nests in holes in trees and cliffs (Cramp, 1998). One distal left radius has been referred to *Otus scops*, a migratory nocturnal species that lives in broad leaved and mixed open woodland and nests in holes in trees or walls (Cramp, 1998; Treggiari et al., 2013). One proximal left tarsometatarsus

has been referred to *Bubo bubo*, a sedentary species that hunts in open woodland and nests in hollow trees, cliff-ledges, or caves (Cramp, 1998). *A. noctua*, *O. scops*, and *S. aluco* are reported in the European fossil record since the Early Pleistocene (Tyrberg, 1998, 2008; Bedetti and Pavia, 2013), whereas *B. bubo*, after a recent revision of its earliest fossil remains, is definitively reported in the fossil record since the Middle Pleistocene (Meijer et al., 2017), and not from the Early Pleistocene as previously thought (Tyrberg, 1998, 2008).

**Accipitriformes - Accipitridae.** One left fourth phalanx of digit IV has been attributed to *Aquila chrysaetos*, which lives in montane areas with rock walls and mountain meadows, respectively used to nest and as hunting grounds (Cramp, 1998). Two remains have been attributed to *Circus aeruginosus*, a partly migratory species that prefers shallow standing fresh or brackish waters fringed by reeds during the breeding season and grassy plains in the winter (Cramp, 1998). *A. chrysaetos* is known since the Early Pleistocene, whereas *C. aeruginosus* is recorded since the Middle Pleistocene (Tyrberg, 1998, 2008).

**Falconiformes - Falconidae.** Four remains have been assigned to *Falco tinnunculus*. The os metacarpale majus of a carpometacarpus is filled by medullary bone, indicating that the species bred in the cave or very close to it (Serjeantson, 2009). This partly migratory species lives in a variety of moorlands, grasslands, and wetlands with open vegetation and nests on trees, rocks, or artifacts (Cramp, 1998). *F. tinnunculus* is known in the fossil record since the Early Pleistocene (Tyrberg, 1998, 2008).

**Passeriformes - Corvidae.** Eleven remains have been referred to *Pyrrhonorax pyrrhonorax*. One tarsometatarsus of *P. pyrrhonorax* belongs to a juvenile individual, testifying to this species breeding near the cave. This sedentary species nests in crevices of coastal cliffs, inland crags, or montane regions in midlatitudes and uses grasslands for feeding (Cramp, 1998). Four remains have been assigned to *Pica pica*, a sedentary bird which lives in a wide variety of habitats, such as open or lightly wooded areas (Cramp, 1998). *Corvus monedula* is present in this avian assemblage with one proximal right carpometacarpus. This partly migratory species is highly sinantropic, lives in open areas with grasslands and scattered woodlands, and nests in holes in trees, cliffs, or buildings (Cramp, 1998). *Corvus corax* is represented by seven ungual phalanxes. This sedentary species nests in cliffs, walls, or high up in trees near open areas that it uses to feed (Cramp, 1998). *P. pyrrhonorax*, *P. pica*, and *C. corax* are known in the fossil record since the Early

Pleistocene (Tyrberg, 1998, 2008). *C. monedula* is known since the Early Pleistocene (Tyrberg, 1998, 2008), with only one Upper Pliocene record (Sánchez Marco, 2005).

**Passeriformes - Alaudidae.** Two bill fragments have been identified as *Melanocorypha calandra*, a migratory bird living in steppe grassland (Cramp, 1998). *M. calandra* is known since the Early Pleistocene (Tyrberg, 1998, 2008; Bedetti and Pavia, 2013).

**Passeriformes - Sylviidae.** One right and one left juvenile humeri have dubitatively been referred to *Sylvia communis*. This migratory species lives in grasslands with low shrubs, preferring dry and sunny terrain, or in open woodland glades and edges (Cramp, 1998). *S. communis* is known in the fossil record since the Middle Pleistocene with two dubitative identifications (*Sylvia* cf. *communis*) from the Early Pleistocene deposits of Betfia (Romania) and Pirro Nord (Italy). The two humeri reported from Grotta del Cavallo (layer I) could represent, if the identification will be confirmed, the second Italian fossil occurrence of this species, as no other fossil remain of this species has been reported in Italy except for Pirro Nord (Tyrberg, 1998, 2008; Mlíkovský, 2002; Bedetti and Pavia 2013).

**Passeriformes - Turdidae.** Two bone remains have been dubitatively referred to *Turdus viscivorus*, a partly migratory species that lives in open woodlands and nests on stout branches of trees or ledges in cliffs (Cramp, 1998). *T. viscivorus* is known since the Early Pleistocene (Tyrberg, 1998, 2008).

**Passeriformes - Emberizidae.** Three remains, a maxilla and two mandibulae have been attributed to *Emberiza calandra*, a partly migratory species living in fully open areas (Cramp, 1998). This species is known in the fossil record since the Late Pleistocene (Tyrberg, 1998, 2008). In the deposits of the Early Pleistocene site of Betfia, this species has been identified in a dubitative form (cf. *E. calandra*) (Kessler, 2014). The *Emberiza calandra* fossil occurrences from Grotta del Cavallo (layer M) represent the first Italian fossil occurrence of this species, witnessing its presence in Italy since at least MIS 7.

## POSITION OF THE FIGURE 5

### 4.2. Taphonomic inferences

Considering the whole dataset, fragmentation and manganese dioxide staining were the most abundant and widespread taphonomic features recovered in all examined sub-units (mean = 0.75, s = 0.13; and = 0.66,

= 0.19 respectively). Concretions and root marks were also widespread but attained lower and highly variable values between examined layers (mean = 0.39, s = 0.26; and = 0.28; = 0.22 respectively; see Tab. S3b for details). Other natural modifications (e.g. weathering or trampling), as well as carnivore bite marks and traces of digestion by nocturnal raptors (here considered jointly) are poor (mean  $\leq 0.06$  in all cases, Tab. S3b). Evidence of anthropic modifications produced by human activity (i.e., cut-marks and combustion-derived traces, considered jointly) is also scarce (mean  $\leq 0.02$ , s = 0.04).

