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# Ecological responses of Western Palearctic avian species to late Quaternary climate oscillations

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## Abstract

This PhD thesis explores the ecological responses of bird species to glacial-interglacial transitions during the late Quaternary in the Western Palearctic, using multiple approaches and at different scales, enhancing the importance of the bird fossil record and quantitative methods to elucidate biotic trends in relation to long-term climate changes.

First, the taxonomic and taphonomic analyses of the avian fossil assemblages from four Italian Middle and Upper Pleistocene sedimentary successions (Grotta del Cavallo, Grotta di Fumane, Grotta di Castelcivita, and Grotta di Uluzzo C) allowed us to reconstruct local-scale patterns in birds' response to climate changes. These bird assemblages are characterized by the regular presence of temperate species and by the occasional presence of cold-dwelling species (or an increase of them) during glacial periods, related to shifts in their distribution towards lower altitudes or lower latitudes. These local patterns are widely supported by those identified at the continental scale. In this respect, I mapped the present-day and LGM climatic envelopes of species with different climatic requirements and migratory behaviors. The results show a substantial stability in the range of temperate species and pronounced changes in the range of cold-dwelling species, supported by their fossil records. Therefore, the responses to climate oscillations are highly related to the thermal niches of investigated species.

I also clarified the dynamics of the presence of boreal and arctic bird species in Mediterranean Europe, due to southern range shifts, during the glacial phases. After a reassessment of the reliability of the existing fossil evidence, I show that this phenomenon is not as common as previously thought, with important implications for the paleoclimatic and paleoenvironmental significance of the targeted species.

In addition, the analyses of the avian fossil assemblages and the identification of the local patterns of species turnover in response to climate shifts, allowed extremely detailed environmental reconstructions during glacial-interglacial cycles.

I have also been able to explore the potential of multivariate and rarefaction methods in the analyses of avian fossils. The ordination analysis applied on the taphonomic dataset of Grotta del Cavallo delineated the main drivers of taphonomic damages, whereas the rarefaction analyses highlighted the dynamics of species diversity in relation to climate-driven paleoenvironmental changes.

As for the cold-dwelling bird species, which were the most impacted after the glacial periods, the knowledge of past response to climatic changes also helps to better understand the current responses to global warming and to forecast its future effects, in order to adopt more suitable conservation strategies.

# 1. Introduction

## 1.1 Climate changes in the late Quaternary

Climatic variability has been particularly pronounced in the Quaternary Period (last 2.58 million years; Cohen & Gibbard, 2019). The alternating glacial and interglacial conditions, marked by smaller oscillations called stadials and interstadials, are superimposed upon an overall global cooling trend. Cores drilled from ice sheets (Greenland and Antarctica) and from beneath the seafloor recorded Earth's climate history, based on the $^{18}O/^{16}O$ isotope ratio found in the ice and in the skeletons of marine planktonic foraminifera entombed in the bottom sediments of the ocean (Lisiecki & Raymo, 2005; Rasmussen et al., 2014; Landais et al., 2015), as shown in Fig. 1.1. The recognition of many different climatic phases based on the variation (δ) of $^{18}O/^{16}O$ through time, led to the current subdivision of the Quaternary in 103 warm and cold periods called Marine Isotope Stages (MIS) (Lisiecki & Raymo, 2005).

Long-term changes in solar radiation, triggered by orbital forcings, and the complex feedback processes of the climate system are the main drivers of cyclical climatic oscillations on Earth (Kamawura et al., 2007; Cheng et al., 2009; Lisiecki, 2010), that also cause eustatic sea-level fluctuations (Fig. 1.2) (Waelbroeck et al., 2002). The three main astronomical parameters affecting Earth's orbital geometry around the Sun and climate variability are precession, obliquity, and eccentricity, with averaged periodicities of ca. 23, 41, and 100 ky respectively (Milankovitch, 1930, 1941; Berger, 1988). Between 1.2 and 0.7 Ma, the so-called mid-Pleistocene transition (MPT) marked the change in the periodicity of glacial-interglacial cycles. The ~41,000-year periodicity driven by the variation in Earth's tilt, which allowed the presence of thin ice sheets, was replaced by the ~100,000-year current cyclicity. The latter is characterized by long cooling phases (glacials) with the build-up of thick ice sheets, followed by relatively short warm phases (interglacials), lasting thousands of years (Clark et al., 2006; Bajo et al., 2020).

Other millennial scale perturbations of the climate system, such as the Dansgaard-Oeschger cycles or the Heinrich events, are commonly attributed to stochastic processes that affect the climate system (e.g., volcanic dust loading) and feedback processes of the Earth's climate system, such as oceanic global circulation patterns and ice-sheet dynamics (Masson-Delmotte et al., 2013).

The Late Pleistocene (126 - 11.7 ky) (Cohen & Gibbard, 2019) witnessed the last complete glacial-interglacial cycle. The Last Interglacial (LIG, 129 - 116 ky) (Shackleton et al., 2003; Dutton & Lambeck, 2012), also known as MIS 5e, was characterized by global mean temperatures warmer by 2°C and the sea level a few meters higher than pre-industrial times (Masson-Delmotte et al., 2013; Dyer et al., 2021). The last glaciation began about 115 ky ago, when temperatures rapidly dropped by several degrees. The buildup of glaciers culminated during the MIS 2, in the Last Glacial Maximum (LGM), which occurred from about 26.5 to 19 ky ago (Clark et al., 2009; Lambeck et al., 2014). During this period, large ice sheets covered Northern

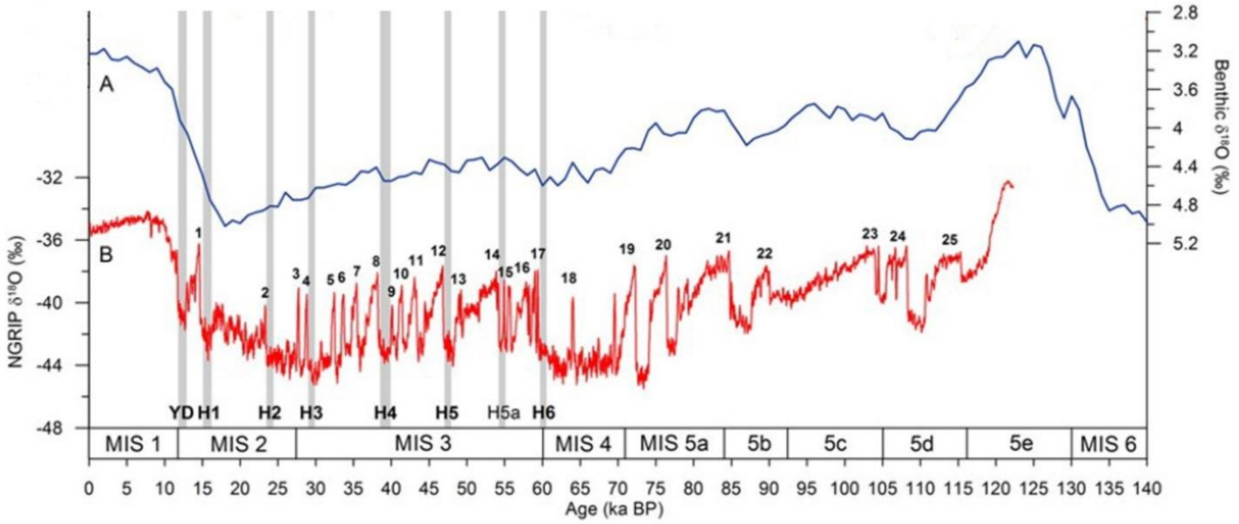

Fig. 1.1. A) Global stack of $\delta^{18}O$ values from benthic foraminifera reflecting changes in global ice volume and temperature (Lisiecki and Raymo, 2005). Peaks in $\delta^{18}O$ values (downwards) indicate warm conditions, reduction of ice volume and increasing global sea level. B) General chronology of the Greenland ice cores, shown using $\delta^{18}O$ data from the NGRIP core. Numbers indicate the rapid warming events, known as Dansgaard–Oeschger (D–O) events or Greenland Interstadials (GI). Heinrich events, characterized by ice rafting events in the North-Atlantic, are shaded grey and labelled. Marine Isotope Stages (MIS) are indicated, where MIS 5e is equivalent to the Last Interglacial and MIS 1 to the current interglacial. Modified after Vasskog et al., 2015.

Europe and North America, whereas sea level dropped by about 125-130 m (Yokoyama et al., 2018). Considering model simulations, data from paleoclimatic archives and the local variability, LGM global mean surface temperature is estimated to be cooler than pre-industrial times by 3° to 8°C (Annan & Hargreaves, 2013; Masson-Delmotte et al., 2013). Colder temperatures, reduced precipitation, and decreased $CO_2$ air concentration produced increased aridity with the expansion of desert areas and grasslands and the retreat of forests (Fig. 1.3) (Prentice et al., 2000; Harrison & Prentice, 2003; Allen et al., 2010; Becker et al., 2015; Binney et al., 2017).

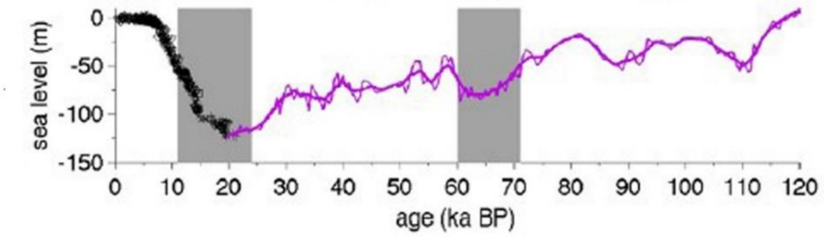

Fig. 1.2. Sea level variations in the last 120 ky. Sea-level data are taken from Waelbroeck et al. (2002) (purple) except for the last 19 ky, which are from coral and other benchmark indicators. Modified after Siddall et al., 2010.

Figure 1.3: LGM paleoenvironments of Europe (modified after Becker et al., 2015). On the right, the legend shows the main climate zones of the Koppen-Geiger classification (B, C, D, E) indicated by the colors in the map.

The onset of the current warm period (Holocene), dated approximately 10 ky BP, was marked by rapid ice melting and retreat. Glacial terminations, i.e., the transitions from glacial to interglacial conditions, represent relatively fast Quaternary climate changes. The early Holocene is marked by the late phases of deglaciation of Pleistocene land ice, sea level rise, and the occurrence of warm phases that affected different regions at different times, centered at around 8.0-6.5 ky BP (Amorosi et al., 2017; Liu et al., 2018; Vacchi et al., 2020).

During this period, often referred to as the Holocene Thermal Maximum (HTM), regional temperatures were up to 1°C higher than pre-industrial time (Kaufman et al., 2020; Gulev et al., 2021). In the present day, Earth is facing global warming, which is acknowledged to be a direct result of human activities. The burning of fossil fuels is causing a rapid increase in greenhouse gases in the atmosphere, which has already triggered an increase in surface temperature of 0.74°C compared to pre-industrial levels, with mean temperature increases over two degrees in certain areas of the temperate and arctic climate zones (Masson-Delmotte et al., 2013; Kaufman et al., 2020). Current estimates predict atmospheric $CO_2$ levels may rise up to 450–500 ppm by the end of this century, potentially driving an increase in global average temperature of 2-5°C (Masson-Delmotte et al., 2013). Ongoing climatic change markedly differs from preceding changes, because it occurs at smaller temporal scales (at least one order of magnitude faster than the last glacial termination) (Collins et al., 2013) and is accompanied by unprecedented changes in land use (Masson-Delmotte et al., 2013).

## 1.2 Birds' response to climate changes

Large-scale changes in climate alter the physicochemical conditions under which plants and animals can live at various points in time. As animals depend on ecosystems of primary producers, there is a cascading effect throughout the whole ecosystem: latitudinal and altitudinal shifts of the different vegetational belts are followed by animal species tracking their ecological niche. Such latitudinal and altitudinal shifts forced plants and animals to modify their geographic ranges, or drove them to extinction, based on species-specific climatic tolerances, dispersal capacity, genetic diversity, reproductive strategies, phenotypic plasticity, and population growth rates. Biotic responses to climatic and environmental changes, as shown by the fossil records, vary from macroevolutionary divergences (at very long-time scales) to phenotypic adjustments in situ (at shorter time scales) (Nogues-Bravo et al., 2018). Birds, like other organisms, developed a broad range of different adaptations to cope with climatic variations. As they represent one of the most studied zoological taxa in terms of ecology and behavior, several studies in the last decades have observed and analyzed the consequences of global warming on bird species, individually or in terms of populations, showing various types and magnitudes of impacts (Dunn & Møller, 2019). Nonetheless, little is known about how they adapted to the major and repeated climatic shifts which characterized the Quaternary Period. The European avian fossil record, which is very rich in terms of the number of localities, abundance of remains, and number of species, represents the main source of information available for investigating the responses of birds to past climate changes. This huge resource is still in part neglected, and more research is needed in the field. The investigation of past biotic dynamics in relation to long-term natural changes will help elucidate the mechanisms of response of bird species to current global warming and forecast near-future avian dynamics in a warmer Earth, in order to provide better conservation strategies. It would also help disentangle the climatic effects from the anthropogenic impacts that threaten present-day avian ecosystems and their biodiversity.

### 1.2.1 Birds and global warming

Climate change has primary consequences in the geographic distribution of birds, in terms of location, range extent, and abundance, as a species' range is related to species-specific physiological tolerance to temperature, precipitation, and other climate-driven environmental variables (Scridel et al., 2017).

In northern temperate regions, global warming has induced range shifts of bird species towards higher latitudes (mainly northeast or northwest) (Huntley et al., 2008; Barbet-Massin et al., 2012; Lehikoinen & Virkkala, 2016; Virkkala et al., 2018) and elevations (Tingley et al., 2009; Reif & Flousek, 2012). Those mountain bird species that occupy only the higher elevations are experiencing a decrease in the potential area available and have declined in numbers (Pernollet et al., 2015; Brambilla et al., 2016; Scridel et al., 2018; Lehikoinen et al., 2019a). Positive aspects of climate change comprise increasing abundance and/or ranges for sedentary, generalist, and warm-dwelling species (Devictor et al., 2008; Davey et al., 2012), whereas climate change impacts are proposed to be more severe for cold-dwelling species, restricted-range species, and species using seasonal habitats (Both et al., 2010; Scridel et al., 2017). To date, climate change-driven global or continental extinction events for bird species remain to be unambiguously proven, but negative impacts are expected to prevail for most species, with vast species losses predicted for the future.

The BirdLife International (2018) report on the conservation state of the birds of the World clearly shows how humans are responsible for most of the threats to birds. The first five most important threats are: agricultural expansion and intensification, which impacts 1,091 globally threatened birds (74%); logging, affecting 734 species (50%); invasive alien species, which threaten 578 (39%) species; and hunting and trapping, which puts 517 (35%) species at risk. Climate change represents an emerging and increasingly serious threat - currently affecting 33% of globally threatened species - and one that often exacerbates existing threats.

Climate changes have produced effects also in bird behavior. Due to earlier onset of spring in the breeding grounds of the northern hemisphere, changes in migration phenology and breeding cycles have been observed in the last decades. In terms of migration phenology, an earlier spring migration has been reported, more pronounced in short distance migrants than in long-distance migrants (Both & Visser, 2001; Crick, 2004; Jonzén et al., 2006; Gordo, 2007; Saino et al., 2011; Bitterlin & Van Buskirk, 2014; Usui et al., 2017; Lehikoinen et al., 2019b; Horton et al., 2020) and also a delay in autumn migration in short-distance migrants (whereas long distance migrants seem to advance the autumn migration) (Jenny & Kery, 2003; Horton et al., 2020). The lasting permanence in the breeding grounds also led to earlier breeding as well as an increased length of the breeding season and numbers of broods (Both et al., 2004; Møller et al., 2010; Smallegange et al., 2010). The ameliorated climate produced an increase in resident individuals in a number of migratory species (especially short-distance migrants), that is mainly the tendency to overwinter in the breeding grounds (particularly regarding populations living in the southerly areas of the breeding range) or also to shorten the migration distance between breeding and wintering grounds by shifting the wintering grounds northwards (La Sorte & Thompson III, 2007; Visser et al., 2009; Smallegange et al., 2010; Morganti, 2015). Overall, a decrease in the share of migratory individuals in many bird species and populations is undergoing due to climate warming (Berthold, 2001; Newton, 2010). The plasticity of migratory behavior plays a pivotal role and represents a successful strategy for coping with climate in continuous change, but often fails to track the speed of global warming. Indeed, the latter is causing one of the main threats for migratory bird species, that is called "ecological mismatch". It is basically a phenological mismatch between the timing of breeding of northern bird populations and the time of maximal food abundance, due to failure to keep pace with progressively earlier peaks in arthropod prey. Unequal climate change in breeding, passage, and wintering areas and less flexibility to adapt to changes represent an even greater threat for long-distance migrants (Hüppop & Winkel, 2006; Møller et al., 2008; Both et al., 2010; Jones & Cresswell, 2010; Saino et al., 2011).

Moreover, many long-distance migrants that winter in sub-Saharan Africa are also dealing with a progressive increase in the migration distances (Huntley et al., 2006; Doswald et al., 2009; Howard et al., 2018) due to poleward shifts of breeding ranges (Huntley et al., 2008; Barbet-Massin et al., 2012; Lehikoinen & Virkkala, 2016) and no consistent directional shift of the wintering grounds (Barbet-Massin et al., 2009; Doswald et al., 2009). Southward shifts of wintering grounds have also been reported, due to droughts and desertification in the Sahel (related to anthropic activities), further lengthening the migration trip (Wilson & Cresswell, 2006; Zwarts et al., 2009; Adams et al., 2014). Only rarely have the wintering grounds been reported to move northwards (Ambrosini et al., 2011). The lengthening of the migration journey, together with competition with resident species, ecological mismatches, loss of habitat due to anthropic land use, and severe poaching along the migration routes, are causing a decline of the long-distance Afro-palearctic migrants (Møller et al., 2008; Saino et al., 2011; Barbet-Massin et al., 2012; Vickery et al., 2014; Bairlein, 2016; Zurell et al., 2018).

Impacts of climate change may involve shifts in body size or appendage size. Declines in body size have been suggested to interest many different organisms as a response to warming climates (Gardner et al., 2011). Ecogeographic rules are involved in these mechanisms, such as Bergmann's rule, that explains why a larger body size is advantageous in cold climates to reduce heat loss (due to the relationship between body volume and body surface area) (Bergmann, 1847), or Allen's rule, that explains why animals tend to have shorter extremities in cold climates to reduce heat loss (Allen, 1877). Several studies have proven that Bergmann's rule works on current geographic variability of birds, with larger birds in northern cooler climates (Zink & Remsen, 1986; Blackburn & Gaston, 1996; Ashton, 2002; Meiri & Dayan, 2003; Olson et al., 2009). Zink & Remsen (1986) surveyed the evidence of validity of Allen's rule on present-day geographic variability and found that the results were conflicting. Indeed, some authors found evidence of validity of Allen's rule for hindlimbs (Fleischer & Johnston, 1982; Cartar & Morrison, 2005) and bills (Symonds & Tattersaal, 2010; Greenberg et al., 2012; Danner & Greenberg, 2015), whereas others do not (Gutiérrez-Pinto et al., 2014). The factors influencing the variation in birds over space are the same as those operating across time. Several studies support general, but not universal, temporal decline in mean body size of birds in response to global warming (Johnston & Selander, 1964; Yom-Tov, 2001; Yom-Tov et al., 2006; Gardner et al., 2009; Salewski et al., 2010; Van Buskirk et al., 2010; Teplitski & Millien, 2014; Weeks et al., 2020). The size of appendages, such as the bill may be responsive to climate warming in accordance with Allen's rule (Campbell-Tennant et al., 2015). The temporal patterns observed in the above-mentioned works, although consistent with ecogeographic rules, may have additional causes, such as changes in primary productivity, habitat, food availability or other environmental factors.

### 1.2.2 Past responses to Quaternary climate changes

The extensive Western Palearctic Quaternary fossil record of birds provides evidence of many species' changes in distribution in response to climatic oscillations. During glacial periods, the environmental conditions at high latitudes were not suitable anymore for the survival of bird species, because of the expansion of the ice cap. Therefore, several species that currently live in arctic, sub-arctic and boreal environments (i.e., *Lagopus lagopus, Surnia ulula, Bubo scandiacus, Strix nebulosa, Falco rusticolus, Loxia pytyopsittacus, Pinicola enucleator*) (Tyrberg, 1991, 1998, 2008; Holm & Svenning, 2014) gradually shifted their distribution southwards, using Mediterranean Europe as a "climate refugium". Species which now live in different habitat and regions once occurred together, giving place to the "no-analog communities". The Mediterranean refugia mostly consisted of Iberia, Italy, and the Balkans (Tyrberg, 1998; Newton, 2003; Sanchez Marco, 2004; Bedetti & Pavia, 2007; Hampe & Jump, 2011; Holm & Svenning, 2014). Cold-adapted species which currently live in the mid-latitude mountain areas (*Bonasa bonasia*, *Lagopus muta*, *Tetrao urogallus*, *Lyrurus tetrix*, *Glaucidium passerinum*, *Aegolius funereus*, *Pyrrhocorax pyrrhocorax*, *Pyrrhocorax graculus*, *Prunella collaris*, *Montifringilla nivalis,* among others), were spread over a wider geographic range during glacial periods with respect to the present day, because of the downward shifting of vegetational zones in the mountains. During interglacials, such as the present one, their range reduced considerably with the shrinking and isolation of populations on the mid-latitude high mountain ranges and in boreal areas. For this reason, these species are often referred to as "glacial relicts" (Tyrberg, 1991, 1998, 2008; Newton, 2003; Holm & Svenning, 2014). The more distinctly Mediterranean and warm-adapted species, during cold phases survived only in the southern offshoots of the refugia with isolated populations, whereas they flourished during warm phases. For instance, in the LIG the distribution of Southern European species extended further north, some as far as the United Kingdom (*Tachymarptis melba*, *Aquila pennata*) (Tyrberg, 1998). A study by Tyrberg (2010) indicates that avifaunal communities from LIG deposits were comparable to the present ones, so that a difference of less than 2°C on average does not substantially alter avifaunal communities, but that changes in precipitation could be more important. The fragmentation and isolation of the populations caused by the climatic oscillations triggered speciation and the differentiation of current subspecies, whereas post-glacial expansion favored genetic re-admixtures between populations. Ultimately, climatic oscillations shaped the extant genetic diversity of bird species and their present geographic distribution (Avise & Walker, 1998; Blondel & Mourer-Chauviré, 1998; Hewitt, 2000, 2004; Newton, 2003; Tietze, 2018). Molecular genetic studies provide evidence of range changes and elucidate glacial distributions and patterns of Holocene range expansions by temperate species (Liukkonen-Anttila et al., 2002; Brito, 2005; Ruokonen et al., 2005; Garcia et al., 2011; Pellegrino et al., 2014, 2015; Drovetski et al., 2018; Raković et al., 2019).