When the taphonomic variables are ordinated by means of NMDS (only sub-unit with  $n \geq 18$  fossils considered), axis 1 is correlated with overall taphonomic damage. With nearly all samples showing average-low taphonomic degradation (mean damage <28%; Tab. S3b) attaining negative NMDS1 values, whereas NMDS1 positive values essentially record samples with overall median to high taphonomic degradation (Fig. 6, Tab. S3b). In addition, post-depositional degradation associated with differential carbonate rich groundwater percolating through the sedimentary succession (i.e. concretions) and, to a certain extent, vegetation cover (root etching), are also associated with NMDS1. As for NMDS2, it seems to reflect a proxy of postmortem taphonomic modifications mainly associated with differential redox conditions of groundwater percolating through the sedimentary succession (i.e., manganese staining).

At the unit level, samples from N show a consistently high degradation in all the sub-units considered (i.e., closely spaced along NMDS1, Fig. 6), with concretions and root etching representing important sources of taphonomic damage. Along the same line, sub-units F and I show a relatively homogenous overall degradation within the analysed sub-units (Fig. 6). On the contrary, layer M (and to a certain extent L) show a high variation in overall taphonomic degradation among sub-units (i.e., more spaced apart along NMDS1), suggesting a changing environmental setting and supporting the presence of important erosional surfaces (Martini and Sarti, in press; Sarti, in press).

POSITION OF THE FIGURE 6

## **5. Discussion**

### ***5.1. Taphonomic processes and fossil accumulation dynamics***

Scoring and ordination of the main taphonomic variables considered (Tab. 1, S3b) indicate physical related processes as the main driver of taphonomic degradation observed in the analysed dataset. Specifically, fragmentation, manganese oxides, root marks, and concretions are the most important and widespread variables here scored (see Tab. S3b). All N and M sub-units (especially N2 and M4) show close association with intense fragmentation in the ordination space (Fig. 6). Fragmentation is mainly associated with sin- or post-depositional processes related to occasional collapses of limestones blocks from the cave vault and, to a lesser extent, with reworking due to erosional processes reported through the entire succession (Martini and Sarti, in press; Sarti, in press).

Manganese oxides and carbonate concretions are common taphonomic marks in cave systems and result from post-depositional processes concerning different redox states affecting the groundwater within the cave environment. The diffuse black stainings on examined bones are due to poorly crystalline manganese oxides, that commonly precipitates from reduced waters percolating in the cave environment. The reduced conditions are typical of waters flowing through fine sediments in the presence of important amounts of organic material (that oxidize the groundwater). A highlighted by ordination analyses (Fig. 6; Tab. S3b), manganese precipitates peak in sub-units F, which record intense human related activity that could have enriched the fine deposits with organic matter, and in M4, associated to clayely-silty deposits that are less porous and retain more organic matter

As for concretions, carbonates precipitate from oxic water rich in calcium ions ( $\text{Ca}^{2+}$ ) while flowing through sediment. When such water flows in  $\text{CO}_2$  rich environments, carbon dioxide reacts with water forming  $\text{HCO}_3^-$  that in turn reacts with  $\text{Ca}^{2+}$  forming calcite which then precipitates as incrustation. Thus, calcite incrustation in cave settings could attain higher prevalence during periods where  $\text{CO}_2$  production in the soils is high due to higher productivity (developed roots networks) and is commonly associated with warmer and wetter climates. Here, ordination analyses point toward an association between root etching and concretion-related features that characterize layers N and Q (even if the latter is excluded from the NMDS), which are attributed to MIS 7. The diffuse presence of concretions and root marks on fossil bones (when added to the relevant degree of fragmentation) from layers N and Q make these deposits the most degraded of the entire studied succession (Fig. 6; Table S3b). Other modifications, like trampling, rodent gnawing, exfoliation, and cracking play a minor and always subordinate role (see Tab. S3b). Overall, the most

widespread and important taphonomic degradation (see above) derive from sin- or post-depositional processes, thus not directly involved in fossil accumulations.

Concerning the main drivers of avian bone accumulation, the feeding activities of carnivores and nocturnal raptors is scarcely supported by performed investigation. Indeed, such taphonomic features (bite marks and nocturnal raptors digestion traces) show relatively low values through the entire succession (Tab. S3b) with a higher contribution detected in subunits I2 and L1. The negligible role of mammals as agents of fossil accumulation is also supported by the scarce presence of such remains in the Mousterian sequence (Sarti et al., 1998-2000, 2002; Cecchetti, 2003; Sarti and Martini, in press). Despite the relatively small percentage of bones showing traces of digestion by nocturnal raptors, their activity in the Mousterian layers of Grotta del Cavallo is supported by other elements. The abundance in the cave deposits of well-preserved micromammals (Berto, in press) and small Passeriformes bones (the latter, which are common prey for nocturnal raptors, constitute the majority of identified bird remains), indirectly suggest a role of nocturnal raptors in the avian bone accumulation within the cave, even if diagnostic traces on bone are low. The bones in the pellets, indeed, often are in a good state of preservation, as they are protected by the fur and feathers of the pellet (Andrews, 1990; Serjeantson, 2009), and because they are devoid from flesh residues, which could undermine the conservation of the bones during post-depositional phases, on the basis of a recent study (Bocheński et al., 2017). The intensity of the digestion traces on the bones of their prey varies among the different raptor species: some of them produce pellets with a very small percentage of corroded bones and/or with only faint traces, such as *Tyto alba* (Andrews, 1990). Furthermore, the finding of four Strigidae species which regularly or occasionally feed on other birds and nest on rocky walls (*Athene noctua*, *Otus scops*, *Strix aluco*, and *Bubo bubo*; Cramp, 1998), supports the contribution of nocturnal raptors in the accumulation of bird bones, that probably took place in the periods when the cave was not occupied by Neanderthal groups.

The relevant presence in the deposit of bird species that regularly or occasionally nest on rocky cliffs or exposures, in addition to the presence of several taxa in open nomenclature which include species that nest on cliffs, suggests that physical short-range transport-related processes carrying the remains within the cave could also have played a relevant role in the accumulation of bones within examined Pleistocene layers. Indeed, the abundance of birds whose presence in the deposit could likely be due to natural death within (or

accidentally transported in) the cave, reaches 28.1% ( $n=228$ ) of the identified remains. The highest relative abundance of these taxa is documented in layer N, followed by the layer I (Tab. 2).

As for taphonomic features related to human behaviour, only a negligible percentage of the remains is affected by such signatures. Therefore, humans played a minor role in the accumulation of avian fossil remains across the studied succession, but their study and significance is beyond the scope of the present.

## **5.2. *Paleoenvironmental, paleoclimatic and diversity remarks***

The bird taxa identified allowed to detail and assess the main features of the landscape in the surrounding of Grotta del Cavallo. Considering the whole assemblage, the species from open and water habitats dominate the assemblage, in terms of the number of taxa, MNI, and NISP (Tab. 2). The species of rocky environments are also represented well numerically, whereas woodland-related species were poorly represented. Several species, such as *Athene noctua*, *Falco tinnunculus*, *Eudromias morinellus*, *Coturnix coturnix*, and *Perdix perdix*, testify to the presence of open areas, such as grasslands and shrublands, that were locally drier as suggested by *Tetrax tetra*, *Emberiza calandra*, and by several Alaudidae species (i.e., *Alaudala rufescens*/*Calandrella brachydactyla*, *Melanocorypha calandra*, *Galerida theklae/cristata*) which feed on bare terrains with low vegetation. One remain belonging to *Falco tinnunculus* shows medullar bone in its inside, thus suggesting that the individual was a breeding female that nested near the site, probably in rock ledges. Two juvenile remains of *Sylvia* cf. *communis* from layer I suggest that this species bred nearby the cave and thus shrublands were present. Rocky exposures with scattered low vegetation were also present, as suggested by *Alectoris grae*, *a. Columba livia*, together with two swift species (*Tachymarptis melba* and *Apus apus*), one owl (*Bubo bubo*), one raptor (*Aquila chrysaetos*), and two Corvidae species (*Pyrrhocorax pyrrhocorax* and *Corvus corax*) indicate the presence of rocky walls, probably corresponding to the 70-100 meters high coastal cliff where the cave opens, and used by these species to nest. The nesting of *P. pyrrhocorax* nearby the cave is supported by the finding of a juvenile remain of this species in layer M. The presence of *Strix aluco* seems to suggest the presence of woodland environments, whereas the presence of *Streptopelia turtur*, *Otus scops*, *Pica pica*, and *Turdus viscivorus* indicate the presence of open woodlands and clumps of trees (Cramp, 1998).

The presence of wet environments around the cave was previously only partially hinted at by the sporadic presence of a few plant taxa in the layers I, L, H, and F (Ricciardi, 2005) and of scattered mollusc specimens of brackish or freshwater (Wilkens, in press). The avian assemblages were able to detail the landscape resolution with respect to previous data, documenting the presence of diffused marshes and wetland systems nearby the cave for the entire succession. This is due to the retrieval of two grebe species (*Podiceps cristatus* and *P. nigricollis*), several duck species (cf. *Aythya nyroca*, *Aythya fuligula*, *Spatula querquedula*, *Mareca strepera/penelope*, *Anas crecca*), one Rallidae (*Fulica atra*), an ibis (*Plegadis falcinellus*), some waders (*Pluvialis squatarola*, *Numenius* sp.), a gull (*Larus genei*), and a raptor (*Circus aeruginosus*). In addition, two goose species (cf. *Branta leucopsis* and *Anser albifrons/erythropus*) point towards the presence of wet meadows in addition to the previously mentioned brackish settings. The analysis of the relative abundances of species from open, water, rocky, and woodland habitat, across the representative layers (i.e. N, M, I and F), showed an higher frequency of occurrence of water bird species (and so their favourite habitats) within layer F (MIS 3), with respect to layers N, M (MIS 7), and I (MIS 6) (Fig. 3). During the MIS 3 interval, a cool-temperate climatic phase (global mean sea level curve between -90 and -50 m), the coastal line was located closer to the cave than during MIS 6 peak (water depth ca. -130 m) (Benjamin et al., 2017), allowing the presence, nearer to the cave, of extensive wetlands related to the coastal system. The aridity linked to glacial phases, such as MIS 6, could also have prevented the development of extensive wetlands. During MIS 7, on the other hand, the lower abundance of water species is possibly due to the sea-level highstand that limited the areal extent of the coastal plain near the cave. In addition, recent geochemical derived findings point, for great part of MIS 3, towards a regional environmental and climatic context characterized by constant humid conditions and vegetated soils (mostly C<sub>3</sub> plants). Within the study area and during MIS 3, Dansgaard-Oeschger (DO) events, which caused strong and rapid climatic shifts at higher latitudes, had a minor impact on humidity and rainfall variability (Columbu et al., 2020). Thus, the combined sea-level dynamics and local climate allowed the creation and maintenance of such wetlands. From a biodiversity point of view, the presence of humid habitats and mild conditions during MIS 3 (layer F) played a key role for a number of migratory and sedentary water birds that used this area to feed, nest, and overwinter. The extension of these habitats during MIS 3 seems to have increased the avian diversity of the study area, as highlighted by the coverage-based rarefied richness of



layer F, which reports the highest standardized by coverage richness-based values among all the analysed layers (Fig. 2). The same analysis reports the lowest values of avian richness in layer I (MIS 6), possibly related to the glacial climatic conditions.

A substantial homogeneity in the overall diversity of the pre-MIS3 Mousterian avian assemblages is shown by rarefaction curves that depict a strong overlap of the estimators for layers I, M, and N when empirical species richness of the layers are standardized by sample size or sample coverage (Fig. 2).