Very few studies based on the osteometry of bird fossils report that past climatic oscillations also produced morphological variations in bird species (Northcote, 1981; Ericson, 1987a; Stewart, 1999a, 2007). One such example is that of grouses (*Lagopus muta* and *Lagopus lagopus*). Several studies (Bocheński, 1974, 1985; Potapova, 1986; Stewart, 1999a, 1999b, 2007; Potapov et al., 2003) suggest that individuals living during glacial periods may have modified their bodily proportions according to Bergmann's and Allen's rules.

Migratory behavior, that likely appeared well before Pleistocene glaciations, is related in birds to an increase in seasonality and deterioration of winter conditions (Bruderer & Salewski, 2008; Louchart, 2008; Finlayson, 2011; Winger et al., 2019). Therefore, migratory behavior probably appeared, disappeared, and adapted multiple times in the past, leveraging its plasticity, in response to changing climatic conditions. Based on traditional interpretations, during glacial maxima in the Western Palearctic, migratory species shifted their breeding grounds southwards, due to the expansion of the ice cap, and continued to migrate shorter distances to the same wintering areas. Other works suggest that migratory behavior could be linked to the recolonization of northern deglaciated areas in postglacial times, and thus it mainly represents a phenomenon of interglacial periods, which considerably reduced during glacial phases (Fiedler, 2003; Milá et al., 2006; Zink, 2011; Zink & Gardner, 2017). Recent research suggests that there is no evidence of the loss of the migratory behavior in Afro-Palearctic migrants during the LGM (Ponti et al., 2020) and that bird migration remained an important global phenomenon throughout the last 50,000 years (Somveille et al., 2020).

As for migratory distance in long-distance migrants, during glacial times it was likely shorter than the present day as the wintering ranges remained basically still whereas breeding ranges shifted southwards (Moreau, 1954; Ponti et al., 2020), even if the Sahara seems to have slightly expanded during the LGM (Dupont, 1993; Hoelzmann et al., 2004; Larrasoana et al., 2013; Hoag & Svenning, 2017). On the other hand, the African Humid Periods, that caused the cyclic greening of the Sahara and occurred in correspondence with the LIG and the HTM (Hoelzmann et al., 2004; Larrasoana et al., 2013; Hoag & Svenning, 2017; Tierney et al., 2017), could have played a pivotal role in the length of the migratory trip of these birds, making northern Africa a huge potential wintering ground for Afro-palearctic migrants with a consequent shortening of the migration trip.

The paucity of the studies dealing with African avian fossil assemblages prevents the clarification of the dynamics of the Afro-Palearctic migration system during past climatic phases. The bulk of evidence of the existence of Afro-Palearctic migrations during Pleistocene is represented by the fossil presence, in Sub-Saharan Africa, of long-distance migratory bird taxa and the absence of medullary bone in African fossils belonging to Afro-Palearctic migratory bird species (Churcher & Smith, 1972; Harrison, 1980; Matthiesen, 1990; Louchart et al., 2008; Prassack, 2010, 2014; Val, 2016; Prassack et al., 2018; Ponti et al., 2020). Moreover, the fossil record indicates that long-distance migration was present, in the Pleistocene, in species which currently do not migrate to Africa anymore, likely due to Sahara aridification and ameliorated conditions in the northern latitudes (Harrison, 1980; Louchart, 2014; Prassack, 2014).

## 1.3 The investigation of the responses to past climatic oscillations in birds

### 1.3.1 Fossil birds and their potential

The study of fossil birds represents a pivotal tool to better understand the evolution dynamics of avian taxa, paleobiogeography, and population dynamics in response to past climatic changes.

Extant bird species, most of which are reported in the fossil record since approximately the Early Pleistocene (Mourer-Chauviré, 1993; Tyrberg, 1998, 2008; Finlayson, 2011; Bedetti & Pavia, 2013), are very sensitive to environmental and climatic changes and have very specific needs concerning the habitat, especially in terms of vegetation (Cramp, 1998). Assuming that the ecological niche (species-specific physiological tolerance to temperature, precipitation and other environmental variables) did not change at least through the Quaternary, fossil avifauna represents a reliable indicator of the type of environments that surrounded the fossil localities in the past, at the time of the death of the individual (Eastham, 1997; Serjeantson, 2009). Furthermore, birds are helpful in paleoenvironmental reconstructions for the whole Quaternary, whereas current mammal species, which have more recent origins with respect to birds, provide reliable paleoenvironment reconstructions only for the most recent part of the Quaternary. From this perspective, birds are even better paleoenvironmental indicators than mammals. Fossil birds can also give insights about past climates. For instance, the finding of boreal or arctic species (i.e., *Lagopus lagopus, Bubo scandiacus*) (for more details see Chapter 1.2.2) in the fossil record of Western Palearctic mid-latitudes represents clear evidence of a climate colder than the present one. These species can therefore be considered climate markers. Likewise, the finding of species at low altitudes that are now spread only at the higher elevations of mountain areas of Southern Europe (i.e., those species defined "glacial relicts" such as *Lagopus muta*, *Pyrrhocorax graculus*) (for more details see Chapter 1.2.2), represents another proxy of cooler climatic conditions than the present (Carrera et al., 2018a, 2018b, 2021). Furthermore, the species turnover in the different stratigraphic units of a deposit (presence/absence of climate markers, changes in the relative abundance of species) can suggest possible climate oscillations across the sedimentary succession of the fossil locality (Cassoli & Tagliacozzo, 1994; Pavia, 2000; Bedetti & Pavia, 2007; Tomek et al., 2012). To provide reliable results, it should be applied to deposits with a high number of bird fossil remains and sedimentary successions spanning long time intervals.

Additionally, it is worth remembering that many different ecological factors, besides climate, can affect the distribution patterns of species and that the current ecological niches of extant species could be slightly different from Late Pleistocene ones, due to anthropic impacts and land-use. Also, fossil birds can provide extremely precise environmental indications when associated with other paleoenvironmental proxies such as micromammals, macromammals and pollen (Romandini et al., 2020; Carrera et al., 2021).

### 1.3.2 The analysis of fossil bird bones

Bird bones are characterized by adaptations to flight (Fig. 1.4), in order to reduce body mass but at the same time maintain strength and resistance. Among these adaptations are the thinning and lightening of the bone cortex, the pneumatization (extension of the hollow air sacs, which originate in the lungs, inside the bones), the fusion of some elements, the absence of teeth, and the presence of trabeculae (thin struts which develop at angles to the bone wall in response to the mechanical loading on the bone) (Baumel & Witmer, 1993; Serjeantson, 2009).

The identification of bird bones is conducted through comparison with present-day bird skeletons and, when needed, with the help of manuals dedicated to the osteological features of selected avian orders or families (Bacher, 1967; Woelfle, 1967; Erbersdobler, 1968; Kellner, 1968; Kraft, 1972; Fick, 1974; Langer, 1980; Otto, 1981; Solti, 1981; Emslie, 1982; Schmidt-Burger, 1982; Janossy, 1983; Moreno, 1985, 1986, 1987; Boev, 1988; Weesie, 1988; Cuisin, 1989; Gruber, 1990; Lorch, 1992; Bocheński, 1994; Cohen & Serjeantson, 1996; Solti, 1996; Stewart, 1999b; Bocheński & Tomek, 2000; Tomek & Bocheński, 2000; Wójcik, 2002; Kessler, 2015, 2016, 2019; Schäfer & Schmitz, 2016; Ujhelyi , 2016 among others). A detailed review of the available literature on bird bones identification is reported in Stewart & Hernandez Carrasquilla, 1997. The presence of medullary bone, a granular calcium deposit within the bone which provides a supply of calcium for the development of eggs, can allow sex assignation to bird skeletal remains. This deposit is present in a short time-period in the bones of the females just before and during the time of lay (Serjeantson, 2009). The size of the bones also helps when sexing, in those species with pronounced sexual size dimorphism. The age at death can be inferred by some characteristic features of juvenile bones, that separate young birds from adult individuals. In the first weeks of life, the bones are porous with undeveloped articular surfaces; soon after fledging, the

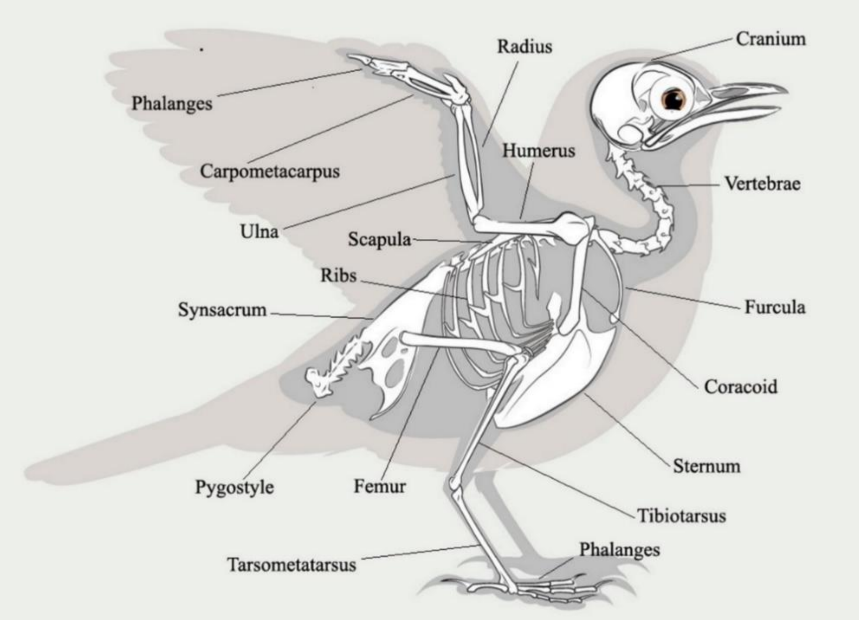

Fig. 1.4. Bird skeleton. Modified from https://academy.allaboutbirds.org/features/birdanatomy/.

bones completely ossify (complete replacement of cartilage by adult bone). The time of ossification is slightly different among families and longer in larger-sized species (Serjeantson, 2009). The presence of medullary bone or juvenile bones also gives precious insights on seasonality, indicating that those birds died during the breeding season, i.e., spring or summer (Serjeantson, 1998, 2009).

The availability and completeness of bird skeletal collections (Olson, 2003; Roselaar, 2003; Mlíkovsky, 2010; Boano & Pavia, 2014; Pavia, 2019) is pivotal to obtaining good results from the taxonomic analysis of fossil birds, but bird skeletal collections are not as common as mammal skeletal collections, due to the higher number of bird species and the difficulty of retrieving dead bird specimens. This is one of the main reasons why the field of paleornithology is not as developed as other paleontological sectors, despite the richness of the avian fossil record in terms of abundance, diversity, and number of localities (Tyrberg, 1998, 2008). The specimens in the reference collections are prepared as disarticulated skeletons. Successively, they are skinned and then the soft parts are eliminated through maceration in water, boiling, burial in the ground or with the use of dermestid beetles. The bones are then cleaned and bleached by passage in an ammonia solution. Eventually, they are stored in the collection and catalogued along with some other information besides the name of the species, such as provenance, date of death, cause of death, age, sex, weight (if available) (Serjeantson, 2009; Pavia, 2019).

The fossil remains can additionally be the subject of taphonomic analysis. Taphonomy is the set of chemical and physical processes that a bone undergoes from the death of the individual to the retrieval of the bone, via burial in the sediment. The analysis consists of the detailed observation of the surface of the bones, in order to find the small traces of the processes that the bone underwent and determine the accumulation agents (Serjeantson, 2009; Fernández-Jalvo et al., 2016). It is conducted using lens, stereomicroscope, or Scanning Electron Microscope (SEM), if necessary. For instance, if a bone was the leftover of a carnivore’s meal, it will show gnawing of the epiphyses or pits and scores left by the carnivore’s teeth (Haynes, 1983; Mallye et al., 2008; Delaney-Rivera et al., 2009; Dominguez-Rodrigo et al., 2012). Otherwise, a bone which was contained in a nocturnal raptor’s pellet will probably carry the traces of the digestive acids of the raptor, which produce a typical slight surface corrosion (Andrews, 1990; Bocheński & Tomek, 1997), whereas the bones belonging to individuals which were butchered by prehistoric men will show cut-marks, burning traces and other typical traces (Potts & Shipman, 1981; Shipman et al., 1984a, 1984b; Nicholson, 1993; Laroulandie, 2005; Dominguez-Rodrigo et al., 2009). Other taphonomic modifications that a bone can show are manganese dioxide staining, concretions, root etching, trampling, weathering etc. (Fernández-Jalvo et al., 2016). The taphonomic analysis, together with the anatomical parts representation (Mourer-Chauviré, 1983; Ericson, 1987b; Livingston, 1989; Bovy, 2002; Bocheński, 2005; Laroulandie, 2010; Lefèvre & Laroulandie, 2014), adds pivotal insight for the interpretation of the fossil assemblage retrieved, as it points out the processes which led to the accumulation of the bones and, consequently, identifies the area around the locality (where the bird individuals came from) that is the objective of the paleoenvironmental reconstruction.

Fig. 1.5: The dresser of the MGPT-MPOC bird Skeletal collection in Turin, with the details of a single drawer and a skeleton of *Corvus corax* (ph. M. Pavia).

### 1.3.3 Species Distribution Models as tools to reconstruct paleodistributions

Bird species are not uniformly distributed and differ in their ecological niches. Current geographic ranges are the result of evolutionary processes, climatic factors and human influences. Species Distribution Models (SDM) represent a useful tool in biogeographic and ecological studies, as they can project the current climatic and ecological requirements of species onto specific geographic areas or other climatic scenarios, in the past or in the future, assuming niche conservatism over time (Wiens & Graham, 2005; Wiens et al., 2010). They achieve this by relating species' observations to environmental predictor variables using statistical and machine-learning methods. Predictions of species distributions are based on current occurrence data that can be downloaded from, for instance, http://datazone.birdlife.org/home, www.gbif.org, www.ebird.org (among others), whereas the predictor variables are GIS layers of current, past or future climate or land-cover data (see https://www.worldclim.org/, Hijmans et al., 2005; https://www.ecoclimate.org, Lima-Ribeiro et al., 2015). Then, an appropriate algorithm relates occurrences to environmental data (BIOCLIM, Maxent, GARP, GAM, BRT, BIOMOD among many others) (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Stiels & Schidelko, 2018). The output is a map that shows areas of different suitability for the occurrence of the species. Recently, avian niche models and their applications were extensively reviewed (Engler et al., 2017), but here I will limit our focus to the applications of SDMs in the study of past avian geographic distribution dynamics, mainly adaptations to late Quaternary climatic changes.

By predicting past species distributions, SDMs allow to explore the responses of species to past changes in climate and environment, reveal changes in the ecological niche over long time scales and provide answers to evolutionary and biogeographical hypotheses (Elith & Leathwick, 2009; Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011; Gavin et al., 2014). SDMs are often integrated with molecular ecology to reconstruct detailed phylogeographic and past population dynamics of bird species, contributing to taxonomic studies (Kozma et al., 2016; Perktas et al., 2017, 2019; Lagerholm et al., 2017; Tietze, 2018; Arcones et al., 2021).

To reconstruct past distributions, climatic models of the past are needed, but those available for the Pleistocene are very few (https://www.worldclim.org, Hijmans et al., 2005; https://www.ecoclimate.org, Lima-Ribeiro et al., 2015). The Last Glacial Maximum climatic layers (Varela et al., 2015) are used in a number of works that explore the LGM dynamics of bird species, in order to clarify refugial dynamics, test niche stability, identify climate threats and effects to optimize current conservation efforts (Peterson et al., 2004; Ruegg et al., 2006; Huntley & Green, 2011; Huntley et al., 2013; Peterson & Ammann, 2013; Smith et al., 2013; Barrientos et al., 2014; Kozma et al., 2016; Lagerholm et al., 2017; Perktas et al., 2017, 2019; Koparde et al., 2019; Kiss et al., 2020; Ponti et al., 2020; Arcones et al., 2021; Sutton et al., 2021). However, only a few of them use the information provided by the fossil record to reinforce, calibrate, or validate the LGM predictive models (Smith et al., 2013; Lagerholm et al., 2017; Ponti et al., 2020; Arcones et al., 2021) and only two include the modelling of LGM wintering grounds of Afro-Palearctic migrants (Ponti et al., 2020; Arcones et al., 2021).

## 2. Aims and research outlines

This work explores the ecological responses of bird species to past glacial-interglacial transitions through several approaches and at different scales, integrating qualitative fossil data with quantitative techniques for paleoecological studies. The knowledge about responses of birds to past climatic changes provides pivotal insight to better understanding birds' responses to global warming and to adopt conservation strategies for the more endangered species. This integrated approach at different scales provides new useful data to disentangle the climate effects from current and future anthropic impacts on bird population dynamics. Furthermore, it improves the interpretation of fossil assemblages in terms of paleoenvironmental and paleoclimatic significance.

In the beginning, I investigated the dynamics of bird paleocommunities in response to climate shifts at a local scale from four different Italian sites that host rich avian fossil assemblages to reconstruct avian responses to past late Quaternary climate changes. The first paper (Manuscript I, published in Palaeogeography, Palaeoclimatology, Palaeoecology) deals with avian assemblages from Grotta del Cavallo, a well-known cave located in Southern Italy (Apulia), which was inhabited by Neanderthals throughout the Mid-Late Pleistocene. The fossil rich sedimentary succession of Grotta del Cavallo allows to explore the avian biodiversity in this refugial area and provides highly detailed paleoenvironmental and paleoclimatic avian-based reconstruction of the landscape that was home to the Neanderthal hunter-gatherer groups during last interglacial-glacial transitions. Grotta del Cavallo succession also shows how bird assemblages can refine the paleoenvironmental reconstruction previously provided by mammal assemblages alone. Finally, when avian fossil data are elaborated by means of ordination and rarefaction analyses, methods that are not commonly applied to bird assemblages, the results outline the main drivers of fossil accumulation and assess diversity dynamics in relation to climate-driven paleoenvironmental changes during the glacial-interglacial transitions, while highlighting the potential of new multidisciplinary exchanges and applications in the analyses of avian fossil assemblages.

The following papers (Manuscripts II and III) focus on how biosedimentary proxies (here, birds and mammals), when jointly considered, complete each other and represent a powerful tool for reconstructing depositional environments and their shifts within sedimentary successions. In addition to highlighting the value of integrated avian and mammal analyses, Manuscript II (published in Quaternary International) presents a state-of-the-art review of avian assemblages from two key sites that witnessed the transition from Neanderthal and modern humans in Italy (e.g., Grotta di Fumane in Northern Italy and Grotta di Castelcivita in Southern Italy). Whereas Manuscript III (published in the Journal of Quaternary Science), other than stressing the value of integrated research on fossil assemblages from Grotta di Uluzzo C (Apulia, Italy), identifies a set of avian species that are more effective in reconstructing paleoenvironments and their dynamics than others. This is because the responses to the climatic oscillations, mainly in terms of latitudinal and altitudinal range shifts, are species-specific and related to the ecological requirements of a species. In this respect, Manuscript IV (submitted to Scientific Reports, status: second reviewer reports received / ready for editor's decision), brings the analysis of the avian responses to past climatic changes at the continental scale, exploring the effects on the distribution of 6 bird species with different climatic requirements and migratory behaviors. This has been achieved with the use of Species Distribution Models and the MIS 2 fossil occurrences of the selected species, in order to test the relation between changes in range size and species climatic requirements. The results suggest that cold-dwelling species experienced more pronounced net changes in range size compared to temperate species and that, consequently, the thermal niche proves to be a key ecological trait to explain the impact of climate change in species distributions. In conclusion, the cold dwelling species are the most impacted by climatic changes, and thus their presence in the fossil record provides a very important paleoclimatic and paleoenvironmental proxy. The dynamics of the presence in Mediterranean Europe of these cold-dwelling species, and in detail of boreal species, during the glacial phases of the Mid-Late Pleistocene, are explored in Manuscript V (in preparation). In detail, the paper presents the current state of the art regarding their fossil presence in Southern Europe by checking documentations in support of the taxonomic attributions in the literature, often coming from old works. A reassessment of the reliability of these fossil records will provide a new and more robust frame of the large-magnitude southern range shifts experienced by these species, showing that the evidence related to this behavior are not as common as previously thought.

## 3. Manuscript I

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

Palaeogeography, Palaeoclimatology, Palaeoecology 567 (2021) 110256

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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.

## 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-Chauvire, 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 sub-optimal 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; Sánchez

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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, 2002, 2017; Benazzi et al., 2011; Romagnoli et al., 2015; Fabbri et al., 2016; Martini, 2016; Martini and Sarti, 2017; Moroni et al., 2018; Zanchetta et al., 2018; Sarti and Martini, 2020a; Zanchetta et al., 2020). The sedimentary succession of Grotta del Cavallo covers a wide time span, from Marine Isotope Stage (MIS) 7 to 1 (Holocene), (Sarti and Martini, 2020a). 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, 2020). 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

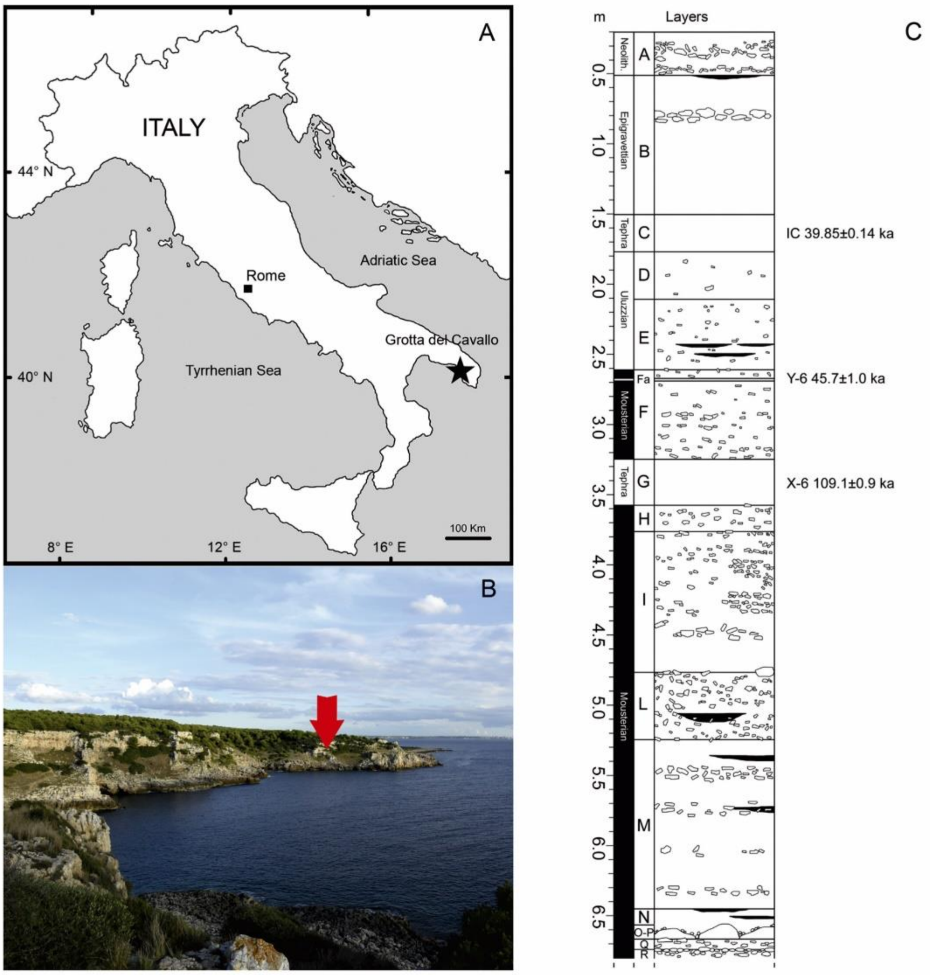

**Fig. 1.** A. Geographic position of the cave, indicated by the black star; B. The Uluzzo bay and Grotta del Cavallo site, indicated by the red arrow (photo by Sarti and Martini, 2020). C. Grotta del Cavallo stratigraphic sequence. In black, on the left, are indicated the Mousterian units which are object of this paper, whereas on the right is reported the age of the tephra layers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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, b). 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 and Cantelli, 2004; Azzarone et al., 2020).