The abundance of birds from open areas and the paucity of woodland taxa (Fig. 3) apparently do not agree with the paleoenvironmental reconstruction provided by the macromammals, where the ungulates of woodland or open woodland (*Cervus elaphus* and *Dama dama*) are numerically well represented (Palma di Cesnola, 1966; Sarti et al., 1998-2000, 2002; Cecchetti, 2003; Boscato et al., 2013; Sala and Berto, in press), but support the habitat indications given by the micromammal sequence (Dalla Valle, 2008; Petruso et al., 2011; Berto, in press). Bird remains, whose accumulation is mainly due to short-range transport-related processes and by the activity of nocturnal raptors, as suggested by the taphonomic analysis, represent the local environment around the cave. Furthermore, nocturnal raptors mainly have a hunting range of about 5 km around the nesting or resting site (Andrews, 1990), and thus the bird and the micromammal assemblages could be affected by this bias. Ungulates (and other macromammals), instead, have been introduced in the deposit mainly by Neanderthal hunters (Sarti et al., 1998-2000, 2002; Cecchetti 2003; Boscato et al. 2013), and thus they could come from farther woodland areas (Vita-Finzi and Higgs, 1970; Serjeantson, 2009). In general terms, woodlands were probably more common far from the cave, but were also probably more spread in the wetter and warmer climatic phases (Allen and Huntley, 2000, 2009; Tzedakis et al., 2006; Brauer et al., 2007; Huntley et al., 2013; Milner et al., 2013). The different accumulation agents of bird and macromammal assemblages provide a possible explanation of the partially disjoint paleoenvironmental signal recorded in the studied succession. The paleoenvironmental insights provided by the bird assemblage also generally agree with the pollen sequence (Ricciardi, 2005).

The paleoenvironmental frame provided by the bird taxa of Grotta del Cavallo agrees with the other Apulian bird fossil assemblages in attesting to the dominance of open environments, the presence of wetlands, and the paucity of woodlands throughout the whole Pleistocene (Giusti, 1979, 1980; Cassoli and Tagliacozzo, 1997; Tyrberg, 1998, 2008; Pavia, 2000; Tagliacozzo and Gala, 2002, 2004; Rustioni et al.,

2003; Bedetti and Pavia, 2007; Petronio et al., 2008; Gala and Tagliacozzo, 2010; Bedetti and Pavia, 2013). Cold-adapted species have been also documented in this refugial area during the Late Pleistocene and the late glacial (Cassoli and Tagliacozzo, 1997; Tyrberg, 1998; Bedetti and Pavia, 2007).

Some of the species identified in this work have provided also significant climatic indications. For instance, the remain referred to cf. *Branta leucopsis* in layer M also has a possible paleoclimatic significance. Its presence in the deposit of Grotta del Cavallo suggests a climate colder than present, as in Apulia this species has never been observed after 1950 (La Gioia et al., 2010) and is currently mostly observed in Northern and Central Italy. In the cooler periods, this species, as with many others, shifted its distribution southwards. In addition, the presence at low heights of *Alectoris graeca*, *Aquila chrysaetos* and *Pyrhacorax pyrrhacorax*, possibly due to the downward shift of the vegetational zones during the harsher phases of the Pleistocene (Tyrberg, 1991, 1998, 2008; Holm and Svenning, 2014; Carrera et al., 2018a, 2018b), have a paleoclimatic significance. These species, that currently live on average at higher altitudes in Italy (Brichetti and Fracasso, 2003, 2004, 2011), could suggest the presence of a climate cooler than the present one, at least in the layers F, I, M, and N.

## 6. Conclusions

The rich bird assemblage from the Mousterian layers of Grotta del Cavallo allowed to explore the avian biodiversity in this refugial area during interglacial-glacial transitions. It supports the environmental framework and climatic trends suggested by the other paleoenvironmental proxies, (e.g., macromammals, micromammals, and pollens) but also adds new insights to detail the characteristics of the landscape that was home to the Neanderthal hunter-gatherer groups.

The landscape near the cave was dominated by extensive open habitats like grasslands and shrublands, mostly located on the plateau above the cave and locally interspersed with rocky exposures and open woodland. In front of the cave, the coastal plain hosted marshes and wetlands that possibly peaked in extension in layer F (MIS 3), due to more humid climatic conditions. The presence of extended brackish or freshwater habitats produced an increase in avian diversity, as highlighted by the coverage-based rarefied richness of layer F. These habitat characteristics perfectly agree with the regional environmental context provided by other bird fossil assemblages from Apulian paleontological or archaeological contexts.

From a paleontological perspective, the taxonomic analysis also provided some interesting taxa, such as the first Palearctic fossil occurrence of *Larus genei*, the first Italian fossil occurrence of *Emberiza calandra*, the second Italian fossil occurrence of *Sylvia communis* (if confirmed), and the oldest Italian occurrence of *Podiceps nigricollis*, testifying to the long-lasting presence of these taxa in the Italian peninsula.

Taphonomic analyses detected the main drivers of taphonomic degradation in avian fossil bones, while elucidating the main agents responsible for bird fossil accumulation in the succession of Grotta del Cavallo. All layers show taphonomic degradations mainly due to physical sin- and post-depositional processes, whereas fossil accumulation is partly due to feeding activities (mainly nocturnal raptors) and short-range transport due to the physical processes of sediment accumulation with the physical agents likely prevailing. In conclusion, fossil birds have proven to be a pivotal source of environmental and climatic data for paleoecologists and archaeologists.

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## **Declaration of interests**

☒ 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.

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**Figure 1.** A. Geographic position of the cave, indicated by the black star; B. The Uluzzo bay and Grotta del Cavallo site, indicated by the red arrow (photo Sarti and Martini, 2020). C. Grotta del Cavallo stratigraphic sequence. In black, on the left, are indicated the Mousterian units which are object of this paper, whereas on the right is reported the age of the tephra layers.