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 (Siena University) 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$^2$ (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, 2020). 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, 2020; Sarti and Martini, 2020b). 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 ± 0.9 kyr B.P. 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; Sarti and Martini, 2020a; Zanchetta et al., 2020). 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-I1c are referred to MIS 6 (191–130 kyr B.P.) (Sala and Berto, 2020).

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, 2020). 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 (Ricciardi, 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, 2020).

## 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 (Table 1) and taxonomical perspectives (Table 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

**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-depostional physical processes | 0 = whole; 1 broken |
| Concretions ($CaCO_3$) | Precipitation of carbonates on the bone surface from percolating waters | 0 = absent-low; 1 moderate to coated |
| Exfoliation | Flaking of the bone during subaereal 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 subaereal 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 | Surficial, 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 | *Coturnix coturnix* | O | | | | | 6/3 | 2/1 | | 8/4 |
| | *Alectoris graeca* | R | | | | | 2/2 | 1/1 | | 3/3 |
| | *Alectoris* sp. | O | 6/4 | 1/1 | 1/1 | 1/1 | 8/7 | 1/1 | | 18/15 |
| | *Perdix perdix* | 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. *Branta leucopsis* | Wa | | | | | 1/1 | | | 1/1 |
| | *Anser albifrons/erythropus* | Wa | | | | | 2/2 | | | 2/2 |
| | cf. *Aythya nyroca* | Wa | | | | | 1/1 | | | 1/1 |
| | *Aythya fuligula* | Wa | 1/1 | | | | | | | 1/1 |
| | *Spatula querquedula* | Wa | 1/1 | | | | | | | 1/1 |
| | *Spatula querquedula/Anas crecca* | Wa | 1/1 | | | | | | | 1/1 |
| | *Mareca strepera/penelope* | Wa | 1/1 | | | | 1/1 | | | 2/2 |
| | *Anas crecca* | Wa | 2/2 | | | | | | | 2/2 |
| | Unidentified | Wa | 13/5 | | | | 6/6 | 1/1 | 1/1 | 21/13 |
| Podicipediformes/Podicipedidae | *Podiceps cristatus* | Wa | | | | | 1/1 | 1/1 | | 2/2 |
| | *Podiceps nigricollis* | Wa | 1/1 | | | | | | | 1/1 |
| Columbiformes/Columbidae | *Columba livia* | R | 1/1 | | | | 3/3 | | | 4/4 |
| | *Columba livia/oenas* | NA | 3/2 | | | 2/2 | 11/7 | 4/4 | 1/1 | 21/16 |
| | *Columba livia/palumbus* | NA | 1/1 | | | | | | | 1/1 |
| | *Columba* sp. | NA | | | | | 2/2 | | | 2/2 |
| | *Streptopelia turtur* | Wo | 2/1 | | | | | | | 2/1 |
| Caprimulgiformes/Apodidae | *Tachymarptis melba* | R | | | | | 1/1 | | | 1/1 |
| | *Apus apus* | R | 1/1 | | | | | | | 1/1 |
| Gruiformes/Rallidae | *Fulica atra* | Wa | 1/1 | | | | | | | 1/1 |
| | Unidentified | NA | 1/1 | | | | | | | 1/1 |
| Otidiformes/Otididae | *Tetrax tetrax* | O | 5/2 | | | | 2/2 | 1/1 | | 8/5 |
| Pelecaniformes/Threskiornithidae | *Plegadis falcinellus* | Wa | | | | | | 1/1 | | 1/1 |
| Charadriiformes/Charadriidae | *Pluvialis squatarola* | Wa | | | | | 1/1 | | | 1/1 |
| | *Pluvialis squatarola/apricaria* | Wa | | 1/1 | 2/2 | | | | | 3/3 |
| | *Eudromias morinellus* | O | | | | | | | 1/1 | 1/1 |
| Charadriiformes/Scolopacidae | *Numenius* sp. | Wa | 1/1 | | | | | | | 1/1 |
| | Unidentified | NA | | | | | 1/1 | | | 1/1 |
| Charadriiformes/Laridae | *Larus genei* | Wa | 1/1 | | | | | | | 1/1 |
| | Unidentified | Wa | | | | 1/1 | | | | 1/1 |
| Strigiformes/Strigidae | *Athene noctua* | O | 9/4 | | | 1/1 | 6/5 | 3/2 | | 19/12 |
| | *Otus scops* | Wo | 1/1 | | | | | | | 1/1 |
| | *Asio otus/flammeus* | NA | 1/1 | | | | | | | 1/1 |
| | *Strix aluco* | Wo | | | | | 1/1 | | | 1/1 |
| | *Bubo scandiacus/bubo* | NA | | | | | | 1/1 | | 1/1 |
| | *Bubo bubo* | R | | | | | 1/1 | | | 1/1 |
| | Unidentified | NA | 4/4 | 2/1 | | 1/1 | 2/2 | 1/1 | | 10/9 |
| Accipitriformes/Accipitridae | *Aquila chrysaetos* | R | | | 1/1 | | | | | 1/1 |
| | *Circus aeruginosus* | Wa | | | | | 2/1 | | | 2/1 |
| | *Buteo lagopus/buteo* | NA | | | | | 1/1 | | | 1/1 |
| Falconiformes/Falconidae | *Falco naumanni/vespertinus* | NA | 1/1 | | | | | | | 1/1 |
| | *Falco tinnunculus* | O | 2/1 | | | | 2/2 | | | 4/3 |
| | *Falco* sp. | NA | 10/4 | 1/1 | 4/3 | | 6/5 | | 1/1 | 22/14 |
| Passeriformes/Corvidae | *Pyrrhocorax pyrrhocorax* | R | | | 1/1 | | 7/4 | 3/3 | | 11/8 |
| | *Pyrrhocorax pyrrhocorax/graculus* | R | 2/2 | | | | 1/1 | | | 3/3 |
| | *Pyrrhocorax graculus/Corvus monedula* | NA | | | | | 1/1 | | | 1/1 |
| | *Pica pica* | Wo | 1/1 | | | | 2/2 | 1/1 | | 4/4 |
| | *Corvus monedula* | NA | | | | | 1/1 | | | 1/1 |
| | *Corvus frugilegus/corone* | NA | 2/2 | | 2/2 | | 4/3 | | | 8/7 |
| | *Corvus corax* | 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 | *Alaudala rufescens/Calandrella brachydactyla* | O | 2/2 | | | | | | | 2/2 |
| | *Melanocorypha calandra* | O | | | 1/1 | | 1/1 | | | 2/2 |
| | *Melanocorypha calandra/Galerida cristata* | O | | | 1/1 | | 1/1 | | | 2/2 |
| | *Galerida theklae/cristata* | O | | | | | 1/1 | | | 1/1 |
| | Unidentified | O | 2/2 | | | | 3/3 | | | 5/5 |
| Passeriformes/Hirundinidae | Unidentified | NA | 7/5 | | | 1/1 | | | | 8/6 |
| Passeriformes/Sylvidae | *Sylvia* cf. *communis* | O | | | 2/1 | | | | | 2/1 |

(*continued on next page*)

**Table 2** (*continued*)

| Order/Family | Species | Habitat | F | H | I | L | M | N | Q | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Passeriformes/Sturnidae | *Sturnus vulgaris/unicolor* | NA | | | | 1/1 | 16/13 | | | 17/14 |
| | Unidentified | NA | | | | | 1/1 | | | 1/1 |
| Passeriformes/Turdidae | cf. *Turdus viscivorus* | Wo | 1/1 | | 1/1 | | | | | 2/2 |
| | *Turdus* sp. | NA | 1/1 | | | | 2/2 | | | 3/3 |
| Passeriformes/Muscicapidae | *Oenanthe* sp. | O | 1/1 | | | | | | | 1/1 |
| Passeriformes/Fringillidae | Unidentified | NA | | | | | 1/1 | | | 1/1 |
| Passeriformes/Emberizidae | *Emberiza calandra* | 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 |

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 Table 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 (Table 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 Table 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 (Table 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 30× magnifying glass, in raking or reflected artificial light, and detected marks have been additionally observed with a 0.75-70× Leica S6D Green Ough stereomicroscope. Remains from each paleosurface were merged and analysed at sub-unit scale (Sarti and Martini, 2020b), 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 (Table S3a, S3b). For each remain, twelve variables were recorded and scored following the protocol defined in Table 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 (Table 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).

## 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 (Table 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).

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 Table 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; Table 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, Table 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, whereas some of the bones identified at the species level are represented in Figure 4 and Figure 5. Further details on the osteological features that support the taxonomic identifications are described in the Supplementary Material (SM-Diagnostic features and taxonomic inferences).

#### 4.1.1. *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).

### 4.1.2. *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).

### 4.1.3. *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.

### 4.1.4. *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).

### 4.1.5. *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).

### 4.1.6. *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).

### 4.1.7. *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).

### 4.1.8. *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).

### 4.1.9. *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).

### 4.1.10. *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

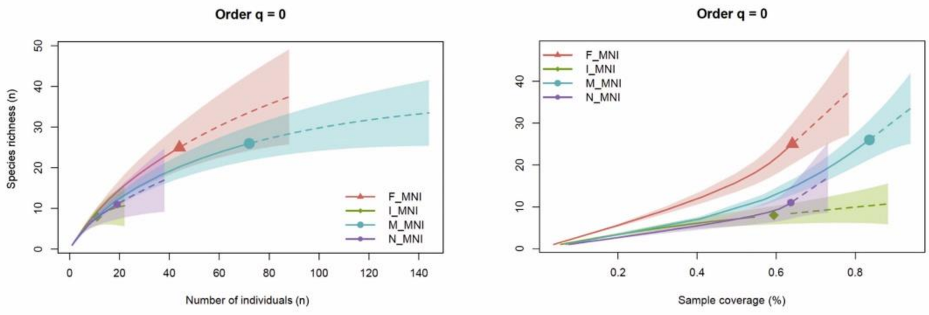

**Fig. 2.** Specimen (left) and coverage-based (right) rarefaction/extrapolation curves of diversity based on species richness (q = 0). Dashed lines represent extrapolation of species diversity until the double of the sample size, shaded bands represent 95% confidence intervals (see also Table S2) for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

**Fig. 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: *Tachymarptis 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.

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.

### 4.1.11. *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).

**Fig. 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: *Pyrrhocorax pyrrhocorax* 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.

### 4.1.12. 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).

### 4.1.13. 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).

### 4.1.14. Passeriformes – Corvidae

Eleven remains have been referred to *Pyrrhocorax pyrrhocorax*. One tarsometatarsus of *P. pyrrhocorax* 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. pyrrhocorax, 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).

### 4.1.15. 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).

### 4.1.16. 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).

### 4.1.17. 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).

#### 4.1.18. *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.

### 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 Table 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, Table 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%; Table S3b) attaining negative NMDS1 values, whereas NMDS1 positive values essentially record samples with overall median to high taphonomic degradation (Fig. 6, Table 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 (Sarti, 2020; Sarti and Martini, 2020b).

## 5. Discussion

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

Scoring and ordination of the main taphonomic variables considered (Table 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 Table 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 (Sarti, 2020; Sarti and Martini, 2020b).

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). As highlighted by ordination analyses (Fig. 6; Table 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

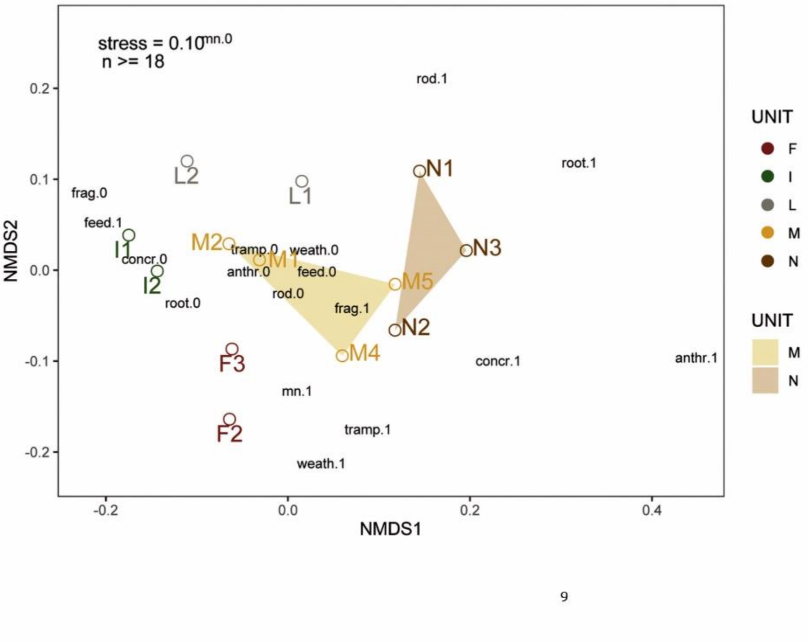

**Fig. 6.** Two-dimensional NMDS output based on Euclidean distance for log-transformed relative abundances of taphonomic variables of avian samples from the Pleistocene succession of Grotta del Cavallo. Both taphonomic variables and sub-units are displayed (here considered only the sub-units with $n \geq 18$ 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.

porous and retain more organic matter.

As for concretions, carbonates precipitate from oxic water rich in calcium ions ($Ca^{2+}$) while flowing through sediment. When such water flows in $CO_2$ rich environments, carbon dioxide reacts with water forming $HCO_3^-$ that in turn reacts with $Ca^{2+}$ forming calcite which then precipitates as incrustation. Thus, calcite incrustation in cave settings could attain higher prevalence during periods where $CO_2$ 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 towards 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 Table 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 (Table 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, 2002; Cecchetti, 2003; Sarti and Martini, 2020a). 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, 2020) 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 (Table 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 (Table 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 tetrax*, *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 graeca*. *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 m 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, 2020). 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 $C_3$ plants). Within the study area and during MIS 3, Dansgaard-

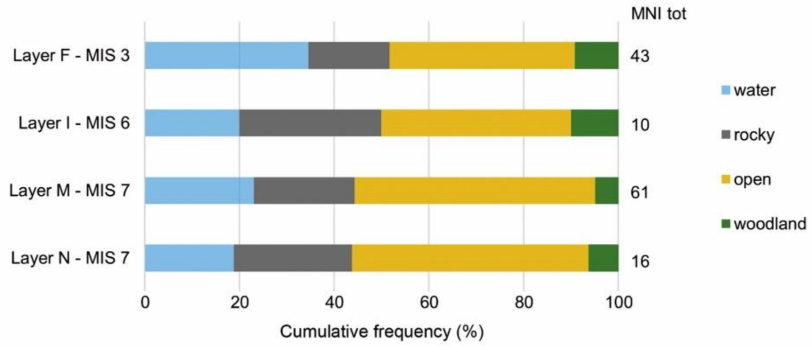

**Fig. 3.** Cumulative frequencies (%) of bird taxa from open, rocky, water, and forest environments retrieved in the layers F, I, M, and N of Grotta del Cavallo. Abundances consider the Minimum Number of Individuals from the four different habitats.

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 maintainance 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, an 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, 2020), but support the habitat indications given by the micromammal sequence (Dalla Valle, 2008; Petruso et al., 2011; Berto, 2020). 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 *Pyrrhocorax pyrrhocorax,* 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.

## 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.

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## Appendix A. Supplementary data

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## SM Supplementary Material Carrera et al. 2021- *Mid-Late Pleistocene Neanderthal landscapes in southern Italy: paleoecological contributions of the avian assemblage from Grotta del Cavallo, Apulia, southern Italy*. Palaeogeography, Palaeoclimatology, Palaeoecology

## Diagnostic features and taxonomic inferences

### Galliformes - Phasianidae

*Coturnix coturnix*: one proximal right coracoid (C498), one proximal left coracoid (C24), two proximal right ulnae (C41, C191), one proximal radius (C617), one left carpometacarpus (C98), one proximal left carpometacarpus (C434), and one distal right tarsometatarsus (C211). The identification of the bones of this species is based on the recognition of the osteological features of the Galliformes and on the size, as *C. coturnix* is clearly smaller than the other Western Palearctic Galliformes (Erbersdobler, 1968; Kraft, 1972). *Alectoris graeca*: one cranial portion of a right scapula (C458), one cranial portion of a left scapula (C163) and one distal left tibiotarsus (C398). The morphology of the bones agrees with the genus *Alectoris* in having the scapula without a foramen on the proximal epiphysis and a well protruding acromion and a distal large tibiotarsus with a tick pons supratendineus and an elongated condylus medialis. *Alectoris rufa* is ruled out because the acromion in the fossils develops straight and not bended, as well as for the smaller size of the tibiotarsus (Kraft, 1972). *Alectoris chukar* and *Alectoris barbara* have not been considered for the identifications for biogeographic reasons, as both are currently considered introduced in Italy (Scandura et al., 2010; Brichetti and Fracasso, 2015). *Perdix perdix*: two proximal right coracoids (C101, C363), one right humerus (C177), one proximal right humerus (C460), three proximal left humeri (C169, C426, C432), one proximal right ulna (C333), one proximal radius (C242), two distal left carpometacarpi (C27, C185), and one distal right tarsometatarsus (C890). This middle to small-sized species (Kraft, 1972) is characterized by a relatively slender coracoid with a slender processus acrocoracoideus and a very shallow foramen in the distal part; a slender humerus with a rather straight diaphysis, a small proximal end with the incisura capitis forming a notch in the proximal outline, and a protruding crista deltopectoralis with a squared cranial outline; a rounded outline of the cotyla dorsalis of the ulna; a relatively squared, in proximal view, and not very laterally protruded proximal epiphysis of the radius; an arched distal epiphysis, in distal view, with a narrow synosseus metacarpalis distalis of the carpometacarpus; a distal tarsometatarsus rather compact and not splayed. We ruled out the fossil species *Perdix paleoperdix*, considered a primitive form of *P. perdix*, on the basis on the size that is clearly smaller than *P. perdix* (Mourer-Chauviré, 1975).

### Anseriformes - Anatidae

Cf. *Branta leucopsis*: one proximal left ulna (C59). The remain is dubitatively referred to *B. leucopsis* for its larger size compared to other *Branta* species (Bacher, 1967), and for the olecranon protruding ventrally. Cf. *Aythya nyroca*: one distal right carpometacarpus (C641). The size of this remain is small and the symphysis metacarpalis distalis is very narrow with a well-marked lateral protrusion in the distal end. *Aythya fuligula*:

one distal right carpometacarpus (C1042). The size corresponds with *A. fuligula* and the protrusion in the distal end is pronounced. The ridges on the shaft of the os metacarpale major are more pronounced than *A. nyroca*. *Spatula querquedula*: one distal left humerus (C857). The general outline of the distal end with the condylus dorsalis not bombed as in *Anas crecca* and without a protrusion just above it, as in *Mergellus albellus*, corresponds to *S. querquedula*. *Anas crecca*: one distal right ulna (C1019) and one right tarsometatarsus (C1041). These remains have been referred to *A. crecca* on the basis of their small size (Woelfle, 1967), the absence of a step above the condylus dorsalis ulnaris, a pronounced tuberculum carpale that points in the proximal direction, and the general stout and stocky look of the tarsometatarsus, with a compact and not splayed distal epiphysis.

**Podicipediformes - Podicipedidae**

*Podiceps cristatus*: one proximal left coracoid (C118) and one distal left tibiotarsus (C447). The size, the very deep curved sulcus on the lateral side of the processus acrocoracoideus and the lack of the pons supratendineus in the distal tibiotarsus (not complete as in *P. grisegena*) identified this remain as *P. cristatus*. *P. nigricollis*: one proximal right tarsometatarsus (C1091). This remain has been identified based on its size and for the presence of three canals for the flexoris digitorum longus, that are four in *Tachybaptus ruficollis* (Bochenski, 1994; Mayr, 2015). The latter can also be ruled out for the eminentia intercotylaris that is more protruding in the proximal direction than the hypotarsus (Bochenski, 1994).

**Columbiformes - Columbidae**

*Columba livia*: one distal right radius (C345), one distal right tibiotarsus (C646) and two distal right tarsometatarsi (C102, C1044). The identifications have been based on the size, on the shape of the distal radius (wider than *C. oenas*), and on the more developed epicondylus medialis of the tibiotarsus. The distal epiphysis of the tarsometatarsus is more splayed compared to *C. oenas*, with the trochlea metatarsi II more protruded in the plantar direction than in *C. palumbus*. *Streptopelia turtur*: one proximal right humerus (C873) and one distal right humerus (C874). These remains have been assigned to *Streptopelia turtur* for their size (Fick, 1974). *Streptopelia decaocto* has been ruled out for its larger size and for biogeographic reasons, as this species has colonised Europe only in the last 50-60 years (Tyrberg, 1998, 2008; Bagi et al., 2018).

**Caprimulgiformes - Apodidae**

*Tachymarptis melba*: one right coracoid (C648). The large size ruled out the other Western Palearctic swift species, as *T. melba* is the largest among them. *Apus apus*: one right tarsometatarsus (C1094). This remain has been identified due to its squat look with the three trochleae obliquely aligned, in dorsal view. It also shows a small bulge, in medial view, in the proximal portion of the dorsal surface. In the same-sized *Apus pallidus* (Boano et al., 2015), the bulge is absent or less pronounced and the tarsometatarsus overall is slightly more slender.

**Gruiformes - Rallidae**

*Fulica atra*: one right quadratum (C1050). The size, the processus orbitalis flat and as long as the processus temporalis, and the processus quadrato-jugalis forming a right angle with the processus mandibolaris in ventral view, correspond with *F. atra*. In addition, the processus temporalis is longer than the processus oticus whereas, in ventral view, the tuberculum mandibulare is pronounced and the processus mandibularis is curved towards the processus orbitalis. *Gallinula chloropus* (the most similar species) is smaller in size.

**Otidiformes - Otididae**

*Tetrax tetrax*: one cranial portion of a right scapula (C937), one proximal right coracoid (C923), one proximal right humerus (C422), one distal right humerus (C96), one distal left carpometacarpus (C1083), one wing phalanx (C974), one distal right tarsometatarsus (C1043), and one posterior phalanx (C53). These remains show typical characteristics of the bustards, such as a flattened proximal end of the acromion with a protruded tuberculum in the scapula; the coracoid shows a round-shaped cotyla scapularis and a wide proximal part of the shaft in medial view; the humerus has a rounded caput humeri, a well-marked incisura capitis, a small single fossa pneumotricipitalis, and a rounded epicondylus ventralis with a hinted processus supracondylaris dorsalis; the carpometacarpus shows a very narrow symphysis metacarpalis distalis; the distal tarsometatarsus is typically splayed with the trochlea metatarsi III more protruded distally; the posterior phalanx is characterized by a longitudinal sulcus on the dorsal side of the bone. The size of the bones from Grotta del Cavallo are comparable with those of *T. tetrax*, the smallest of the Western Palaearctic Otididae.

**Pelecaniformes - Threskiornithidae**

*Plegadis falcinellus*: one proximal right radius (C439). The size is clearly smaller than the only other Western Palearctic ibis *Geronticus eremita* (Pavia, 2019), and the oblique depression located between the cotyla humeralis and the tuberculum bicipitale radiale is well defined and oval.

**Charadriiformes - Charadriidae**

*Pluvialis squatarola*: one distal left tibiotarsus (C213). The distal condyles are flattened, the distal part of the shaft is relatively wide, and the size is slightly larger than *Pluvialis apricaria*. *Eudromias morinellus*: one right coracoid (C499). The size, the flat outline of the facies articularis humeralis, and the not very pronounced facies articularis clavicularis allowed the identification of this remain.

**Charadriiformes - Laridae**

*Larus genei*: one distal right ulna (C999). The tuberculums carpale, pronounced and pointingproximally, and the straight distal shaft allowed us to recognize this remain as belonging to the Laridae family. Among the gulls, the condylus dorsalis is less longitudinally extended than *Larus canus*, whereas the outline of same condylus is less rounded than *Larus ridibundus* and *Larus melanocephalus*. The condylus dorsalis is also less extended distally than *Rissa tridactyla*. In the latter species, the tuberculum carpale points in the proximal direction more than in *L. genei*.

**Strigiformes - Strigidae**

*Athene noctua*: one cranial portion of a right scapula (C453), one cranial portion of a left scapula (C477), one distal right humerus (C943), one proximal right carpometacarpus (C1153), one distal left carpometacarpus (C861), one left first anterior phalanx of the major digit (C1085), one right proximal femur (C904), one left proximal femur (C1066), one left distal femur (C849), one distal right tibiotarsus (C205), one proximal right tarsometatarsus (C370), two distal right tarsometatarsi (C369, C858), two first posterior phalanges of the digit 1 (C139, C629), two second posterior phalanges of the digit 3 (C150, C667), one posterior phalanx (C868), and one ungual phalanx (C455). The various remains from Grotta del Cavallo perfectly agree with the morphological characteristics of this genus and with the size of *Athene noctua* (Langer, 1980; Pavia and Mourer-Chauviré, 2002; Pavia et al., 2015), including the posterior phalanges (Torres-Roig et al., 2019). *Otus scops*: one distal radius (C1124). The radius is small and lacks the bump on the dorsal side just before the distal epiphysis, which is typical of *A. noctua*. *Strix aluco*: a distal portion of the rostrum mandibulae (C220). The diagnostic feature of this bone is the presence of an x shaped sulcus on the internal surface of the mandibular symphysis and the outline of the two rami of the mandible. *Bubo bubo*: one proximal left tarsometatarsus (C1). The size of this remain is larger than *B. scandiacus* (Mejier et al., 2017).

**Accipitriformes - Accipitridae**

*Aquila chrysaetos*: one left fourth posterior phalanx of digit 4 (C758). This remain is large and robust, with the latter character eliminating the large vultures (Louchart et al., 2005; Manegold et al., 2014). *Circus aeruginosus*: one proximal right ulna (C354) and one distal right tibiotarsus (C119). The identification has been based on the size of these remains (Otto, 1981; Schmidt-Burger, 1982), on the shape of the olecranon projecting ventrally in  the proximal ulna, and on the narrow and shallow proximal part of the sulcus extensorius, placed more laterally than in other Accipitridae, in the distal tibiotarsus.

**Falconiformes - Falconidae**

*Falco tinnunculus*: one proximal left carpometacarpus (C281), one distal left femur (C860), one distal left tibiotarsus (C845), and one distal right tarsometatarsus (C372). The size is similar to *F. columbarius* and *subbuteo* and larger than *F. vespertinus* and *F. naumanni* (according to Solti, 1996). The bones can be referred to *F. tinnunculus* based on the pronounced concavity between the trochlea carpalis and the processus extensorius in the proximal carpometacarpus, the relatively rounded outline of the condylus medialis in the distal femur, the distal epiphysis developed straight in the same direction of the bone axis and symmetrical, with a thick pons supratendineus, in the distal tibiotarsus, and the relatively wide shaft of the tarsometatarsus with a notch in the distal side of the trochlea metatarsi II. The carpometacarpus C281 belonged to a breeding female due to the presence of medullary bone in the bone cavity.

**Passeriformes - Corvidae**

Many of the identifications of the following Corvidae species have been based on the osteological characteristics and the bone measurements reported in Tomek and Bocheński (2000) and on the direct comparisons with the recent skeletons available. Here following we describe in detail only the diagnostic features that have not been described in the previously mentioned contribution. *Pyrrhocorax pyrrhocorax*: one cranial portion of a right scapula (C495), two distal right coracoids (C277, C420), two proximal left carpometacarpi (C77, C80), one proximal right femur (C433), one distal left femur (C70), one distal right tarsometatarsus (C195), one proximal left tarsometatarsus (C743), and two distal left tarsometatarsi (C63, C314). The tarsometatarsus C314 belonged to a juvenile individual due to the presence of porous bone tissue. These remains show a relative stout aspect and a bigger size than *P. graculus* (Tomek and Bocheński, 2000). In addition, they show the acromion and the tuberculum coracoideum of the same size in the cranial portion of the scapula, a weak processus pisiformis, the processus alularis not reaching a bony plate on the shaft (Tomek and Bocheński, 2000), the crista trochanteris not pronounced, a flat outline of the cranial side of the proximal epiphysis of the femur in proximal view, the absence of a saddle in the eminentia intercondylaris in the proximal epiphysis, and the presence of two foramina in the distal epiphysis in the tarsometatarsus. *Pica pica*: one cranial portion of a left scapula (C978), one proximal right coracoid (C452), one distal right humerus (C312), and one proximal left femur (C35). The identifications have been based on the absence of a nodule below the facies articularis humeralis of the scapula with the tuberculum coracoideum slightly developed, the narrow processus acrocoracoideus, the wide and laterally protruded processus flexorius of the distal humerus, and the rounded and scarcely protruded crista trochanteris of the proximal femur. *Corvus monedula*: one proximal right carpometacarpus (C61). *Corvus corax*: seven ungual phalanxes (C635, C643, C714, C742, C859, C941, C1060). The phalanges have been identified based on their large size and the well-marked processus flexorius (Tomek and Bocheński, 2000).

**Passeriformes - Alaudidae**

*Melanocorypha calandra*: one maxilla fragment (C245) and one mandibula fragment (C773). The two bill fragments show the typical narrowing just at the rostral end of the nostril, and a size which rules out any other Alaudidae (Moreno, 1985; Cuisin, 1989; Bedetti and Pavia, 2013; Kessler, 2015).

**Passeriformes - Sylviidae**

*Sylvia* cf. *communis*: one proximal right humerus (C775) and one left humerus (C774). Both the remains come from the same layer and horizon and show juvenile bone characteristics, therefore they likely belong to the same individual. It was probably a juvenile individual in a rather advanced development stage, as the presence of porous bone tissue is limited and the bone features are already recognizable. The flattened fossa tricipitalis, the rather developed fossa pneumoanconea, and the shape of the caput humeri identify this individual as a Sylvidae, sensu Janossy, 1983. This family has currently been split into several families (Acrocephalidae, Phylloscopidae, Scotocercidae, Sylvidae, Regulidae) (del Hoyo et al., 2016). Among the similar sized representatives of these families, the bones recall the morphology and size of *Sylvia communis*, with some uncertainty due to the presence of juvenile bone tissue that could hide some osteological features.

**Passeriformes - Turdidae**

Cf. *Turdus viscivorus*: one proximal right carpometacarpus (C842) and one distal left femur (C800). The size of these remains, which is even larger than the recent *T. viscivorus* specimens examined, suggests a likely attribution to *T. viscivorus* as this species is the largest Western Palearctic Turdidae. The small Corvidae have been ruled out based on the size and morphology (Tomek and Bochenski, 2000).

**Passeriformes - Emberizidae**

*Emberiza calandra*: one maxilla fragment (C247) and two mandibula fragments (C193, C287). This species is the largest among the European Emberizidae, thus the identifications have been based on the size and on the recognition of the typical osteological beak features of the Emberizidae, such as the bending, near the angulus mandibulae, of the os maxillare and of the os spleniale in the mandibula (Cuisin, 1989). Both the maxilla and the madibulae are particularly large and thick.

## Modern osteological comparative collections

Museum acronyms are as follows: AMNH (American Museum Natural History, New York, USA); IPH (Institut de Paléontogie Humaine, Museum National d'Histoire Naturelle, Paris, France); ISIPU (Istituto Italiano Paleontologia Umana, Anagni, Italy); MCCI (Museo Civico di Storia Naturale, Carmagnola, Italy); MGPT-MPOC (Marco Pavia Ornithological Collection, University of Torino, Italy); MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain); MNHN (Museum National d'Histoire Naturelle, Paris France); NHMUK (Natural History Museum, London UK); SMF (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main, Germany); TM (Ditsong Natural History Museum, Pretoria, South Africa); UCBL (Université Claude Bernard Lyon 1, Villeurbanne, France); USNM (National Museum of Natural History, Smithsonian Institution, Washington DC, USA); ZMB (Museum für Naturkunde, Berlin, Germany); ZMUC (Natural History Museum of Denmark, Copenhagen, Denmark). We have also used the bird skeletal collection held at the Sezione di Scienze Preistoriche e Antropologiche of the University of Ferrara, organized by Benedetto Sala and Matteo Romandini, but as the specimens in this collection are only provisionally catalogued and numbered, they are indicated with the abbreviation “FE spec.”, without any catalogue acronym or number.

The modern osteological comparative specimens used in this study were: Phasianidae - *Coturnix coturnix* FE 1 spec., MGPT-MPOC 85, MGPT-MPOC 172, MGPT-MPOC 335, MGPT-MPOC 476, MGPT-MPOC 1656, UCBL 130-1, ZMB 1980/66, ZMUC CN155; *Alectoris graeca* MGPT-MPOC 198, MGPT-MPOC 460, MGPT-MPOC 1163, MGPT-MPOC 1332, MGPT-MPOC 1662; *Alectoris rufa* MGPT-MPOC 1590; *Perdix perdix* FE 1 spec., ISIPU 793, MGPT-MPOC 126, MGPT-MPOC 192, MGPT-MPOC 487, MGPT-MPOC 862, MGPT-MPOC 1146, MGPT-MPOC 1649, MGPT-MPOC 1661, ZMB 2000/34767; *Bonasa bonasia* MGPT-MPOC 844, MGPT-MPOC 1309; *Lagopus muta* FE 1 spec., MGPT-MPOC 243, MGPT-MPOC 1162, MGPT-MPOC 1341, MGPT-MPOC 1533, MGPT-MPOC 1874. Anatidae - *Branta bernicla* IPH 1034, MGPT-MPOC 736, MGPT-MPOC 879, MGPT-MPOC 880; *Branta leucopsis* IPH 1520, MGPT-MPOC 1348, MGPT-MPOC 1515, MGPT-MPOC 1516; *Branta ruficollis* MGPT-MPOC 64, MGPT-MPOC 479, MGPT-MPOC 1085, MGPT-MPOC 1210, MGPT-MPOC 1588; *Anser albifrons* MGPT-MPOC 165, MGPT-MPOC 1586; *Anser erythropus* IPH 1503, MGPT-MPOC 942, 943, 950; *Mergellus albellus* MGPT-MPOC 331, MGPT-MPOC 1717; *Netta rufina* MGPT-MPOC 623; *Aythya ferina* FE 2 spec., MGPT-MPOC 521, MGPT-MPOC 1314, MGPT-MPOC 1370, MGPT-MPOC 1541, MGPT-MPOC 1549, MGPT-MPOC 1614; *Aythya nyroca* MGPT-MPOC 620, MGPT-MPOC 707, MGPT-MPOC 1343, MGPT-MPOC 1391, MGPT-MPOC 1409; *Aythya fuligula* FE 2 spec., MGPT-MPOC 194; *Spatula querquedula* FE 1 spec., MGPT-MPOC 625, MGPT-MPOC 1412, MGPT-MPOC 1430, MGPT-MPOC 1446, MGPT-MPOC 1526, MGPT-MPOC 1650, UCBL 57-1; *Spatula clypeata* MGPT-MPOC 70, MGPT-MPOC 726, MGPT-MPOC 1188, MGPT-MPOC 1355, MGPT-MPOC 1484; *Mareca strepera* MGPT-MPOC 435, MGPT-MPOC 486, MGPT-MPOC 1411, MGPT-MPOC 1425, MGPT-MPOC 1528, MGPT-MPOC 1535; *Mareca penelope* MGPT-MPOC 91, MGPT-MPOC 485, MGPT-MPOC 1404, MGPT-MPOC 1421, MGPT-MPOC 1429, MGPT-MPOC 1431, MGPT-MPOC 1471, MGPT-MPOC 1656, MGPT-MPOC 1781; *Anas platyrhynchos* FE 2 spec., MGPT-MPOC 144, MGPT-MPOC 295, MGPT-MPOC 1548; *Anas acuta* MGPT-MPOC 392, MGPT-MPOC 523, MGPT-MPOC 1094, MGPT-MPOC 1539, MGPT-MPOC 1657; *Anas crecca* FE 2 spec., MGPT-MPOC 112, MGPT-MPOC 443, MGPT-MPOC 490, MGPT-MPOC 558, MGPT-MPOC 698, MGPT-MPOC 1610, MGPT-MPOC 1707, UCBL 55-1. Podicipedidae - *Tachybaptus ruficollis* MGPT-MPOC 653, MGPT-MPOC 657, MGPT-MPOC 1286, MGPT-MPOC 1349, MGPT-MPOC 1679, MGPT-MPOC 1684; *Podiceps grisegena* MGPT-MPOC 840; *Podiceps cristatus* MGPT-MPOC 86, MGPT-MPOC 121, MGPT-MPOC 821, MGPT-MPOC 1620, MGPT-MPOC 1701; *Podiceps auritus* MGPT-MPOC 1503; *Podiceps nigricollis* MGPT-MPOC 7, MGPT-MPOC 122, MGPT-MPOC 439, MGPT-MPOC 464, MGPT-MPOC 1439, MGPT-MPOC 1643. Columbidae - *Columba livia* MGPT-MPOC 55, MGPT-MPOC 205, MGPT-MPOC 268, MGPT-MPOC 1792, UCBL 237-2; *Columba oenas* MGPT-MPOC 472, MGPT-MPOC 1570, MGPT-MPOC 1611, MGPT-MPOC 1722, MGPT-MPOC 1785; *Columba palumbus* MGPT-MPOC 54, MGPT-MPOC 195, MGPT-MPOC 813, MGPT-MPOC 1450, MGPT-MPOC 1478, MGPT-MPOC 1479, MGPT-MPOC 1485, MGPT-MPOC 1538, UCBL-239-2; *Streptopelia turtur* MGPT-MPOC 396, MGPT-MPOC 552, MGPT-MPOC 1150, MGPT-MPOC 1253, MGPT-MPOC 1583, UCBL 240-1. Apodidae - *Tachymarptis melba* MGPT-MPOC 170, MGPT-MPOC 317, MGPT-MPOC 366, MGPT-MPOC 375, MGPT-MPOC 387, MGPT-MPOC 388, MGPT-MPOC 560, MGPT-MPOC 634; *Apus pallidus* MGPT-MPOC 102, MGPT-MPOC 536, MGPT-MPOC 569, MGPT-MPOC 572, MGPT-MPOC 1189, MGPT-MPOC 1288, MGPT-MPOC 1559, MGPT-MPOC 1575; *Apus apus* MGPT-MPOC 49, MGPT-MPOC 566, MGPT-MPOC 582, MGPT-MPOC 1113, MGPT-MPOC 1560. Rallidae - *Crex crex* MGPT-MPOC 709, MGPT-MPOC 751, MGPT-MPOC 1438, MGPT-MPOC 1567, MGPT-MPOC 1576, MGPT-MPOC 1600, MGPT-MPOC 1640, MGPT-MPOC 1652, MGPT-MPOC 1740; *Gallinula chloropus* FE 1 spec., MGPT-MPOC 36, MGPT-MPOC 1353, MGPT-MPOC 1428, MGPT-MPOC 1470, MGPT-MPOC 1603; *Fulica atra* FE 1 spec., MPOC 68, MGPT-MPOC 216, MGPT-MPOC 383, MGPT-MPOC 393, MGPT-MPOC 1204, MGPT-MPOC 1367, MGPT-MPOC 1445, MGPT-MPOC 1447, MGPT-MPOC 1696, MGPT-MPOC 1771. Otididae - *Tetrax tetrax* IPH 157, NHMUK 1858.2.3.6. Threskiornithidae - *Geronticus eremita* AMNH 32870, AMNH 32871, NHMUK S/2006.12.1, TM 76544, UCBL Lyon 1974, UCBL Mar 1992, USNM 647320; *Plegadis falcinellus* MGPT-MPOC 14, MGPT-MPOC 871, TM 61724, TM 61884, TM 61885, TM 77508. Charadriidae - *Pluvialis squatarola* MGPT-MPOC 301, MGPT-MPOC 358, MGPT-MPOC 361, MGPT-MPOC 752, MGPT-MPOC 1486, MGPT-MPOC 1720; *Pluvialis apricaria* MGPT-MPOC 59, MGPT-MPOC 180, MGPT-MPOC 369, MGPT-MPOC 743, MGPT-MPOC 940, MGPT-MPOC 1086, MGPT-MPOC 1453; *Eudromias morinellus* MGPT-MPOC 711, MGPT-MPOC 712, MGPT-MPOC 713, MGPT-MPOC 1068, MGPT-MPOC 1754; *Vanellus vanellus* FE 1 spec., MGPT-MPOC 9, MGPT-MPOC 44, MGPT-MPOC 267, MGPT-MPOC 446, MGPT-MPOC 856, MGPT-MPOC 1377, MGPT-MPOC 1466, MGPT-MPOC 1663, MGPT-MPOC 1705. Scolopacidae - *Limosa lapponica* MGPT-MPOC 105, MGPT-MPOC 727, MGPT-MPOC 1354, MGPT-MPOC 1742; *Numenius phaeopus* IPH 403, MGPT-MPOC 1077, MGPT-MPOC 1299, MGPT-MPOC 1326, MGPT-MPOC 1546; *Numenius tenuirostris* AMNH 547, IPH 406; *Numenius arquata* MGPT-MPOC 236, MGPT-MPOC 483, MGPT-MPOC 689, MGPT-MPOC 1454, MGPT-MPOC 1463, MGPT-MPOC 1550, MGPT-MPOC 1664; *Tringa erythropus* MGPT-MPOC 391, MGPT-