**Figure 2.** Specimen (left) and coverage-based (right) rarefaction/extrapolation curves of diversity based on species richness ( $q=0$ ). Dashed lines represent extrapolation of species diversity until the double of the sample size, shaded bands represent 95% confidence intervals (see also Tab. S2) for estimates derived by Simpson and Shannon indexes. Abbreviation MNI: Minimum Number of Individuals.

**Figure 3.** Cumulative frequencies (%) of bird taxa from open, rocky, water, and forest environments retrieved in the layers F, I, M, and N of Grotta del Cavallo. Abundances consider the Minimum Number of Individuals from the four different habitats.

**Figure 4.** Fossil birds from Grotta del Cavallo. A: *Alectoris graeca* distal left tibiotarsus (C398), cranial view; B: *Perdix perdix* proximal left humerus (C432), caudal view; C: cf. *Branta leucopsis* proximal left ulna (C59), ventral view; D: *Aythya fuligula* distal right carpometacarpus (C1042), dorsal view; E: *Podiceps cristatus* distal right tibiotarsus (C447), cranial view; F: *Podiceps nigricollis* proximal right tarsometatarsus (C1091), dorsal view; G: *Streptopelia turtur* distal right humerus (C874), cranial view; H: *Tachymarpitis melba* right coracoid (C648), dorsal view; I: *Apus apus* right tarsometatarsus (C1093), dorsal view; J: *Fulica atra* right quadratum (C1050), dorsal view; K: *Tetrax tetrax* distal right humerus (C96), cranial view; L: *Plegadis falcinellus* proximal right radius (C439), caudal view; M: *Pluvialis squatarola* distal left tibiotarsus (C213), cranial view; N: *Eudromias morinellus* right coracoid (C499), dorsal view; O: *Larus genei* distal right ulna (C999), ventral view. Scale bars: 1 cm.

**Figure 5.** Fossil birds from Grotta del Cavallo. A: *Athene noctua* proximal right tarsometatarsus (C370), dorsal view; B: *Otus scops* distal left radius (C1124), caudal view; C: *Strix aluco* distal mandibula (C220), dorsal view; D: *Bubo bubo* proximal left tarsometatarsus (C1), dorsal view; E: *Aquila chrysaetos* left fourth phalanx of the digit IV (C758), lateral view; F: *Circus aeruginosus* distal right tibiotarsus (C119), cranial view; G: *Pyrhcorax pyrrhcorax* distal left tarsometatarsus (C63), plantar view; H: *Pica pica* proximal right coracoid (C452), lateral view; I: *Corvus corax* ungual phalanx (C714), lateral view; J: *Melanocorypha calandra* maxilla (C245), dorsal view; K: *Sylvia* cf. *communis* left humerus (C774), caudal view; L: *Emberiza calandra* distal mandibula (C287), dorsal view. Scale bars: 1 cm.

**Figure 6.** Two-dimensional NMDS output based on Euclidean distance for log-transformed relative abundances of taphonomic variables of avian samples from the Pleistocene succession of Grotta del Cavallo. Both taphonomic variables and sub-units are displayed (here considered only the sub-units with  $n \geq 18$  items), stress plot and correlation statistic on the goodness of fit are reported in Fig. S2. Abbreviations:

concr–concretion; frag–fragmentation; root–root etching; mn–manganese; weath–exfoliation and cracking; anthr–anthropic related (cut-marks, combustion); feed–feeding activity (carnivore bites and digestion by mammals or raptors); rod–rodent gnawing; tramp–trampling.

**Table 1.** Taphonomic variables identified, their main characteristics (Bocheński and Tomek, 1997; Fernández-Jalvo and Andrews, 2016), and the damage states used to score avian bones from the Mousterian layers of Grotta del Cavallo.

Taphonomic primer		
Variable	Evaluation of	State
Fragmentation	Bone breakage related to syn- and post-depositional physical processes	0 = whole; 1 broken
Concretions (CaCO <sub>3</sub> )	Precipitation of carbonates on the bone surface from percolating waters	0 = absent-low; 1 moderate to coated
Exfoliation	Flaking of the bone during subaerial exposure related to weathering agents (e.g., sun, wind, temperature)	0 = pristine-rare; 1 moderate to high
Cracking	Fracture of the surface of the bones during subaerial exposure, mainly related to differential temperature and humidity	0 = absent-low; 1 moderate to widespread
Manganese	Black staining of bones related to manganese precipitation from percolating water	0 = absent-low; 1 moderate to coated
Root etching	Linear, branching marks with U-shaped cross-section and conical perforations related to roots of plants impinging on the bone surface	0 = not visible-low; 1 moderate to advanced stage
Trampling	Superficial, irregular linear traces with V-shaped cross section naturally produced (i.e., sedimentary abrasion)	0 = absent-low; 1 moderate to widespread
Carnivore bites	Pits, punctures, and grooves (with U-shaped cross-section) produced by carnivores during feeding	0 = absent; 1 moderate to widespread
Rodent gnawing	Parallel groove marks produced by the incisors of a rodent that chew the bones to gain bone mineral, wear their teeth or eat flesh residues	0 = absent; 1 moderate to widespread
Digestion marks	Surface corrosion due digestive enzymes that can be produced by carnivores (diffuse on bone surface) or raptors (often localized on the epiphyses)	0 = absent; 1 moderate to widespread
Cut-marks	Linear marks, with V-shaped cross-section produced by stone tools and due to anthropic activity	0 = absent; 1 moderate to widespread
Combustion	Fire-related modification on bones: shrinkage, cracking and heat-derived colors (e.g., brown, black, or white)	0 = absent-low; 1 moderate with secondary color/pattern

**Table 2.** Bird taxa identified in the Middle Paleolithic layers of Grotta del Cavallo. The numbers indicate, for each taxon, the NISP at the numerator and the MNI at the denominator. The habitat category has also been reported for each taxon: O (open), R (rocky), Wa (water/wetland), Wo (woodland), and NA (not assigned, i.e., those taxa that are not considered “environmental markers” due to their ecologic characteristics or because of their open nomenclature).