MPOC 459, MGPT-MPOC 466, MGPT-MPOC 470, MGPT-MPOC 539, MGPT-MPOC 1488; *Tringa nebularia* MGPT-MPOC 455; *Tringa totanus* MGPT-MPOC 309, MGPT-MPOC 355, MGPT-MPOC 377, MGPT-MPOC 491, MGPT-MPOC 840, MGPT-MPOC 946, MGPT-MPOC 1741; *Actitis hypoleucos* MGPT-MPOC 318, MGPT-MPOC 1598, MGPT-MPOC 1642. Laridae - *Rissa tridactyla* MGPT-MPOC 416, MGPT-MPOC 437, MGPT-MPOC 458, MGPT-MPOC 770; *Larus genei* MGPT-MPOC 434, MGPT-MPOC 1139; *Larus ridibundus* MGPT-MPOC 8, MGPT-MPOC 397, MGPT-MPOC 837, MGPT-MPOC 1066, MGPT-MPOC 1373; *Larus melanocephalus* MGPT-MPOC 700, MGPT-MPOC 808, MGPT-MPOC 833, MGPT-MPOC 834, MGPT-MPOC 835, MGPT-MPOC 836; *Larus canus* MGPT-MPOC 118, MGPT-MPOC 453, MGPT-MPOC 892, MGPT-MPOC 1589. Tytonidae - *Tyto alba* IPH 244, MGPT-MPOC 37, MGPT-MPOC 436, MGPT-MPOC 621, MGPT-MPOC 646, MGPT-MPOC 663, MGPT-MPOC 671, MGPT-MPOC 708, MGPT-MPOC 823, MGPT-MPOC 1093, MGPT-MPOC 1616, MGPT-MPOC 1693, MGPT-MPOC 1706, MGPT-MPOC 1776. Strigidae - *Surnia ulula* IPH 1101, MGPT-MPOC 1499; *Glaucidium passerinum* IPH 883, MGPT-MPOC 876, MGPT-MPOC 1497, MGPT-MPOC 1504; *Athene noctua* FE 2 spec., IPH 145, MGPT-MPOC 38, MGPT-MPOC 255, MGPT-MPOC 385, MGPT-MPOC 497, MGPT-MPOC 498, MGPT-MPOC 680, 719, MGPT-MPOC 816, MGPT-MPOC 863, MGPT-MPOC 964, MGPT-MPOC 1787, SMF 10240; *Aegolius funereus* IPH 882, MCCI 146 MGPT-MPOC 1082, MGPT-MPOC 1156, MGPT-MPOC 1496; *Otus scops* IPH 1243, MGPT-MPOC 41, MGPT-MPOC 113, MGPT-MPOC 502, MGPT-MPOC 556, MGPT-MPOC 587, MGPT-MPOC 642, MGPT-MPOC 648, MGPT-MPOC 649, MGPT-MPOC 662, MGPT-MPOC 677, MGPT-MPOC 860, MGPT-MPOC 1061, MGPT-MPOC 1211, MGPT-MPOC 1232; *Asio flammeus* IPH 1048; MGPT-MPOC 241, MGPT-MPOC 654, MGPT-MPOC 694, MGPT-MPOC 1342, MGPT-MPOC1383, MGPT-MPOC 1618, MGPT-MPOC 1789, MGPT-MPOC 1795; *Asio otus* FE 1 spec., IPH 999, MCCI ingr 1191, MGPT-MPOC 33, MGPT-MPOC 212, MGPT-MPOC 718, MGPT-MPOC 756, MGPT-MPOC 963, MGPT-MPOC 1547, MGPT-MPOC 1593, MGPT-MPOC 1752; *Strix aluco* FE 1 spec., IPH 1022, MGPT-MPOC 18, MGPT-MPOC 40, MGPT-MPOC 196, MGPT-MPOC 260, MGPT-MPOC 508, MGPT-MPOC 510, MGPT-MPOC 814, MGPT-MPOC 1651, MGPT-MPOC 1783; *Strix nebulosa* MGPT-MPOC 1089, MGPT-MPOC 1508, MGPT-MPOC 1511; *Strix uralensis* MGPT-MPOC 1505, MGPT-MPOC 1507; *Bubo scandiacus* MGPT-MPOC 838, MGPT-MPOC 1364, NHMUK S/1998.59.1, ZMB 2000/44555; *Bubo bubo* FE 1 spec., MGPT-MPOC 67, MGPT-MPOC 1543, MGPT-MPOC 1580, NHMUK S/2007.62.1. Accipitridae - *Pandion haliaetus* IPH 482, MGPT-MPOC 66, MGPT-MPOC 227, MGPT-MPOC 484, MGPT-MPOC 640, MGPT-MPOC 1386; *Pernis apivorus* FE 1 spec., IPH 1264, MGPT-MPOC 25, MGPT-MPOC 193, MGPT-MPOC 380, MGPT-MPOC 382, MGPT-MPOC 517, MGPT-MPOC 522, MGPT-MPOC 824, MGPT-MPOC 853, MGPT-MPOC 1631; *Gypaetus barbatus* MGPT-MPOC 504; *Gyps fulvus* IPH 1057, NHMUK 1861.3.24.6, NHMUK 1954.30.55; *Aegypius monachus* AMNH 28556, MGPT-MPOC 270, NHMUK 1848.3.8.2, USNM 614152; *Aquila adalberti* MNCN 161, MNCM 172; *Aquila heliaca* MGPT-MPOC 716, NHMUK 1954.30.48; *Aquila chrysaetos* IPH 126, IPH 576, MNHN AC 1997.103, NHMUK 1898.5.7.2; *Circus aeruginosus* FE 1 spec., IPH 124, IPH 417, MGPT-MPOC 183, MGPT-MPOC 234, MGPT-MPOC 374, MGPT-MPOC 398, MGPT-MPOC 622, MGPT-MPOC 739, MGPT-MPOC 758, MGPT-

MPOC 817; *Circus cyaneus* IPH 557, MGPT-MPOC 20, MGPT-MPOC 478, MGPT-MPOC 1194, MGPT-MPOC 1347, MGPT-MPOC 1619, MGPT-MPOC 1773; *Circus macrourus* IPH 503, MGPT-MPOC 1608; *Circus pygargus* IPH 798, MGPT-MPOC 367, MGPT-MPOC 1381, MGPT-MPOC 1637; *Accipiter gentilis* MGPT-MPOC 88, MGPT-MPOC 372, MGPT-MPOC 520, MGPT-MPOC 530, MGPT-MPOC 532, MGPT-MPOC 851, MGPT-MPOC 852, MGPT-MPOC 932, MGPT-MPOC 1476, MGPT-MPOC 1659, MGPT-MPOC 1700; *Haliaeetus albicilla* IPH 1432, MGPT-MPOC 1494, NHMUK 1858.2.3.1; *Buteo buteo* FE 1 spec., IPH 1265, MGPT-MPOC 22, MGPT-MPOC 65, MGPT-MPOC 512, MGPT-MPOC 811, MGPT-MPOC 822, MGPT-MPOC 952, MGPT-MPOC 1665; NHMUK 1930.3.24.316; *Buteo lagopus* IPH 976, MGPT-MPOC 839, MGPT-MPOC 1509, MGPT-MPOC 1517; NHMUK 1954.30.36; *Buteo rufinus* MGPT-MPOC 1540. Falconidae - *Falco naumanni* IPH 585 MGPT-MPOC 82, MGPT-MPOC 643, MGPT-MPOC 652, MGPT-MPOC 679, MGPT-MPOC 682, MGPT-MPOC 702, MGPT-MPOC 703, MGPT-MPOC 704, MGPT-MPOC 706, MGPT-MPOC 1062, MGPT-MPOC 1063, MGPT-MPOC 1229, MGPT-MPOC 1236, MGPT-MPOC 1695, MGPT-MPOC 1786; *Falco tinnunculus* FE 1 spec., IPH 351, MGPT-MPOC 51, MGPT-MPOC 111, MGPT-MPOC 440, MGPT-MPOC 513, MGPT-MPOC 815, MGPT-MPOC 944, MGPT-MPOC 959; *Falco vespertinus* IPH 330, MGPT-MPOC 720, MGPT-MPOC 1595, MGPT-MPOC 1761; *Falco eleonorae* IPH 87; *Falco columbarius* FE 1 spec., MGPT-MPOC 11, MGPT-MPOC 759, MGPT-MPOC 1501, MGPT-MPOC 1512, MGPT-MPOC 1514, MGPT-MPOC 1728*; Falco subbuteo* FE 1 spec., IPH 513, MGPT-MPOC 39, MGPT-MPOC 201, MGPT-MPOC 384, MGPT-MPOC 531, MGPT-MPOC 937, MGPT-MPOC 947, MGPT-MPOC 1231, MGPT-MPOC 1252, MGPT-MPOC 1609, MGPT-MPOC 1713. Corvidae - *Pyrrhocorax pyrrhocorax* IPH 664, NHMUK 1930.3.24.635, UCBL 305-1; *Pyrrhocorax graculus* IPH 216, ISIPU B 41, MGPT-MPOC 89, MGPT-MPOC 336, MGPT-MPOC 447, MGPT-MPOC 1187, MGPT-MPOC 1531, NHMUK 1917.8.1; *Garrulus glandarius* FE 1 spec., MGPT-MPOC 109, MGPT-MPOC 854, MGPT-MPOC MGPT-MPOC 855, MGPT-MPOC 977, MGPT-MPOC 987, MGPT-MPOC 1034, MGPT-MPOC 1186, MGPT-MPOC 1235, MGPT-MPOC 1527; *Pica pica* FE 1 spec., MGPT-MPOC 27, MGPT-MPOC 56, MGPT-MPOC 626, MGPT-MPOC 737, MGPT-MPOC 933, MGPT-MPOC 1239, MGPT-MPOC 1436, MGPT-MPOC 1451, MGPT-MPOC 1456; *Nucifraga caryocatactes* MGPT-MPOC 444, MGPT-MPOC 1689; *Corvus monedula* MGPT-MPOC 461, MGPT-MPOC 469, MGPT-MPOC 578, MGPT-MPOC 1035; *Corvus frugilegus* IPH 191, MGPT-MPOC 456, MGPT-MPOC 526, NHMUK 1852.1.23.11; *Corvus corax* MCCI 62, MGPT-MPOC 136, MGPT-MPOC 308, MGPT-MPOC 1346, MGPT-MPOC 1371, MGPT-MPOC 1578, MGPT-MPOC 1625, MGPT-MPOC 1779; *Corvus corone* MGPT-MPOC 107, MGPT-MPOC 189, MGPT-MPOC 202 MGPT-MPOC 283, MGPT-MPOC 298, MGPT-MPOC 509, MGPT-MPOC 1209, NHMUK 1930.3.24.606, UCBL 296-2. Alaudidae - *Calandrella brachydactyla* MGPT-MPOC 248; *Eremophila alpestris* MGPT-MPOC 917, MGPT-MPOC 1014, MGPT-MPOC 1015, MGPT-MPOC 1016, MGPT-MPOC 1017; *Lullula arborea* MGPT-MPOC 247; *Alauda arvensis* MGPT-MPOC 103, MGPT-MPOC 333, MGPT-MPOC 1247; *Galerida cristata* MGPT-MPOC 182, MGPT-MPOC 1020, MGPT-MPOC 1606. Hirundinidae - *Delichon urbicum* MGPT-MPOC 75; *Hirundo rustica* MGPT-MPOC 58, *Ptyonoprogne rupestris* MGPT-MPOC 1159; *Riparia riparia* MGPT-MPOC 132. Acrocephalidae - *Acrocephalus scirpaceus* MGPT-MPOC

1000. Sylvidae - *Sylvia atricapilla* MGPT-MPOC 73, MGPT-MPOC 968, MGPT-MPOC 988, MGPT-MPOC 1244, MGPT-MPOC 1251, MGPT-MPOC 1318; *Sylvia borin* MGPT-MPOC 134, MGPT-MPOC 1435, MGPT-MPOC 1674; *Sylvia curruca* MGPT-MPOC 1029, MGPT-MPOC 1038, MGPT-MPOC 1041; *Sylvia melanocephala* MGPT-MPOC 10, MGPT-MPOC 1228; *Sylvia communis* MGPT-MPOC 61, MGPT-MPOC 1031, MGPT-MPOC 1033. Sturnidae - *Sturnus vulgaris* FE 3 spec., MGPT-MPOC 46, MGPT-MPOC 1755; *Sturnus unicolor* MGPT-MPOC 185, MGPT-MPOC 675; *Pastor roseus* MGPT-MPOC 1048, MGPT-MPOC 1049. Turdidae - *Turdus viscivorus* MGPT-MPOC 495, MGPT-MPOC 866, MGPT-MPOC 1028, MGPT-MPOC 1308; *Turdus philomelos* MGPT-MPOC 186, MGPT-MPOC 570, MGPT-MPOC 972; *Turdus iliacus* MGPT-MPOC 775, MGPT-MPOC 1366, MGPT-MPOC 1604; *Turdus merula* FE 1 spec., MGPT-MPOC 973, MGPT-MPOC 995, MGPT-MPOC 1238; *Turdus pilaris* MGPT-MPOC 116, MGPT-MPOC 561, MGPT-MPOC 568, MGPT-MPOC 1289, MGPT-MPOC 1613; *Turdus torquatus* MGPT-MPOC 1322. Muscicapidae - *Erithacus rubecula* MGPT-MPOC 129; *Luscinia megarhynchos* MGPT-MPOC 160, MGPT-MPOC 346, MGPT-MPOC 978, MGPT-MPOC 1242, MGPT-MPOC 1433; *Phoenicurus ochruros* MGPT-MPOC 78, MGPT-MPOC 1114, MGPT-MPOC 1224; *Phoenicurus phoenicurus* MGPT-MPOC 128, MGPT-MPOC 982, MGPT-MPOC 1434; *Monticola saxatilis* MGPT-MPOC 1026; *Monticola solitarius* MGPT-MPOC 197, MGPT-MPOC 690, MGPT-MPOC 693; *Oenanthe oenanthe* MGPT-MPOC 79, MGPT-MPOC 327; *Oenanthe hispanica* MGPT-MPOC 1044. Fringillidae - *Fringilla coelebs* MGPT-MPOC 77, MGPT-MPOC 994, MGPT-MPOC 1563, MGPT-MPOC 1678; *Fringilla montifringilla* MGPT-MPOC 351, MGPT-MPOC 1214, MGPT-MPOC 1769, MGPT-MPOC 1778; *Coccothraustes coccothraustes* MGPT-MPOC 48, MGPT-MPOC 979, MGPT-MPOC 983, MGPT-MPOC 990, MGPT-MPOC 1493, MGPT-MPOC 1506; *Carpodacus erythrinus* MGPT-MPOC 1032, MGPT-MPOC 1036; *Pyrrhula pyrrhula* MGPT-MPOC 63, MGPT-MPOC 275, MGPT-MPOC 338, MGPT-MPOC 546, MGPT-MPOC 1565; *Chloris chloris* MGPT-MPOC 250, MGPT-MPOC 352, MGPT-MPOC 1605; *Linaria cannabina* MGPT-MPOC 106, MGPT-MPOC 155; *Loxia curvirostra* MGPT-MPOC 749, MGPT-MPOC 1753; *Carduelis carduelis* MGPT-MPOC 104, MGPT-MPOC 1561, MGPT-MPOC 1636; *Serinus serinus* MGPT-MPOC 1633. Emberizidae - *Emberiza calandra* MGPT-MPOC 251, MGPT-MPOC 1352, MGPT-MPOC 1615; *Emberiza cia* MGPT-MPOC 1148 *Emberiza hortulana* MGPT-MPOC 981, MGPT-MPOC 986; *Emberiza cirlus* MGPT-MPOC 345, MGPT-MPOC 1669; *Emberiza citrinella* MGPT-MPOC 1790; *Emberiza schoeniclus* MGPT-MPOC 62, MGPT-MPOC 1243, MGPT-MPOC 1250, MGPT-MPOC 1638.

**Table S1.** List of taxa used for rarefaction analyses with the MNI values for each layer.

| **Taxa** | **F_MNI** | **I_MNI** | **M_MNI** | **N_MNI** |
|---|---|---|---|---|
| *Coturnix coturnix* | 0 | 0 | 3 | 1 |
| *Alectoris graeca* | 0 | 0 | 2 | 1 |
| *Perdix perdix* | 1 | 0 | 4 | 3 |
| cf. *Branta leucopsis* | 0 | 0 | 1 | 0 |
| *Anser albifrons*/*erythropus* | 0 | 0 | 2 | 0 |
| cf. *Aythya nyroca* | 0 | 0 | 1 | 0 |
| *Aythya fuligula* | 1 | 0 | 0 | 0 |
| *Spatula querquedula*/*Anas crecca* | 4 | 0 | 0 | 0 |
| *Mareca strepera*/*penelope* | 1 | 0 | 1 | 0 |
| *Podiceps cristatus* | 0 | 0 | 1 | 1 |
| *Podiceps nigricollis* | 1 | 0 | 0 | 0 |
| *Columba livia*/*palumbus*/*oenas* | 4 | 0 | 10 | 4 |
| *Streptopelia turtur* | 1 | 0 | 0 | 0 |
| *Tachymarptis melba* | 0 | 0 | 1 | 0 |
| *Apus apus* | 1 | 0 | 0 | 0 |
| *Fulica atra* | 1 | 0 | 0 | 0 |
| *Tetrax tetrax* | 2 | 0 | 2 | 1 |
| *Plegadis falcinellus* | 0 | 0 | 0 | 1 |
| *Pluvialis squatarola*/*apricaria* | 0 | 2 | 1 | 0 |
| *Eudromias morinellus* | 0 | 0 | 0 | 0 |
| *Numenius* sp. | 1 | 0 | 0 | 0 |
| *Larus genei* | 1 | 0 | 0 | 0 |
| *Athene noctua* | 4 | 0 | 5 | 2 |
| *Otus scops* | 1 | 0 | 0 | 0 |
| *Asio flammeus*/*otus* | 1 | 0 | 0 | 0 |
| *Strix aluco* | 0 | 0 | 1 | 0 |
| *Bubo scandiacus*/*bubo* | 0 | 0 | 1 | 1 |
| *Aquila chrysaetos* | 0 | 1 | 0 | 0 |
| *Circus aeruginosus* | 0 | 0 | 1 | 0 |
| *Buteo lagopus*/*buteo* | 0 | 0 | 1 | 0 |
| *Falco naumanni*/*vespertinus* | 1 | 0 | 0 | 0 |
| *Falco tinnunculus* | 1 | 0 | 2 | 0 |
| *Pyrrhocorax pyrrhocorax*/*graculus*/*C. monedula* | 2 | 1 | 7 | 3 |
| *Pica pica* | 1 | 0 | 2 | 1 |
| *Corvus frugilegus*/*corone* | 2 | 2 | 3 | 0 |
| *Corvus corax* | 3 | 1 | 1 | 0 |
| *Alaudala rufescens*/*Calandrella brachydactyla* | 2 | 0 | 0 | 0 |
| *Galerida theklae*/*cristata*/*M. calandra* | 0 | 2 | 3 | 0 |
| *Sylvia* cf. *communis* | 0 | 1 | 0 | 0 |
| *Sturnus vulgaris*/*unicolor* | 0 | 0 | 13 | 0 |
| cf. *Turdus viscivorus* | 1 | 1 | 0 | 0 |
| *Oenanthe* sp. | 1 | 0 | 0 | 0 |
| Fringillidae indet. | 0 | 0 | 1 | 0 |
| *Emberiza calandra* | 0 | 0 | 2 | 0 |
| Hirundinidae indet | 5 | 0 | 0 | 0 |
| **Tot_MNI** | 44 | 11 | 72 | 19 |

**Table S2.** Estimates of the rarefaction values standardized by 20 specimens (a) and by 70% coverage (b). In the column "order" are reported the species diversity measures used (*q*=0 refers to species richness, *q*=1 to Shannon diversity and *q*=2 to Simpson diversity). Abbreviations: int. - interpolated, ext - extrapolated, SC - Sample Coverage, qD - estimated diversity value, qD_LCL - lower confidence limit, qD_UCL - upper confidence limit.

| **a) Specimens** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **site** | **m** | **method** | **order** | **SC** | **qD** | **qD.LCL** | **qD.UCL** |
| 1 | F_MNI | 20 | int. | 0 | 0.473 | 14.679 | 12.572 | 16.785 |
| 2 | F_MNI | 20 | int. | 1 | 0.473 | 13.258 | 10.746 | 15.771 |
| 3 | F_MNI | 20 | int. | 2 | 0.473 | 11.744 | 9.203 | 14.285 |
| 4 | I_MNI | 20 | ext. | 0 | 0.854 | 10.422 | 6.285 | 14.559 |
| 5 | I_MNI | 20 | ext. | 1 | 0.854 | 10.223 | 6.426 | 14.02 |
| 6 | I_MNI | 20 | ext. | 2 | 0.854 | 9.821 | 5.859 | 13.784 |
| 7 | M_MNI | 20 | int. | 0 | 0.591 | 12.531 | 10.983 | 14.079 |
| 8 | M_MNI | 20 | int. | 1 | 0.591 | 10.561 | 8.819 | 12.303 |
| 9 | M_MNI | 20 | int. | 2 | 0.591 | 8.692 | 6.802 | 10.583 |
| 10 | N_MNI | 20 | ext. | 0 | 0.643 | 11.363 | 7.628 | 15.097 |
| 11 | N_MNI | 20 | ext. | 1 | 0.643 | 9.55 | 5.642 | 13.459 |
| 12 | N_MNI | 20 | ext. | 2 | 0.643 | 8.182 | 3.744 | 12.619 |
| **b) 70% coverage** | | | | | | | | |
| 1 | F_MNI | 60 | ext. | 0 | 0.701 | 30.281 | 23.585 | 36.977 |
| 2 | F_MNI | 60 | ext. | 1 | 0.701 | 23.742 | 17.038 | 30.445 |
| 3 | F_MNI | 60 | ext. | 2 | 0.701 | 18.851 | 12.14 | 25.562 |
| 4 | I_MNI | 14 | ext. | 0 | 0.711 | 9.092 | 6.437 | 11.747 |
| 5 | I_MNI | 14 | ext. | 1 | 0.711 | 8.611 | 5.869 | 11.353 |
| 6 | I_MNI | 14 | ext. | 2 | 0.711 | 8.191 | 5.301 | 11.082 |
| 7 | M_MNI | 34 | int. | 0 | 0.699 | 17.475 | 15.016 | 19.934 |
| 8 | M_MNI | 34 | int. | 1 | 0.699 | 13.545 | 10.916 | 16.175 |
| 9 | M_MNI | 34 | int. | 2 | 0.699 | 10.431 | 7.878 | 12.984 |
| 10 | N_MNI | 31 | ext. | 0 | 0.7 | 14.997 | 8.785 | 21.209 |
| 11 | N_MNI | 31 | ext. | 1 | 0.7 | 11.73 | 6.058 | 17.401 |
| 12 | N_MNI | 31 | ext. | 2 | 0.7 | 9.449 | 3.933 | 14.965 |

**Table S3.** Abundances (3a) and relative abundances (3b) of selected taphonomic variables in the sub-units with more than 10 items. The lithological composition (LITH), the thickness, the Marine Isotopic Stage (MIS), the total number of items (n) and the sample degradation values (S. degr.) are reported for each sub-unit. Abbreviations: ss-sandy silt, sm-sandy mud, sg-sand gravel, ms-muddy silt, m-mud, mss-muddy sand, frag-fragmentation, tramp-trampling, concr-concretion, feed-feeding activity (carnivore bites and digestion by mammals or raptors), rod-rodent gnawing, mn-manganese, root-root etching, weath-exfoliation and cracking, anthr-anthropic related (cut-marks, combustion), degrsample degradation.

**S3a**

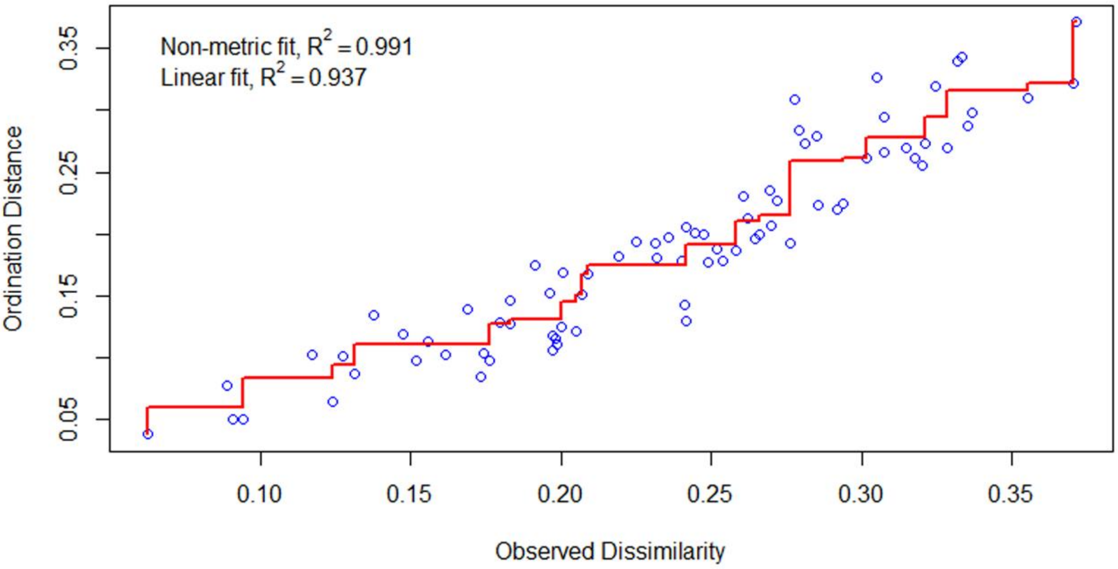
| Sub-unit | OBS | LITH | THICK (cm) | MIS | n | frag-1 | tramp-1 | concr-1 | feed-1 | rod-1 | mn-1 | root-1 | weath-1 | anthr-1 | frag-0 | tramp-0 | concr-0 | feed-0 | rod-0 | mn-0 | root-0 | weath-0 | anthr-0 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| F1 | 1 | ss | 5_7 | MIS3 | 13 | 8 | 0 | 4 | 0 | 0 | 12 | 1 | 0 | 0 | 5 | 13 | 9 | 13 | 13 | 1 | 12 | 13 | 13 |
| F2 | 2 | ss | 7_10 | MIS3 | 57 | 38 | 3 | 27 | 1 | 0 | 56 | 1 | 5 | 0 | 19 | 54 | 30 | 56 | 57 | 1 | 56 | 52 | 57 |
| F3 | 3 | sm | 25_50 | MIS3 | 266 | 193 | 14 | 108 | 9 | 5 | 217 | 17 | 29 | 4 | 73 | 252 | 158 | 257 | 261 | 49 | 249 | 237 | 262 |
| H | 4 | sg | 4_8 | MIS5? | 12 | 9 | 2 | 3 | 0 | 0 | 6 | 0 | 1 | 0 | 3 | 10 | 9 | 12 | 12 | 6 | 12 | 11 | 12 |
| I1 | 5 | ss | >5_33 | MIS6? | 34 | 17 | 0 | 7 | 1 | 0 | 16 | 1 | 0 | 0 | 17 | 34 | 27 | 33 | 34 | 18 | 33 | 34 | 34 |
| I2 | 6 | ms | 23_37 | MIS6 | 27 | 18 | 1 | 8 | 3 | 0 | 14 | 0 | 1 | 0 | 9 | 26 | 19 | 24 | 27 | 13 | 27 | 26 | 27 |
| L1 | 9 | mss | 26_41 | MIS6 | 34 | 20 | 0 | 8 | 3 | 1 | 20 | 20 | 0 | 0 | 14 | 34 | 26 | 31 | 33 | 14 | 14 | 34 | 34 |
| L2 | 10 | m | 8_20 | MIS6 | 36 | 23 | 2 | 0 | 1 | 2 | 16 | 11 | 3 | 1 | 13 | 34 | 36 | 35 | 34 | 20 | 25 | 33 | 35 |
| M1 | 11 | mss | na | MIS7 | 86 | 69 | 9 | 18 | 0 | 2 | 51 | 23 | 6 | 1 | 17 | 77 | 68 | 86 | 84 | 35 | 63 | 80 | 85 |
| M2 | 12 | m | 15_70 | MIS7 | 175 | 148 | 16 | 16 | 8 | 2 | 100 | 45 | 16 | 0 | 27 | 159 | 159 | 167 | 173 | 75 | 130 | 159 | 175 |
| M4 | 14 | mss | >14_36 | MIS7 | 47 | 45 | 8 | 14 | 1 | 0 | 42 | 20 | 2 | 1 | 2 | 39 | 33 | 46 | 47 | 5 | 27 | 45 | 46 |
| M5 | 15 | mss | na | MIS7 | 140 | 116 | 14 | 78 | 4 | 7 | 108 | 80 | 9 | 6 | 24 | 126 | 62 | 136 | 133 | 32 | 60 | 131 | 134 |
| N1 | 17 | sm | 10_33 | MIS7 | 40 | 30 | 3 | 29 | 0 | 1 | 16 | 18 | 0 | 2 | 10 | 37 | 11 | 40 | 39 | 24 | 22 | 40 | 38 |
| N2 | 18 | sm | na | MIS7 | 20 | 18 | 2 | 9 | 1 | 1 | 17 | 11 | 3 | 3 | 2 | 18 | 11 | 19 | 19 | 3 | 9 | 17 | 17 |
| N3 | 19 | sm | na | MIS7 | 18 | 16 | 0 | 14 | 0 | 0 | 11 | 10 | 1 | 0 | 2 | 18 | 4 | 18 | 18 | 7 | 8 | 17 | 18 |
| Q | 20 | sm | 33 | MIS7 | 17 | 14 | 0 | 16 | 1 | 1 | 10 | 5 | 1 | 0 | 3 | 17 | 1 | 16 | 16 | 7 | 12 | 16 | 17 |

**S3b**

| Sub-unit | OBS | LITH | THICK (cm) | MIS | n | frag-1 | tramp-1 | concr-1 | feed-1 | rod-1 | mn-1 | root-1 | weath-1 | anthr-1 | frag-0 | tramp-0 | concr-0 | feed-0 | rod-0 | mn-0 | root-0 | weath-0 | anthr-0 | S. degr. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | | | | | | | | | | *mean* | *median* |
| F1 | 1 | ss | 5_7 | MIS3 | 13 | 0.615 | 0.000 | 0.308 | 0.000 | 0.000 | 0.923 | 0.077 | 0.000 | 0.000 | 0.385 | 1.000 | 0.692 | 1.000 | 1.000 | 0.077 | 0.923 | 1.000 | 1.000 | 0.21 | 0.00 |
| F2 | 2 | ss | 7_10 | MIS3 | 57 | 0.667 | 0.053 | 0.474 | 0.018 | 0.000 | 0.982 | 0.018 | 0.088 | 0.000 | 0.333 | 0.947 | 0.526 | 0.982 | 1.000 | 0.018 | 0.982 | 0.912 | 1.000 | 0.26 | 0.05 |
| F3 | 3 | sm | 25_50 | MIS3 | 266 | 0.726 | 0.053 | 0.406 | 0.034 | 0.019 | 0.816 | 0.064 | 0.109 | 0.015 | 0.274 | 0.947 | 0.594 | 0.966 | 0.981 | 0.184 | 0.936 | 0.891 | 0.985 | 0.25 | 0.06 |
| H | 4 | sg | 4_8 | MIS5? | 12 | 0.750 | 0.167 | 0.250 | 0.000 | 0.000 | 0.500 | 0.000 | 0.083 | 0.000 | 0.250 | 0.833 | 0.750 | 1.000 | 1.000 | 0.500 | 1.000 | 0.917 | 1.000 | 0.19 | 0.08 |
| I1 | 5 | ss | >5_33 | MIS6? | 34 | 0.500 | 0.000 | 0.206 | 0.029 | 0.000 | 0.471 | 0.029 | 0.000 | 0.000 | 0.500 | 1.000 | 0.794 | 0.971 | 1.000 | 0.529 | 0.971 | 1.000 | 1.000 | 0.14 | 0.03 |
| I2 | 6 | ms | 23_37 | MIS6 | 27 | 0.667 | 0.037 | 0.296 | 0.111 | 0.000 | 0.519 | 0.000 | 0.037 | 0.000 | 0.333 | 0.963 | 0.704 | 0.889 | 1.000 | 0.481 | 1.000 | 0.963 | 1.000 | 0.19 | 0.04 |
| L1 | 9 | mss | 26_41 | MIS6 | 34 | 0.588 | 0.000 | 0.235 | 0.088 | 0.029 | 0.588 | 0.588 | 0.000 | 0.000 | 0.412 | 1.000 | 0.765 | 0.912 | 0.971 | 0.412 | 0.412 | 1.000 | 1.000 | 0.24 | 0.09 |
| L2 | 10 | m | 8_20 | MIS6 | 36 | 0.639 | 0.056 | 0.000 | 0.028 | 0.056 | 0.444 | 0.306 | 0.083 | 0.028 | 0.361 | 0.944 | 1.000 | 0.972 | 0.944 | 0.556 | 0.694 | 0.917 | 0.972 | 0.18 | 0.06 |
| M1 | 11 | mss | na | MIS7 | 86 | 0.802 | 0.105 | 0.209 | 0.000 | 0.023 | 0.593 | 0.267 | 0.070 | 0.012 | 0.198 | 0.895 | 0.791 | 1.000 | 0.977 | 0.407 | 0.733 | 0.930 | 0.988 | 0.23 | 0.10 |
| M2 | 12 | m | 15_70 | MIS7 | 175 | 0.846 | 0.091 | 0.091 | 0.046 | 0.011 | 0.571 | 0.257 | 0.091 | 0.000 | 0.154 | 0.909 | 0.909 | 0.954 | 0.989 | 0.429 | 0.743 | 0.909 | 1.000 | 0.22 | 0.09 |
| M4 | 14 | mss | >14_36 | MIS7 | 47 | 0.957 | 0.170 | 0.298 | 0.021 | 0.000 | 0.894 | 0.426 | 0.043 | 0.021 | 0.043 | 0.830 | 0.702 | 0.979 | 1.000 | 0.106 | 0.574 | 0.957 | 0.979 | 0.31 | 0.17 |
| M5 | 15 | mss | na | MIS7 | 140 | 0.829 | 0.100 | 0.557 | 0.029 | 0.050 | 0.771 | 0.571 | 0.064 | 0.043 | 0.171 | 0.900 | 0.443 | 0.971 | 0.950 | 0.229 | 0.429 | 0.936 | 0.957 | 0.33 | 0.10 |
| N1 | 17 | sm | 10_33 | MIS7 | 40 | 0.750 | 0.075 | 0.725 | 0.000 | 0.025 | 0.400 | 0.450 | 0.000 | 0.050 | 0.250 | 0.925 | 0.275 | 1.000 | 0.975 | 0.600 | 0.550 | 1.000 | 0.950 | 0.28 | 0.08 |
| N2 | 18 | sm | na | MIS7 | 20 | 0.900 | 0.100 | 0.450 | 0.050 | 0.050 | 0.850 | 0.550 | 0.150 | 0.150 | 0.100 | 0.900 | 0.550 | 0.950 | 0.950 | 0.150 | 0.450 | 0.850 | 0.850 | 0.36 | 0.15 |
| N3 | 19 | sm | na | MIS7 | 18 | 0.889 | 0.000 | 0.778 | 0.000 | 0.000 | 0.611 | 0.556 | 0.056 | 0.000 | 0.111 | 1.000 | 0.222 | 1.000 | 1.000 | 0.389 | 0.444 | 0.944 | 1.000 | 0.32 | 0.06 |
| Q | 20 | sm | 33 | MIS7 | 17 | 0.824 | 0.000 | 0.941 | 0.059 | 0.059 | 0.588 | 0.294 | 0.059 | 0.000 | 0.176 | 1.000 | 0.059 | 0.941 | 0.941 | 0.412 | 0.706 | 0.941 | 1.000 | 0.31 | 0.06 |
| **Taphonomic damage** | | | | | ***mean*** | 0.75 | 0.06 | 0.39 | 0.03 | 0.02 | 0.66 | 0.28 | 0.06 | 0.02 | | | | | | | | | | | |
| | | | | | ***s*** | 0.13 | 0.06 | 0.26 | 0.03 | 0.02 | 0.19 | 0.22 | 0.04 | 0.04 | | | | | | | | | | | |

**Figure S1.** Main categories of taphonomic variables examined in the bird assemblages from Grotta del Cavallo and employed in the ordination analysis (as for fragmentation the reader is referred to Fig. 4). A: Concretions; B: Root etching; C: Manganese staining; D: Cracking; E: Rodent gnawing; F: Trampling; G: Digestion by nocturnal raptors; H: Cut-mark. The scale bar is indicated in each picture.

**Figure S2.** Shepard stress plot showing the relationship between the actual dissimilarities between samples (from the original dissimilarity matrix) and the ordination distances (i.e. the distances on the NMDS plot). In addition, it displays two correlation-like statistics on the goodness of fit in the graph. The nonmetric fit is based on stress S and defined as R2 = 1-S*S. The "linear fit" is the squared correlation between fitted values and ordination distances. These series of data are well correlated and the amount of scatter is low, then the ordination could be considered representative of the original distance and effectively reduced the multivariate space in two dimensions.



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## 4. Manuscript II

# Macromammal and bird assemblages across the late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review

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# Macromammal and bird assemblages across the late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review

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## ABSTRACT

Evidence of human activities during the Middle to Upper Palaeolithic transition is well represented from rock-shelters, caves and open-air sites across Italy. Over the past decade, both the revision of taphonomic processes affecting archaeological faunal assemblages and new zooarchaeological studies have allowed archaeologists to better understand subsistence strategies and cultural behaviors attributed to groups of Neandertal and modern humans living in the region.

This work presents the preliminary results of a 5-years research programme (ERC n. 724046 – SUCCESS) and offers a state-of-the-art synthesis of archaeological faunal assemblages including mammals and birds uncovered in Italy between 50 and 35 ky ago. The present data were recovered in primary Late Mousterian, Uluzzian, and Protoaurignacian stratigraphic contexts from Northern Italy (Grotta di Fumane, Riparo del Broion, Grotta Maggiore di San Bernardino, Grotta del Rio Secco, Riparo Bombrini), and Southern Italy (Grotta di Castelcivita, Grotta della Cala, Grotta del Cavallo, and Riparo l'Oscurusciuto). The available Number of Identified Specimens (NISP) is analysed through intra- and inter-site comparisons at a regional scale, while aoristic analysis is applied to the sequence documented at Grotta di Fumane. Results of qualitative comparisons suggest an increase in the number of hunted taxa since the end of the Middle Palaeolithic, and a marked change in ecological settings beginning with the Protoaurignacian, with a shift to lower temperatures and humidity. The distribution of carnivore remains and taphonomic analyses hint at a possible change in faunal exploitation and butchering processing between the Middle and Upper Palaeolithic. A preliminary comparison between bone frequencies and the distribution of burned bones poses interesting questions concerning the management of fire. Eventually, the combined use of relative taxonomic abundance and aoristic analysis explicitly addresses time averaging and

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temporal uncertainty embedded in NISP counts and offers estimates of absolute change over time that can be used to support hypotheses emerging from taxon relative frequencies.

## 1. Introduction

Evidence for change in human behaviour and adaptive strategies linked to palaeoenvironmental change has been consistently documented for contexts dated to Marine Isotope Stage 3 (MIS 3: 60-30 ky BP) across Europe. The different subsistence strategies developed by Neandertals and modern humans in response to change in the underlying climatic conditions has been of particular interest in all transitional contexts of continental and Mediterranean Europe (among others: Bietti and Manzi, 1990-91; Guidi and Piperno, 1992; Stiner, 1994; Bietti and Grimaldi, 1996; Milliken, 1999–2000; Kuhn and Bietti, 2000; Mussi, 2001; Peresani, 2009, 2011; Moroni et al., 2013, 2019).

Investigations into hominin diets, specifically those of the Neandertals, ineluctably feed into debates that revolve around the presumed capabilities, or lack thereof, of these hominins in the exploitation of small game as a food resource (Stiner, 2001; Stiner and Munro, 2002, 2011; Hockett and Haws, 2005).

Nevertheless, multiple data have induced some authors to suggest that the exploitation of small animals has been important for human subsistence since ca. 250ka (Klein and Scott, 1986; Stiner, 2005; Romandini et al., 2018b; Morin et al., 2019).

The Italian Peninsula plays a pivotal role as it connects Alpine Europe to the centre of the Mediterranean, and it provides a privileged perspective on interaction and replacement of Neandertals by modern humans in a very diverse set of ecological and climatic regions (Benazzi et al., 2011; Higham et al., 2011; Peresani, 2011; Moroni et al., 2018; Villa et al., 2018; Peresani et al., 2016, 2019). All scholars agree for example on the role played by geographic barriers (Alps and Apennines) in segregating – from a climatic and ecological point of view – a western Mediterranean region form an eastern continental one, the latter affected by the cyclical emersion of the northern Adriatic platform (Sala, 1990; Sala and Marchetti, 2006). Such a diversity, however, made the reconstruction of past ecosystems, of the spatio-temporal distribution of resources, and of population-level subsistence strategies particularly difficult, especially in light of the intense glacial/interglacial cycles of the past 200,000 years. Notwithstanding the many detailed studies carried out at a local scale, a global understanding of change in mobility, adaptive strategies, and settlement pattern across the Middle-Upper Palaeolithic Transition across Italy is still elusive. The few exceptions (Van Andel and Davies, 2003) draw on very scant and heterogeneous data generated with different aims and at different scales, and the emerging scenarios are far from the temporal coherence exhibited by recent global (Bond et al., 1992; Dansgaard et al., 1993; Rasmussen et al., 2014) and Mediterranean palaeoclimatic and palaeecological records (Allen et al., 1999; Sánchez Goñi et al., 2000; Tzedakis et al., 2002; Margari et al., 2009; Fletcher et al., 2010; Müller et al., 2011; Wulf et al., 2018).

The present paper aims to fill this gap and lay the foundations for a finer and more systematic comparison across the whole of the Italian Peninsula by presenting a state-of-the-art review of available data on faunal remains in a number of key dated Italian sites. By carefully documenting and comparing the distribution of faunal remains, we also generate hypotheses on the different subsistence strategies developed by Neandertals and modern humans in response to change in the underlying climatic conditions. Inferences about paleoclimate and ecological settings are based on well-established links between ungulate families/avifaunal groups and the very specific environmental settings to which they were and still are adapted today. More specifically, the review focuses on relative taxon frequency of macromammals (ungulates, carnivores, rodents and lagomorphs) and birds across Late Mousterian, Uluzzian, and Protoaurignacian layers documented for 9 Italian sites for which quantitative data are available (Fig. 1, Areas 1–3). Other assemblages from central and northwestern Italy are also briefly described in this context, but their data are not directly integrated in more detailed investigations of regional trends. Finally, one particularly well-documented site (Grotta di Fumane) is also investigated through aoristic analysis, a probabilistic approach never before applied to the Palaeolithic of Italy. The method explicitly addresses temporal uncertainty and depositional factors affecting the observed number of specimens (NISP) and offers estimates of absolute change over time that can be used to support hypotheses emerging from taxon relative frequencies, as well as to allow a direct comparison between layers of different coeval sites. Finally, the available taphonomic evidence is also presented to provide preliminary insights on change over time in animal exploitation strategies and butchering processes.

This work is still preliminary, as it describes the initial results of an ongoing 5-year project aimed at reaching a deeper understanding of the mechanisms that underpinned the geographic overlap between Neandertals and modern humans in the Italian Peninsula, as well as the final replacement of the former by the latter. While future research will be able to support or disprove part of the picture that emerges from this first assessment, it nonetheless offers a first attempt to generate a coherent synthesis of all the data published to date concerning the region of interest.

## 2. Regional contexts

### 2.1. Northeastern (Adriatic) Italy

In the northern Adriatic Area archaeologists uncovered a considerable number of rock shelters and caves which yielded evidence of the last Neandertals and of the earliest modern humans. The geographic location of such sites is a key element to understanding regional differences in the faunal assemblages they have yielded (Sala, 1990; Sala and Marchetti, 2006; Sala and Masini, 2007; Masini and Sala, 2007, 2011). From a paleoecological point of view, pollen records from Lake Fimon and Azzano Decimo (north-eastern Alpine foothills; Pini et al., 2009, 2010), document long-term vegetation trends during MIS 3. Phases of expansion of conifer-dominated forest (*Pinus sylvestris/mugo* and *Picea*), rich in broad-leaved trees (*Alnus* cf. *incana* and tree *Betula*), are accompanied by a reduction in the amount of warm-temperate elements (e.g. *Tilia*). Middle Würm stadials experienced summer temperatures very close to the growth limit of oaks, but still within the range of lime (MAW 13–15 °C) which persisted, together with other temperate trees (e.g. *Abies*), up to ca. 40 ka (Pini et al., 2009, 2010; Badino et al., this Special Issue). Interestingly, peaks of *Tilia* pollen have been identified in layers preserving Mousterian artifacts and dated to 40.6–46.4 ka $^{14}$C BP from cave deposits at the Broion (Leonardi and Broglio, 1966; Cattani and Renault-Miskowski, 1983-84). Despite evidence of afforestation persisting at a long-term scale south of the Alps, forest withdrawals with expansion of grasslands and dry shrublands (Gramineae, *Artemisia*, Chenopodiaceae) occurred, possibly related to the establishment of drier/colder conditions (i.e. Greenland Stadials/Heinrich events). Such drier and colder stadial conditions likely favoured the presence of Alpine ibex, chamois, and marmot at low altitudes (in the Colli Berici), as well as the presence of micromammals in steppic environments, and the diffusion of birds in tundra-like environments. The Po alluvial valley was, in contrast, inhabited by woolly rhinoceros, mammoth, and bison (Sala, 1990).

Only a few contexts offer data on the Middle to Upper Palaeolithic transition, and their number further decreases for the temporal interval comprised between 50 and 35 ky.

At present, data on faunal remains and the relative chronology are available from Grotta di Fumane (Verona), Grotta Maggiore di San Bernardino (Vicenza), Riparo del Broion and Grotta del Broion (Vicenza), Grotta del Rio Secco (Pordenone) (Table 1, Fig. 1, Area 1). **Grotta di Fumane** is a key site for northern Italy, located at 350 m asl in the western part of the Lessini Mountains (Table 1, Fig. 1). Its archaeological sequence includes the Middle-Upper Palaeolithic transition (Peresani et al., 2008; Higham et al., 2009; López-García et al., 2015). Faunal assemblages consist of a rich association of ungulates, carnivores, and birds from diverse environments and climates. Quantitative comparisons between the Uluzzian assemblage (A3) (Tagliacozzo et al., 2013) and the late Mousterian ones (A4, A5-A6, A9) has highlighted only modest ecological and economic adjustments within a humid forested landscape (Peresani et al., 2011a,b; Romandini, 2012; Romandini et al., 2014a, 2016a,b, 2018a,b, Fiore et al., 2016; Gala et al., 2018; Terlato et al., 2019). Considerable change, on the other hand, emerged from the Protoaurignacian occupations (A2), coinciding with a shift towards colder and steppic environments (Cassoli and Tagliacozzo, 1994a; Fiore et al., 2004).

**Riparo del Broion** is located in the northern part of the Berici eastern slope, at 135 m asl, along a steep slope comprising escarpments, cliffs and remnants of collapsed sinkholes that connects the top of Mount Brosimo (327 m asl) to the marshy and swampy plain (De Stefani et al., 2005; Gurioli et al., 2006; Romandini et al., 2012; Peresani et al., 2019).

Slope-waste clay deposits can be found at the feet of Mount Brosimo. Uluzzian faunal assemblages (levels 1f-1g) show a high richness due to the different environments of the surroundings. Alongside the presence of marmot, hare, chamois, ibex, bison and possibly aurochs, the number of red deer and roe deer bones as well as the abundance of wild boar remains indicate the existence of humid woodlands located in the alluvial plain to the east of Mount Brosimo (Peresani et al., 2019).