Order/Family	Species	Habitat	F	H	I	L	M	N	Q	Total
Galliformes/Phasianidae	<i>Coturnix coturnix</i>	O					6/3	2/1		8/4
	<i>Alectoris graeca</i>	R					2/2	1/1		3/3
	<i>Alectoris</i> sp.	O	6/4	1/1	1/1	1/1	8/7	1/1		18/15
	<i>Perdix perdix</i>	O	1/1				8/4	3/3		12/8
	Unidentified	NA	5/4		1/1	1/1	17/6	1/1		25/13
Anseriformes/Anatidae	cf. <i>Branta leucopsis</i>	Wa					1/1			1/1
	<i>Anser albifrons/erythropus</i>	Wa					2/2			2/2
	cf. <i>Aythya nyroca</i>	Wa					1/1			1/1
	<i>Aythya fuligula</i>	Wa	1/1							1/1
	<i>Spatula querquedula</i>	Wa	1/1							1/1
	<i>Spatula querquedula/Anas crecca</i>	Wa	1/1							1/1

	<i>Mareca strepera/penelope</i>	Wa	1/1				1/1		2/2
	<i>Anas crecca</i>	Wa	2/2						2/2
	Unidentified	Wa	13/5				6/6	1/1	1/1 21/13
Podicipediformes/Podicipedidae	<i>Podiceps cristatus</i>	Wa					1/1	1/1	2/2
	<i>Podiceps nigricollis</i>	Wa	1/1						1/1
Columbiformes/Columbidae	<i>Columba livia</i>	R	1/1				3/3		4/4
	<i>Columba livia/oenas</i>	NA	3/2		2/2		11/7	4/4	1/1 21/16
	<i>Columba livia/palumbus</i>	NA	1/1						1/1
	<i>Columba</i> sp.	NA					2/2		2/2
	<i>Streptopelia turtur</i>	Wo	2/1						2/1
Caprimulgiformes/Apodidae	<i>Tachymarptis melba</i>	R					1/1		1/1
	<i>Apus apus</i>	R	1/1						1/1
Gruiformes/Rallidae	<i>Fulica atra</i>	Wa	1/1						1/1
	Unidentified	NA	1/1						1/1
Otidiformes/Otididae	<i>Tetrax tetrax</i>	O	5/2				2/2	1/1	8/5
Pelecaniformes/Threskiornithidae	<i>Plegadis falcinellus</i>	Wa						1/1	1/1
Charadriiformes/Charadriidae	<i>Pluvialis squatarola</i>	Wa					1/1		1/1
	<i>Pluvialis squatarola/apricaria</i>	Wa		1/1	2/2				3/3
	<i>Eudromias morinellus</i>	O						1/1	1/1
Charadriiformes/Scolopacidae	<i>Numenius</i> sp.	Wa	1/1						1/1
	Unidentified	NA					1/1		1/1
Charadriiformes/Laridae	<i>Larus genei</i>	Wa	1/1						1/1
	Unidentified	Wa				1/1			1/1
Strigiformes/Strigidae	<i>Athene noctua</i>	O	9/4			1/1	6/5	3/2	19/12
	<i>Otus scops</i>	Wo	1/1						1/1
	<i>Asio otus/flammеus</i>	NA	1/1						1/1
	<i>Strix aluco</i>	Wo					1/1		1/1
	<i>Bubo scandiacus/bubo</i>	NA						1/1	1/1
	<i>Bubo bubo</i>	R					1/1		1/1
	Unidentified	NA	4/4	2/1		1/1	2/2	1/1	10/9
Accipitriformes/Accipitridae	<i>Aquila chrysaetos</i>	R			1/1				1/1
	<i>Circus aeruginosus</i>	Wa					2/1		2/1
	<i>Buteo lagopus/buteo</i>	NA					1/1		1/1
Falconiformes/Falconidae	<i>Falco naumanni/vespertinus</i>	NA	1/1						1/1
	<i>Falco tinnunculus</i>	O	2/1				2/2		4/3
	<i>Falco</i> sp.	NA	10/4	1/1	4/3		6/5		1/1 22/14
Passeriformes/Corvidae	<i>Pyrrhocorax pyrrhocorax</i>	R			1/1		7/4	3/3	11/8
	<i>Pyrrhocorax pyrrhocorax/graculus</i>	R	2/2				1/1		3/3
	<i>Pyrrhocorax graculus/Corvus monedula</i>	NA					1/1		1/1
	<i>Pica pica</i>	Wo	1/1				2/2	1/1	4/4
	<i>Corvus monedula</i>	NA					1/1		1/1
	<i>Corvus frugilegus/corone</i>	NA	2/2		2/2		4/3		8/7
	<i>Corvus corax</i>	R	3/3		1/1	1/1	2/1		7/6
	Unidentified	NA	12/5		13/5	11/2	33/12	11/9	80/33
Passeriformes/Alaudidae	<i>Alaudala rufescens/Calandrella brachydactyla</i>	O	2/2						2/2
	<i>Melanocorypha calandra</i>	O			1/1		1/1		2/2
	<i>Melanocorypha calandra/Galerida cristata</i>	O			1/1		1/1		2/2
	<i>Galerida theklae/cristata</i>	O					1/1		1/1
	Unidentified	O	2/2				3/3		5/5
Passeriformes/Hirundinidae	Unidentified	NA	7/5			1/1			8/6
Passeriformes/Sylviidae	<i>Sylvia</i> cf. <i>communis</i>	O			2/1				2/1
Passeriformes/Sturnidae	<i>Sturnus vulgaris/unicolor</i>	NA				1/1	16/13		17/14
	Unidentified	NA					1/1		1/1
Passeriformes/Turdidae	cf. <i>Turdus viscivorus</i>	Wo	1/1		1/1				2/2
	<i>Turdus</i> sp.	NA	1/1				2/2		3/3



Passeriformes/Muscicapidae	<i>Oenanthe</i> sp.	O	1/1							1/1
Passeriformes/Fringillidae	Unidentified	NA					1/1			1/1
Passeriformes/Emberizidae	<i>Emberiza calandra</i>	O					3/2			3/2
Passeriformes	Unidentified (NISP)	NA	138	5	26	27	204	19	7	426
Unidentified	Unidentified (NISP)	NA	88	2	25	22	74	24	6	241
Total Aves (NISP)			337	12	82	70	453	79	17	1050

**Highlights Carrera et al. - *Pleistocene Neanderthal landscapes in Southern Italy: the paleoecological contribution of the avian assemblage from Grotta del Cavallo (Apulia, Southern Italy)*. Palaeogeography, Palaeoclimatology, Palaeoecology**

- Fossil birds from Mousterian layers are analysed in detail for the first time
- The bird taxa showed the presence of open habitats and wetlands
- First fossil occurrence ever of *Larus genei* and first occurrence in Italy of *Emberiza calandra*
- The accumulation of bird bones is mainly due to activity of nocturnal raptors and physical processes
- Eco-taphonomic patterns detail the landscape exploited by Neanderthals

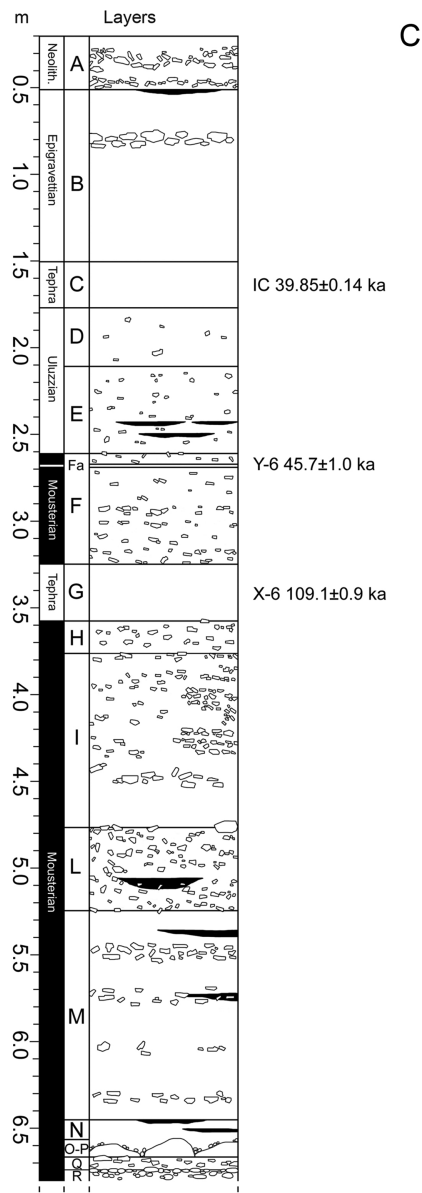


Figure 1

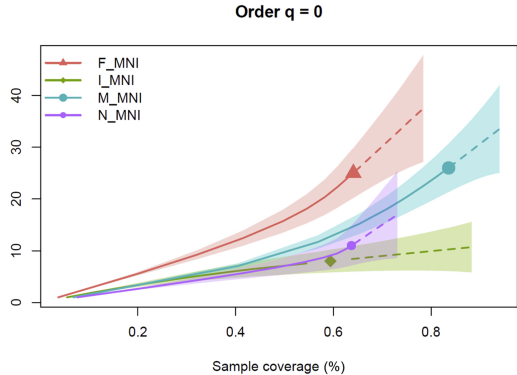
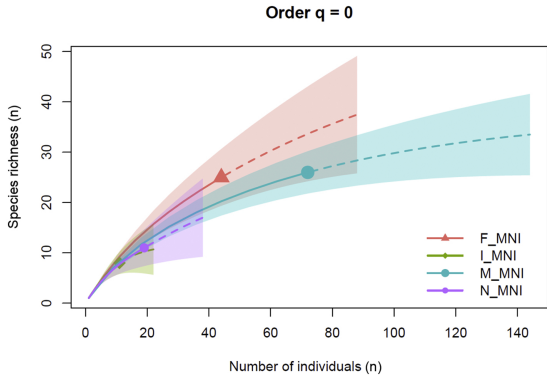