**Grotta Maggiore di San Bernardino** opens on the eastern slope of the Berici karst plateau 135 m asl, to the west of the alluvial plain of the Bacchiglione River. Eight lithological units compose a Middle-Late Pleistocene stratigraphic sequence (Cassoli and Tagliacozzo, 1994b; Peresani, 2001). The majority of the total faunal remains found at the

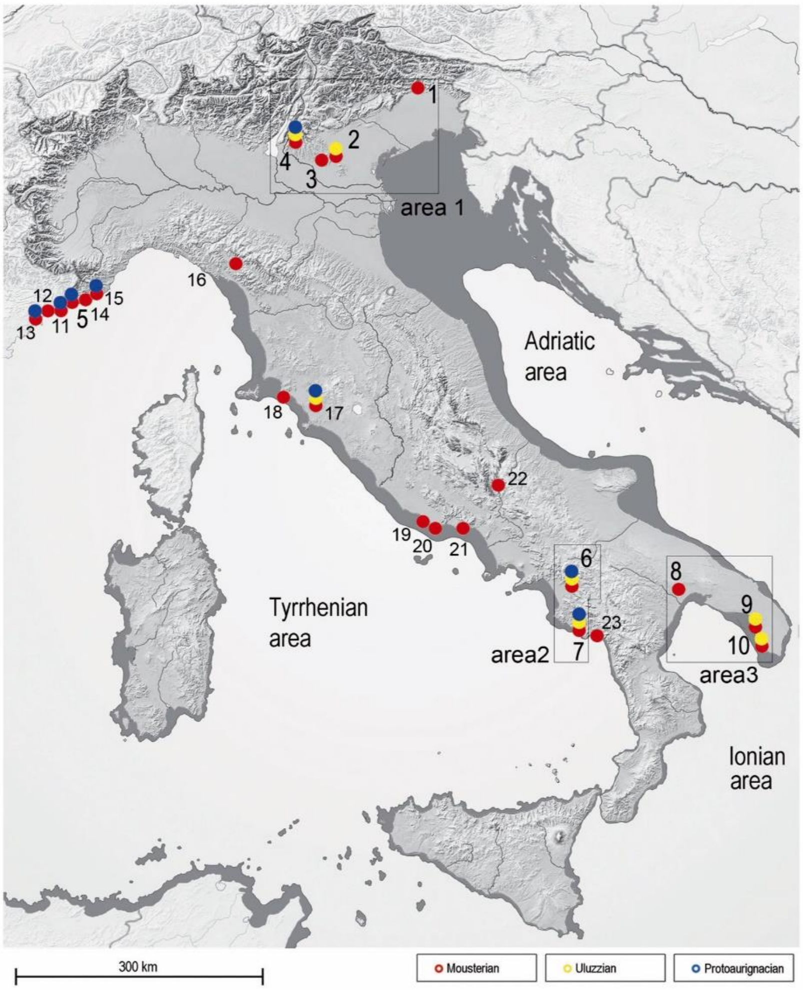


**Fig. 1.** MIS 3 map of Italy (modified from Moroni et al., 2018) and the geographic location of the sites with previously published faunal assemblages mentioned in this work and dated between ca. 50 and 38 ky ago. Sites that are part of the project ERC n. 724046 - SUCCESS are numbered from 1 to 10. Sites analysed in this work are assigned numbers 1-9 (with the exclusion of 5), and are located in study Areas 1-3 (Northeastern, Southwester/Tyrrhenian, and Southeastern/Ionian respectively). For each site the colors represent the presence of levels, USS and/or layers chronologically and technologically linked respectively to the Protoaurignacian = blue; Uluzzian = yellow; Late Mousterian = red. 1) Grotta del Rio Secco; 2) Riparo del Broion; 3) Grotta di San Bernardino; 4) Grotta di Fumane; 5) Riparo Bombrini; 6) Grotta di Castelcivita; 7) Grotta della Cala; 8) Riparo l'Oscurusciuto; 9) Grotta del Cavallo; 10) Grotta di Uluzzo C; 11) Riparo Mochi; 12) Grotta del Principe; 13) Observatoire; 14) Arma Manie; 15) Arma degli Zerbi; 16) Buca della Iena; 17) Grotta la Fabbrica; 18) Grotta dei Santi; 19) Grotta Breuil; 20) Grotta del Fossellone; 21) Grotta S. Agostino; 22) Grotta Reali; 23) Riparo del Poggio. The Italian Peninsula shows a sea level of 70 m below the present-day coastline, based on the global sea-level curve (Benjamin et al., 2017) but lacking the estimation of post-MIS3 sedimentary thickness and eustatic magnitude (sketch map courtesy of S. Ricci, University of Siena). (For interpretation of color coding in this figure legend, the reader is referred to the Web version of this article.)

site (78%) belongs to ungulates, although the frequency of ungulate remains varies between stratigraphic units (Table 1). Units II + III, associated to late Mousterian frequentation, is the only layer to have undergone a detailed zooarchaeological study. Its assemblage suggests the presence of humid climatic conditions, the expansion of woodlands (Cassoli and Tagliacozzo, 1994b; Peresani, 2011; López-García et al., 2017; Romandini et al., 2018b; Terlato et al., 2019).

**Grotta del Rio Secco** is located in a stream gorge at 580 m asl on the Pradis Plateau in the eastern part of the Carnic Pre-Alps (Fig. 1 and Table 1), an orographic system dissected by N–S and W-E valleys separating mountains with peaks of 2000–2300 m asl. The site is a flat and wide south-facing shelter, with a gallery completely filled with sediments. The outer area of the shelter presents with a heap of large boulders collapsed from the original, larger roof. Human occupation has been dated (Tables 1 and A.1) to the Late Mousterian (layers 5top, 7, 5, and 8) and to the Gravettian (layers 6 and 4) (Peresani et al., 2014; Talamo et al., 2014). In layers 7 and 8 archaeologists found evidence of the use of fire and of an intensive exploitation of carnivores (*Ursus arctos*, *Ursus spelaeus*, mustelids, and canids), which are more numerous than ungulates (Peresani et al., 2014; Romandini et al., 2018a). Although bird remains are rare, a terminal pedal phalanx of a golden eagle with anthropic cut marks on the proximal articular facet was recovered from layer 7 (Romandini et al., 2014b).

### 2.2. Northwestern (Tyrrhenian) Italy

The coastal area of this region is characterized by a particular relief pattern with middle-range mountains and a narrow littoral plain between the Mediterranean Sea and the southern Alps (Fig. 1). Faunal assemblages of the region date to between Marine Isotope Stage (MIS) 6 and 3, in agreement with geochronological, pollen and cultural data (Valensi and Psathi, 2004; Bertola et al., 2013; Romandini, 2017). From a general point of view, faunal assemblages attributed to the Middle to Upper Palaeolithic transition exhibit high taxonomical richness, reflecting a variety of biotopes such as forest hills, coastal plains, narrow valleys in the hinterland and numerous cliffs. Consistently high values in species richness, in particular for carnivores, were recorded in Liguria during MIS 3 and 2 (Valensi and Psathi, 2004). The most frequent species of ungulates and small mammals point to the extensive presence of forested environments.

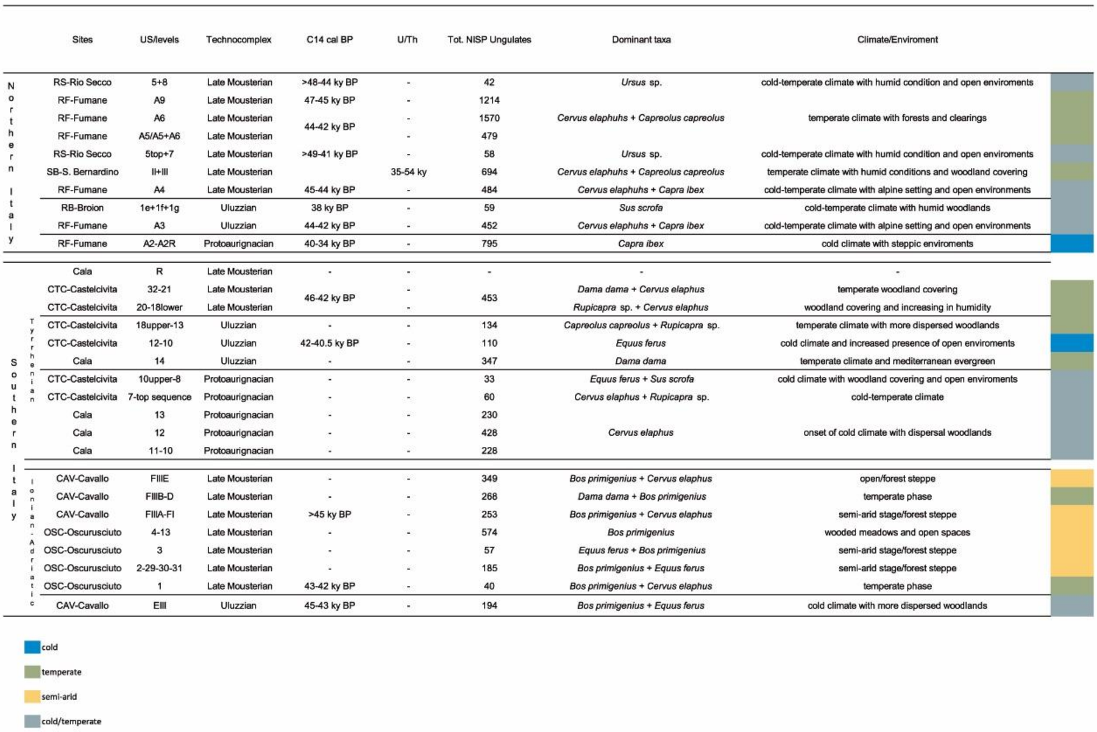
A variety of Late Mousterian sites are reported (Fig. 1): Arma delle Manie, Grotta degli Zerbi, Riparo Bombrini, Riparo Mochi, Grotta del Principe in Italy, and Grotte de l'Observatoire in the Principality of Monaco. The arrival of modern humans in the region is associated to a marked change in the archaeological record (Negrino and Riel-Salvatore, 2018; Riel-Salvatore and Negrino, 2018a). At present, Protoaurignacian evidence has been uncovered at Riparo Mochi (Alhaique, 2000; Kuhn and Stiner, 1998; Douka et al., 2012; Grimaldi et al., 2014), Riparo Bombrini (Bertola et al., 2013; Holt et al., 2019; Negrino and Riel-Salvatore, 2018; Riel-Salvatore et al., 2013; Riel-Salvatore and Negrino, 2018a, 2018b), Arma degli Zerbi and Grotte de l'Observatoire (Rossoni-Notter et al., 2016; Onoratini, 2004; Onoratini and Simon, 2006; Porraz et al., 2010; Romandini, 2017).

### 2.3. Southern Italy

Palaeoecological data for southern Italy come from the Lago Grande di Monticchio record (Monte Vulture, Basilicata). During MIS 3, pollen

**Table 1**

Detailed context table of sites analysed in this work with reference to dominant taxa and to the most represented environmnetal setting recorded at each site.



| | | Sites | US/levels | Technocomplex | C14 cal BP | U/Th | Tot. NISP Ungulates | Dominant taxa | Climate/Enviroment | |
|---|---|---|---|---|---|---|---|---|---|---|
| Northern Italy | | RS-Rio Secco | 5+8 | Late Mousterian | >48-44 ky BP | - | 42 | *Ursus* sp. | cold-temperate climate with humid condition and open enviroments | ◼ |
| | | RF-Fumane | A9 | Late Mousterian | 47-45 ky BP | - | 1214 | *Cervus elaphuhs* + *Capreolus capreolus* | temperate climate with forests and clearings | 🟩 |
| | | RF-Fumane | A6 | Late Mousterian | 44-42 ky BP | - | 1570 | | | 🟩 |
| | | RF-Fumane | A5/A5+A6 | Late Mousterian | | - | 479 | | | 🟩 |
| | | RS-Rio Secco | 5top+7 | Late Mousterian | >49-41 ky BP | - | 58 | *Ursus* sp. | cold-temperate climate with humid condition and open enviroments | ◼ |
| | | SB-S. Bernardino | II+III | Late Mousterian | | 35-54 ky | 694 | *Cervus elaphuhs* + *Capreolus capreolus* | temperate climate with humid conditions and woodland covering | 🟩 |
| | | RF-Fumane | A4 | Late Mousterian | 45-44 ky BP | - | 484 | *Cervus elaphuhs* + *Capra ibex* | cold-temperate climate with alpine setting and open environments | ◼ |
| | | RB-Broion | 1e+1f+1g | Uluzzian | 38 ky BP | - | 59 | *Sus scrofa* | cold-temperate climate with humid woodlands | ◼ |
| | | RF-Fumane | A3 | Uluzzian | 44-42 ky BP | - | 452 | *Cervus elaphuhs* + *Capra ibex* | cold-temperate climate with alpine setting and open environments | ◼ |
| | | RF-Fumane | A2-A2R | Protoaurignacian | 40-34 ky BP | - | 795 | *Capra ibex* | cold climate with steppic enviroments | 🟦 |
| Southern Italy | Tyrrhenian | Cala | R | Late Mousterian | - | - | - | - | - | |
| | | CTC-Castelcivita | 32-21 | Late Mousterian | 46-42 ky BP | - | 453 | *Dama dama* + *Cervus elaphus* | temperate woodland covering | 🟩 |
| | | CTC-Castelcivita | 20-18lower | Late Mousterian | | - | | *Rupicapra* sp. + *Cervus elaphus* | woodland covering and increasing in humidity | 🟩 |
| | | CTC-Castelcivita | 18upper-13 | Uluzzian | - | - | 134 | *Capreolus capreolus* + *Rupicapra* sp. | temperate climate with more dispersed woodlands | 🟩 |
| | | CTC-Castelcivita | 12-10 | Uluzzian | 42-40.5 ky BP | - | 110 | *Equus ferus* | cold climate and increased presence of open enviroments | 🟦 |
| | | Cala | 14 | Uluzzian | - | - | 347 | *Dama dama* | temperate climate and mediterranean evergreen | 🟩 |
| | | CTC-Castelcivita | 10upper-8 | Protoaurignacian | - | - | 33 | *Equus ferus* + *Sus scrofa* | cold climate with woodland covering and open enviroments | ◼ |
| | | CTC-Castelcivita | 7-top sequence | Protoaurignacian | - | - | 60 | *Cervus elaphus* + *Rupicapra* sp. | cold-temperate climate | ◼ |
| | | Cala | 13 | Protoaurignacian | - | - | 230 | *Cervus elaphus* | onset of cold climate with dispersal woodlands | ◼ |
| | | Cala | 12 | Protoaurignacian | - | - | 428 | | | ◼ |
| | | Cala | 11-10 | Protoaurignacian | - | - | 228 | | | ◼ |
| | Ionian-Adriatic | CAV-Cavallo | FIIIE | Late Mousterian | - | - | 349 | *Bos primigenius* + *Cervus elaphus* | open/forest steppe | 🟨 |
| | | CAV-Cavallo | FIIIB-D | Late Mousterian | - | - | 268 | *Dama dama* + *Bos primigenius* | temperate phase | 🟩 |
| | | CAV-Cavallo | FIIIA-FI | Late Mousterian | >45 ky BP | - | 253 | *Bos primigenius* + *Cervus elaphus* | semi-arid stage/forest steppe | 🟨 |
| | | OSC-Oscurusciuto | 4-13 | Late Mousterian | - | - | 574 | *Bos primigenius* | wooded meadows and open spaces | 🟨 |
| | | OSC-Oscurusciuto | 3 | Late Mousterian | - | - | 57 | *Equus ferus* + *Bos primigenius* | semi-arid stage/forest steppe | 🟨 |
| | | OSC-Oscurusciuto | 2-29-30-31 | Late Mousterian | - | - | 185 | *Bos primigenius* + *Equus ferus* | semi-arid stage/forest steppe | 🟨 |
| | | OSC-Oscurusciuto | 1 | Late Mousterian | 43-42 ky BP | - | 40 | *Bos primigenius* + *Cervus elaphus* | temperate phase | 🟩 |
| | | CAV-Cavallo | EIII | Uluzzian | 45-43 ky BP | - | 194 | *Bos primigenius* + *Equus ferus* | cold climate with more dispersed woodlands | ◼ |

🟦 cold

🟩 temperate

🟨 semi-arid

◼ cold/temperate

data associations indicate an alternation between cold/dry steppic vegetation (*Artemisia*-dominated steppe/wooded steppe), related to Greenland Stadials/Heinrich events (GSs/HEs), and an increased range of woody taxa including deciduous *Quercus*, *Abies* and *Fagus* (up to 30–60% of arboreal pollen), referred to Greenland Interstadials (GIs) with a maximum expansion between ca. 55-50 ka (i.e. GI 14) (Allen et al., 1999; Fletcher et al., 2010; Badino et al., this Special Issue). Nevertheless, faunal assemblages coming from MIS3-aged stratigraphic sequences highlight different climatic trends between Tyrrhenian (southwestern) and Ionian (southeastern) contexts (Boscato, 2017) due to an almost persistent moisture availability on the former, mainly generated by the orographic uplift of air charged with moisture from the Tyrrhenian Sea, and to Balkan influence on the latter. The Ionian area is characterized by open environment taxa (e.g. *Bos primigenius*) while the Tyrrhenian one shows an abundance of forest species (Cervidae).

### 2.3.1. Central - southwestern (Tyrrhenian) Italy

Southwestern Italy (Tyrrhenian Area – Table 1, Fig. 1 - Area 2) is best represented by **Grotta di Castelcivita** (Salerno). This site is located 94 m asl and is about 20 km far from the modern coastline, in a territory encompassing the valley of the Calore river and the Alburni mountains (m 1742). The archaeological sequence is dated to MIS 3 (Gambassini, 1997) and is about 2.5 m thick. The lowermost portion (layers cgr, gar, lower rsi, spits 32-18lower) contains Late Mousterian deposits and is overlaid by Uluzzian layers (upper rsi, pie, rpi, rsa'', spits 18upper-10lower). The sequence is capped by Protoaurignacian layers (rsa'-gic-ars, spits 10upper-top of sequence), which are sealed by the Campanian Ignimbrite (Giaccio et al., 2017). From a zooarchaeological point of view, a unique aspect of this site is the presence of freshwater fish in all chronological phases (Cassoli and Tagliacozzo, 1997).

**Grotta della Cala** (Marina di Camerota – Salerno) opens close to the present coastline into a steep calcareous cliff which is part of a hilly/mountain range characterized by plateaus and valleys. The MIS 3 coastline was about 5 km from the cave entrance. The stratigraphic sequence is about 3 m thick and starts from the bottom with Middle Palaeolithic layers in a succession of stalagmites and clastic sediments (Martini et al., 2018). At the entrance of the cave, the Middle Palaeolithic is followed by early Upper Palaeolithic deposits, containing Uluzzian (spit 14) and Protoaurignacian (spits 13-10) evidence (Benini et al., 1997; Boscato et al., 1997). These are covered, after a stratigraphic hiatus, by Gravettian, Epigravettian, Mesolithic and Neo-Eneolithic layers (Palma di Cesnola, 1993).

Beyond these well-documented sites, the only other Uluzzian deposit with faunal assemblages in the region is documented at the Tuscan site of Grotta la Fabbrica (Grosseto; Pitti et al., 1976). Here the abundance of equids points to open environments (less evident in the Protoaurignacian layers). As far as the Late Mousterian is concerned, a similar faunal composition is recorded at Buca della Iena (Lucca; Stiner, 1994). Cervidae are, in contrast, the most abundant family in coeval deposits of Grotta dei Santi (Monte Argentario, Grosseto), suggesting a more humid/temperate climate. In Latium a temperate/humid phase connoted by abundant aurochs and deer remains is recorded at Grotta del Fossellone (Alhaique and Tagliacozzo, 2000) and at Grotta di S. Agostino (Stiner, 1994). A similar trend is found at Grotta Breuil (Alhaique and Tagliacozzo, 2000) where Cervidae are the most abundant in layers 6 and 3a, although ibex remains become more frequent in the latter. In Campania, at Riparo del Poggio (Marina di Camerota), located near Grotta della Cala, faunal assemblages are dominated by Cervidae and are typically linked to temperate climates (fallow deer is the most abundant species; Boscato et al., 2009).

### 2.3.2. Central - southeastern (Adriatic-Ionian) Italy

In the Ionian area (Table 1, Fig. 1 - Area 3) **Grotta del Cavallo** opens into the rocky coast of Uluzzo Tower Bay, at the margin of a vast rolling plain. This cave contains a 7- meter thick stratigraphy which has at its bottom a marine conglomerate attributed to MIS 5e. This is overlaid by a Mousterian sequence dated between MIS 5 and MIS 3 (Table 1) (layers N-FI). These layers are followed by an Uluzzian sequence (EIII – DIb; Moroni et al., 2018) sandwiched between two *tephra* layers (Fa and CII) attributed to the Y-6 and the Y-5 (Campanian Ignimbrite) events, respectively (Zanchetta et al., 2018).

**Riparo l'Oscurusciuto** opens inside the ravine of Ginosa (Taranto), to the north of the modern village and about 20 km from the present coastline (Fig. 1). The zooarchaeological data suggest that Neandertal hunters exploited both the main regional environments, i.e. forest steppe located on flat hills and forested area on the humid bottom of the gorge.

The Middle Palaeolithic stratigraphy is 6-m thick. A tephra (US 14) attributed to the Green Tuff of Monte Epomeo (Ischia) and dated to ca. 55 ky seals the surface of a living floor currently under excavation (US 15) (Boscato et al., 2004, 2011; Boscato and Crezzini, 2006, 2012; Boscato and Ronchitelli, 2008). All the cultural assemblages investigated can be referred to MIS 3 and fall in a chronological interval of ca. 12,000 years. Recurrent Levallois is the most abundant lithic production system (Marciani et al., 2016, 2018; Spagnolo et al., 2016, 2018).

In Molise (Adriatic area) Grotta Reali (Rocchetta a Volturno) yielded Late Mousterian assemblages mostly consisting of Cervidae that can be linked to cold and humid climatic conditions (Sala et al., 2012).

## 3. Materials and methods

Of all the archaeological contexts mentioned in the introduction, the present research only focuses on the 9 ones that present with quantitative evidence on the distribution of faunal assemblages in Middle-to-Upper Palaeolithic transition deposits across Italy ( > 50-35 ky, Tables 1 and A.9 and Fig. 1). Sampled archaeological sites were grouped into three geographic areas based on site location and ecological/environmental context: 1) Northeastern Italy (4 sites); 2) Southwestern/Tyrrhenian Italy (2 sites) and 3) Southeastern/Ionian Italy (3 sites; Fig. 1). New zooarchaeological data for Northwestern Italy are now available from Riparo Bombrini (Pothier Bouchard et al., in this issue), while for the southeastern/Ionian area the zooarchaeological analysis from Grotta di Uluzzo C is currently in progress (Fig. 1). Both sites are part of the ERC n. 724046 – SUCCESS project, but they are not included in the present synthesis.