Figure 2

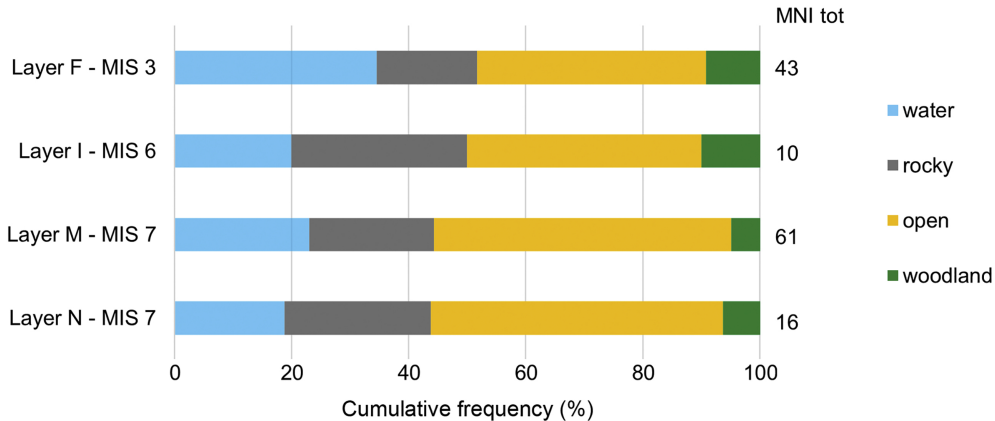


Figure 3

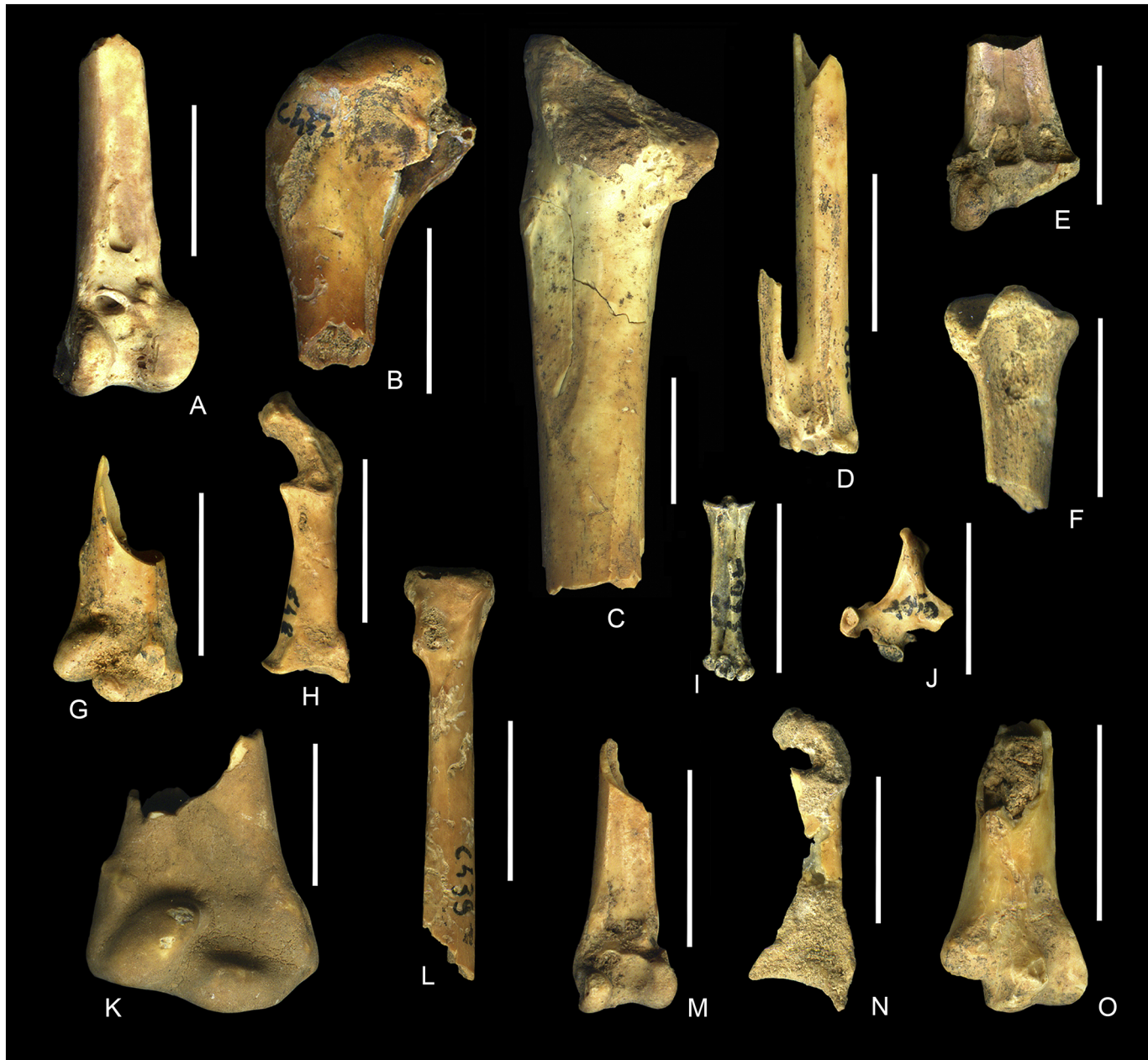


Figure 4



Figure 5

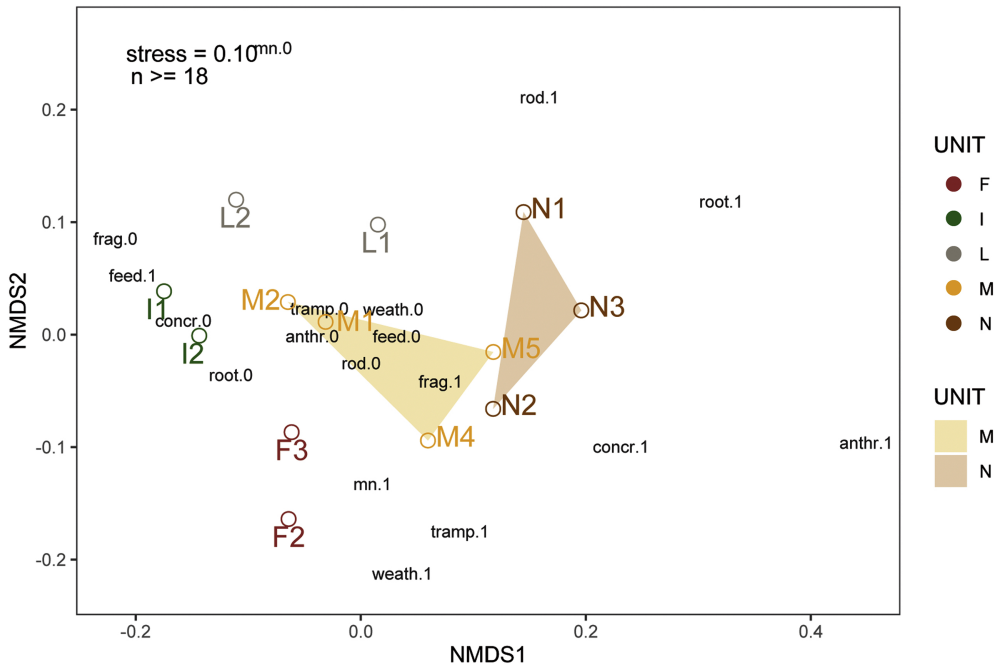


Figure 6