All faunal remains used to compute species abundance based on taxon frequency were uncovered by sieving sediment using 0.5 mm and 1 mm meshes in Northeastern, Southwestern, and Southeastern Italy. Based on currently available evidence, specimens were nonetheless grouped into three size classes in Northeastern Italian contexts (0.1–1 cm, 1–3 cm, > 3 cm; Table 2) and into two size classes in Southwestern and Southeastern Italian contexts (1–3 cm, > 3 cm; Table 5).

Different sources of surface bone alteration (anthropic cut marks vs. animal tooth marks, trampling, postdepositional and modern modifications generated during excavation) were discriminated drawing criteria outlined in a on well-established body of taphonomic literature (Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1984; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Lyman, 1994; Blumenschine, 1995; Fisher, 1995; Fernández-Jalvo and Andrews, 2016; Duches et al., 2016). The degree of combustion was estimated using the method developed by Stiner et al. (1995) and, in Northeastern Italian contexts, burned and calcined bones were separated from unburned materials.

Faunal remains were attributed to species and genus and, when these were not determinable, to families. Unidentified mammal bones were grouped into three classes based on body size: large (red deer, moose, giant deer, bison, aurochs, horse, lion and bear); medium (alpine ibex, chamois, roe deer, fallow deer, wild boar, wolf, lynx, leopard and hyena); and small (hare, marmot, beaver, mustelids, wild cat and

**Table 2**
Different size classes of mammals bones and burned remains (with relative %) identified in the MP/UP transitional contexts of Northern Italy (see Fig. 1 - Area 1). RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

| US - Levels | Technocomplex | 0.1–1 cm | % | 1–3 cm | % | > 3 cm | % | TOTAL Rem. | Burn. + Calc. | % | Burned | % | Calcined | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RF A2-A2R | PA | 13042 | 65.8 | 6280 | 31.7 | 507 | 2.6 | 19829 | 7861 | 40 | | | | |
| RF A3 | UL | 7831 | 46.1 | 8231 | 48.4 | 927 | 5.5 | 16989 | 4723 | 28 | 2840 | 60.1 | 1883 | 39.9 |
| RB 1e + 1f + 1g | UL | 33199 | 88.8 | 3748 | 10 | 443 | 1.2 | 37390 | 18464 | 49 | 15595 | 84.5 | 2869 | 15.5 |
| RF A4 | LM | 9770 | 49 | 9287 | 46.5 | 898 | 4.5 | 19955 | 7321 | 37 | 5187 | 70.9 | 2134 | 29.1 |
| SB II + III | LM | 2744 | 29.8 | 5337 | 57.9 | 1136 | 12.3 | 9217 | 5431 | 59 | 4747 | 87.4 | 684 | 12.6 |
| RS 5top + 7 | LM | 43 | 8.2 | 47 | 9 | 434 | 82.8 | 524 | 693 | 8 | 42 | 97.7 | 1 | 2.3 |
| RF A5/A5 + A6 | LM | 35342 | 52.7 | 29767 | 44.4 | 1974 | 2.9 | 67083 | 38255 | 57 | 30442 | 79.6 | 7813 | 20.4 |
| RF A6 | LM | 62692 | 56.5 | 43944 | 39.6 | 4408 | 4 | 111044 | 53413 | 48 | 46854 | 87.7 | 6559 | 12.3 |
| RF A9 | LM | 78119 | 69.8 | 30763 | 27.5 | 2959 | 2.6 | 111841 | 54411 | 49 | 50398 | 92.6 | 4013 | 7.4 |
| RS 5 + 8 | LM | 2307 | 53.6 | 1538 | 35.8 | 456 | 10.6 | 4301 | 43 | 16 | 671 | 96.8 | 22 | 3.2 |

fox). In addition, unidentified specimens from the southern sites were grouped according to anatomical categories such as “skull”, “jaw”, “teeth”, “vertebrae”, “ribs” etc. or more general categories such as “epiphysis” “diaphysis” and “spongy bones”.

As far as northern Italy is concerned, taxonomic and skeletal identification were based on the reference collections stored at the Bioarchaeology Section of the National Prehistoric Ethnographic Museum “Luigi Pigorini” (Lazio Museum Pole, Rome), at the Prehistoric and Anthropological Sciences Section in the Department of Humanities, University of Ferrara and at the Laboratory of Osteoarchaeology and Palaeoanthropology at the Department of Cultural Heritage, University of Bologna (Ravenna). Bone assemblages recovered from the southern Italian sites were compared with the reference collection stored at the Research Unit of Anthropology and Prehistory of the University of Siena. Differences between the Uluzzian layer of Grotta del Cavallo and the Late Mousterian layers at Grotta del Cavallo and Riparo l’Oscurusciuto (i.e. the only layers which displayed no sign of carnivore activity on ungulate bones) were formally assessed for percentages of carpal and tarsal bones, and of phalanges and sesamoides (relative frequencies were based on both total ungulate counts and on the remains of *Bos Primigenius*). In addition, the presence of significant differences was tested for remnant diaphysis, epiphysis, and spongy bones between the same layers. To do so we measured effect size as Cohen's *h* using the function ES.h in the package pwr in R (Champely, 2018), we then measured statistical power using the dedicated pwr.2p2n.test function in the same package, and performed a two-tailed test for equality in proportions between the chosen layers (with continuity correction for cases in which the number of successes or failures was lower or equal to 5; Tab. A.13 – A.17). We also tested the hypothesis of differences in the degree of fragmentation across sites of Northern Italy by running arcsine transformation of proportions fragment-size classes at all sites (1–3 cm, > 3 cm; following Morin et al., 2019) and then comparing the distribution of transformed values between Uluzzian and Late Mousterian layers via a two-tailed Mann-Whitney test for independent sample design. As for southern Italy, we once again only focused on Riparo l’Oscurusciuto and Grotta del Cavallo in Southeastern Italy. We tested for significant differences in proportions and also calculated effect size and statistical power to support the obtained results.

Species abundance was quantified using the Number of Identified Specimens (NISP; Grayson, 1984). Notwithstanding its limitations (e.g. inflation of the count of rare parts, lower predictive power when limited to long bones), this particular species estimate offers accuracy and reproducibility at the ratio scale (Morin et al., 2017). The ubiquitous recording of NISP in all the examined contexts made it the best available method to directly compare different sites across the study region. Once NISP of each mammal group or species was obtained for all layers of the 9 sampled archaeological sites across Italy, we grouped layers belonging to the same region (i.e. Northeastern, Southwestern, and Southeastern Italy) and within each region we ordered them into a single diachronic sequence, based on absolute dates (Tables 1 and A.9) and associated material cultural evidence. Avifaunal remains were comapred only for Fumane and Castelcivita caves for abundance reasons and lack of comparable sequences in any other sites. Relative taxon abundance was calculated in each layer and variability in relative frequency over time was inspected through bar charts, in order to highlight any differences between trends emerging in different regions.

Comparing NISP proportions across different archaeological layers (in the same context or between different contexts), however, presents a number of potential issues. In addition to post-depositional processes, substantial differences in the time of accumulation of different layers may have deleterious effects on the accurate representation of faunal spectra. This process, known as time-averaging, is extremely frequent in geologic and anthropic contexts (Binford, 1981; Kowalewski, 1996; Premo, 2014; Madsen, 2018), and has a direct impact on the reliability of the quantification of abundance, richness, evenness, and diversity in time-averaged samples (Leonard and Jones, 1989). Specifically, the longer the duration of layer formation, the more inflated richness and diversity will be. This makes tracking change over time more problematic and increases the risk of misidentifying inflated counts for actual human choices (i.e. Type I error when testing hypotheses; Premo, 2014; Madsen, 2018). The presence of differential accumulation rates, palimpsests, and taphonomic processes therefore complicates any attempt at quantifying the effective temporal scale of individual layers solely based on stratigraphy.

In addition, inference made by comparing NISP proportions is hampered by the limitations of closed datasets (Lyman, 2008; Orton et al., 2017). Species relative frequencies are by definition computed over the total number of collected remains and their sum is bound to be equal to 1. No relative frequency is free to vary over time without affecting or being affected by change in the frequency of another class, i.e. the relative abundance of one particular taxon will always be negatively correlated to the relative abundance of another taxon. Interpreting such increases and decreases as the effect of some independent mechanism (e.g. environmental change, cultural selection) is therefore not always straightforward.

In order to overcome the limitations mentioned above while providing support for the trends that might emerge from relative taxonomic abundance analysis across the time-ordered layers of different sites, we also built long-term time-series of zooarchaeological data documented at Grotta di Fumane (Northeastern Italy) that can directly be compared against independent sources of information (e.g. palaeoclimatic models, palinological and palaeoenvironmental data), and across mismatched and differentially overlapping contexts. Grotta di Fumane was chosen as a case study because it offers the longest and best-dated sequence among all the available sites.

More specifically, we computed aoristic sums (i.e. the sum of the probability of existence of all events for a given temporal interval) of taxon abundance to obtain estimates of taxon frequency based on absolute radiocarbon dates. Aoristic analysis has been already employed in a few archaeological and zooarchaeological studies (Ratcliffe, 2000; Johnson, 2004; Crema, 2012; Bevan et al., 2013; Orton et al., 2017), although the method is still generally rarely used and, to the best of our knowledge, it has never been applied to palaeolithic contexts. This approach consists of: a) assigning a start and end date to each archaeological layer from which fossil fragments had been retrieved; b) dividing the entire time span of the study period into temporal bins of fixed width; c) based on the start and end dates of the relevant layer, and drawing on Laplace's principle of insufficient reason (see Crema, 2012; Orton et al., 2017 for a detailed discussion), dividing the total probability mass of each deposition event/fragment (equal to 1) across the $t$ temporal bins comprised in the date interval of the layer. Each deposition event therefore exhibits a uniform probability of existence at each bin calculated as $1/t$; d) summing all the probabilities falling in the same bin, and repeating the same operation for the entire study period.

The result is an estimate of species frequency distribution which incorporates all the temporal uncertainty embedded in the data. Better dating leads to shorter temporal intervals for each deposition event, that in turn allows researchers to assign a higher probability of existence at each temporal bin. As a consequence, worse dating leads to higher dispersion in the probability of existence, i.e. to stable time series which do not show clear evidence of increase or decrease as an artefact due to lack of resolution. In the present work, we first set the temporal limits for each layer at Grotta di Fumane. When start and end dates were already available from the literature (as in the case of layers A9) these intervals were directly taken (Table A.9). As far as all the remaining layers are concerned (A6, A5/A5 + A6, A4, A3, and A2), start and end dates were calculated in OxCal 4.3 (Bronk Ramsey, 2009) as the median of the 68.2% interval taken from the posterior probability distribution of already published layer boundaries (Higham et al., 2014). This particular model was chosen to fully exploit the potential of aoristic analysis and considering that at this site Uluzzian and final Mousterian are reported as temporally indistinguishable (Douka et al., 2014).

Raw NISP counts were then used to compute aoristic sums of each taxon across 50-year bins through the function *aorist* in the package *archSeries* in R version 3.4.4 (Orton, 2017, R Core Team 2018). To avoid generating artifacts due to empty bins at the interval 41600-41100 cal BP, 10 years were added to the median date for the end boundary of level A3. Taxon-specific aoristic values were then summed and used to calculate estimates of taxon relative frequencies. To further ascertain the presence of absolute shifts in estimated frequency, we also plotted the aoristic sum of ungulates. In this case, absolute frequency estimates were compared against 95% confidence envelopes generated through Monte-Carlo simulation (n. iterations = 5000) as well as against a dummy model generated assuming a uniform frequency distribution following Crema (2012) and Orton (Orton et al., 2017). Both the empirical and dummy simulations were computed using the function *date.simulate* in the package *archSeries*. Using the same function, rates of change were also computed for ungulate families. The aim was to assess whether there were temporal bins exhibiting shifts in the abundance of families compared to other bins. Following Crema (2012) and Orton (2017), rates of change were examined by observing (in this case through boxplots) the distribution of simulated standardised differences between each chronological bin and the preceding one. Temporal intervals with median and interquartile range falling above the zero line (suggesting stability or absence of change) were interpreted as a sign of increase, while boxes falling under the zero line were interpreted as instances of decrease. Such distributions were compared against the 95% confidence envelopes of the null model based on the aoristic sum of carnivores, which provides a null expectation independent from palaeoenvironmental change.

## 4. Results

Northeastern Italian contexts yielded a total of 323,964 remains (NISP = 9044) while for Southern Italy as a whole 33,340 remains were documented (NISP = 2351). From a zooarchaeological point of view, Late Mousterian layers have been investigated more intensively than later ones in both regions. Despite the difference in absolute counts, the proportion of mammal orders and classes is roughly the same across all contexts (Fig. 2), with ungulates being the most abundant category followed by carnivores, birds (at Grotta di Fumane and Castelcivita), and rodents, in decreasing order of importance.

Uluzzian layers exhibit an increase in the relative abundance of carnivore and bird remains, matched by a considerably lower number of remains attributed to large rodents (e.g. marmot and beaver) and lagomorphs (Fig. 2). Protoaurignacian phases invert this trend, with an appreciable decrease in the number of carnivore and bird remains.

### 4.1. Mammals

Despite the specificities that may bias the abundance of faunal remains in each of the examined contexts (e.g., Grotta del Rio Secco being consistently used by bears which, in turn, were routinely exploited by Neandertals; Romandini et al., 2018b), most of Late Mousterian levels and layers in Northeastern Italy show an increase in the prevalence of cervidae, followed by a decrease of *Cervus elaphus* and *Capreolus capreolus* matched by a gradual increase, in the Uluzzian and Protoaurignacian, in caprinae, especially *Capra ibex* and *Rupicapra rupicapra (*Fig. 3 and Table A.1*)*. This change over time in the relative abundance between cervidae and caprinae may hint at a shift from a temperate climate characterised by forests and meadows to an alpine setting with open environments.

The archaeological sites are located in a region that included habitats suitable for bovinae, ranging from dense forests with wetlands and small streams more attractive to *Bos primigenius*, to hilly grasslands and plains, populated by bison. However, bovids are generally less abundant than the previous families, and their presence remains roughly constant across the entire study sequence.

Moose (*Alces alces*) and giant deer (*Megaloceros giganteus*) are less frequent and well attested in Mousterian and Uluzzian layers. Their presence suggests – during this period – the existence of humid woodlands near the sampled archaeological sites. Wild boar is rarer yet, being present anecdotally in the Late Mousterian at Grotta di Fumane, while it is more abundant at lower elevations (Grotta di San Bernardino, Mousterian Units II + III; Riparo del Broion, Uluzzian layers 1e + 1f + 1g). The presence of woolly rhinoceros (*Coelodonta antiquitatis*) in the Uluzzian layer A3 at Grotta di Fumane and of *Stephanorhinus* sp. at Grotta di San Bernardino indicates decreasing temperatures and presence of cold arid conditions.

In this region, carnivores are quantitatively more represented in Late Mousterian and Uluzzian assemblages, while their frequency steadily decreases in Protoaurignacian layers (Fig. 2). Nevertheless, variety of carnivores taxa increase beginning with the Uluzzian (Romandini et al., 2018a), and the presence of wolverine (*Gulo gulo*), ermine (*Mustela erminea*), and arctic fox (*Alopex* cfr. *lagopus*) further supports the onset of colder and arid climate conditions during the MP-UP transition (Fig. 4 and Table A.2). Rodents and lagomorphs (Table A.3) are represented by beaver and marmot, already present in Late Mousterian assemblages, and by lagomorphs in the Uluzzian and Protoaurignacian (Romandini et al., 2018a). Upper Palaeolithic contexts also yielded remains of *Lepus* cfr. *timidus,* further supporting the diffusion of increasingly colder environments in the latest phase of the studied sequences.

In Southwestern/Tyrrhenian Italy, the Late Mousterian sequence at Grotta di Castelcivita (spits 32-24) yielded a conspicuous amount of cervidae fragments (*Cervus elaphus, Dama Dama, Capreolus capreolus*); fallow deer in particular is the most abundant species (Fig. 5 and Table A.4). Later on, in spits 23-18 lower, there is an increase in the abundance of red and roe deer and of chamois (*Rupicapra* sp.), correlated to an increase in humidity (Masini and Abbazzi, 1997). The beginning of the Uluzzian sequence (spits 18 upper-15) is characterised by higher frequencies of horse (*Equus ferus*) and large bovids (*Bison priscus* and *Bos/Bison*) suggesting the occurrence of colder climates and sparse woodland. In the following Uluzzian layers (spits 14-10 lower), an additional increase in the occurrence of equids and a decrease in the frequency of fallow deer suggest more open environments. The Early Protoaurignacian (spits 10 upper – 8 lower) shows comparable environmental conditions, while spits 8upper-7 can be linked to an increase in woodland cover as suggested by the higher presence of deer and the decrease in the frequency of horse (Fig. 5 and Table A.4), followed by cold-temperate phases (spit 6) (Masini and Abbazzi, 1997). The anthracological evidence supports the climatic and ecological trend inferred from zooarchaeological remains (Castelletti and Maspero, 1997).

At Grotta della Cala (Marina di Camerota, Salerno), faunal remains from the Uluzzian (spit 14) are characterised by a conspicuous presence of cervidae (representing on the whole 74% of ungulates) and in particular of fallow deer, typical of temperate climates and Mediterranean evergreen forest. In the Protoaurignacian layers (spits 13-10), lower frequencies of fallow deer and higher frequencies of red deer indicate the onset of colder conditions (Fig. 5 and Table A.4). Low frequencies of ungulates linked to open environments/wooded steppe (such as horse, alpine ibex and aurochs) are also recorded (Benini et al., 1997). Cervids account for over 70% of the ungulates recovered in these layers (Boscato et al., 1997).

In the same region, carnivores occur in all phases. Whilst in the Middle Palaeolithic, most of the remains are referable to the spotted hyaena and the leopard, species richness increase in the Uluzzian and in the Protoaurignacian (Table A.5). Rodents and lagomorphs are very rare.

The record of Southeastern/Ionian Italy, on the other hand, is based on the sequences uncovered at Riparo l'Oscurusciuto (Ginosa – Taranto) and Grotta del Cavallo (Nardò – Lecce) (Figs. 1 and 6 and Tables A.6). At Riparo l'Oscurusciuto, layers 13:4 are characterised by the substantial presence of *Bos primigenius*, counterbalanced by low frequencies of horse, rhinoceros and caprinae, and by anecdotal frequencies of cervidae (especially fallow deer), all of which hints at an environment characterised by wooded meadows and open spaces (Fig. 6). Aurochs is less frequent in SU 3, while in the same unit, deer is more abundant, the presence of rhinoceros can be inferred by tooth fragments, and horse

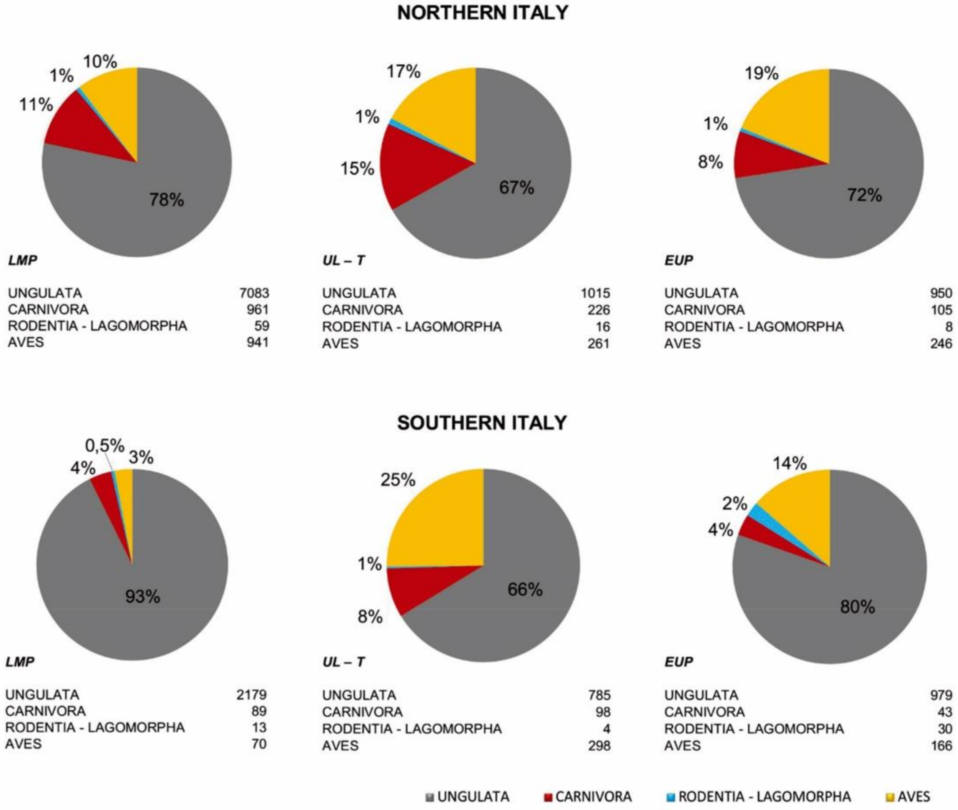


**Fig. 2.** Comparison of the relative frequency of the NISP of Ungulata, Carnivora, Rodentia-Lagomorpha and birds (the latter only for Grotta di Fumane and Castelcivita) documented in all sampled sites (Fig. 1) and divided by macro-geographical area and cultural phase: LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

becomes the most represented ungulate (Table A.6). At the end of the sequence (SU2-1), aurochs is once again the most abundant ungulate, while the increase in abundance of fallow deer suggests the onset of a temperate phase (Boscato and Crezzini, 2012).

The Late Mousterian sequence at Grotta del Cavallo (layers FIII-FI) also yields evidence of the climatic fluctuations known for MIS 3 (Table A.6), which agrees with the sequence described for Riparo l'Oscurusciuto. An initial phase characterised by open/steppic forests indicated by the dominance of aurochs remains (layer FIIIE) is followed, in layers FIIID-FIIIB, by a more temperate phase (as suggested by higher frequency of fallow deer) and by a third, more arid stage in layers FIII-FI associated with the presence of aurochs and horse (Sarti et al., 2000, 2002) (Table A.6). The lowermost Uluzzian level EIII5 suggests, in contrast, a shift to an increasingly colder climate with more dispersed woodlands, indicated by the absence of fallow deer and by the increased presence of horses (Table A.6; Boscato and Crezzini, 2012).

With the only exception of red fox which has been found in the Late Mousterian of Grotta del Cavallo, carnivores, rodents and lagomorphs are almost absent in the assemblages of Ionic area (Table A.7).

### 4.2. Avifaunal remains

Substantial evidence on the exploitation of avifauna was documented for Grotta di Fumane and Grotta di Castelcivita (Cassoli and Tagliacozzo, 1994a, 1997; Masini and Abbazzi, 1997; Gala and Tagliacozzo, 2005; Peresani et al., 2011a; Romandini, 2012;

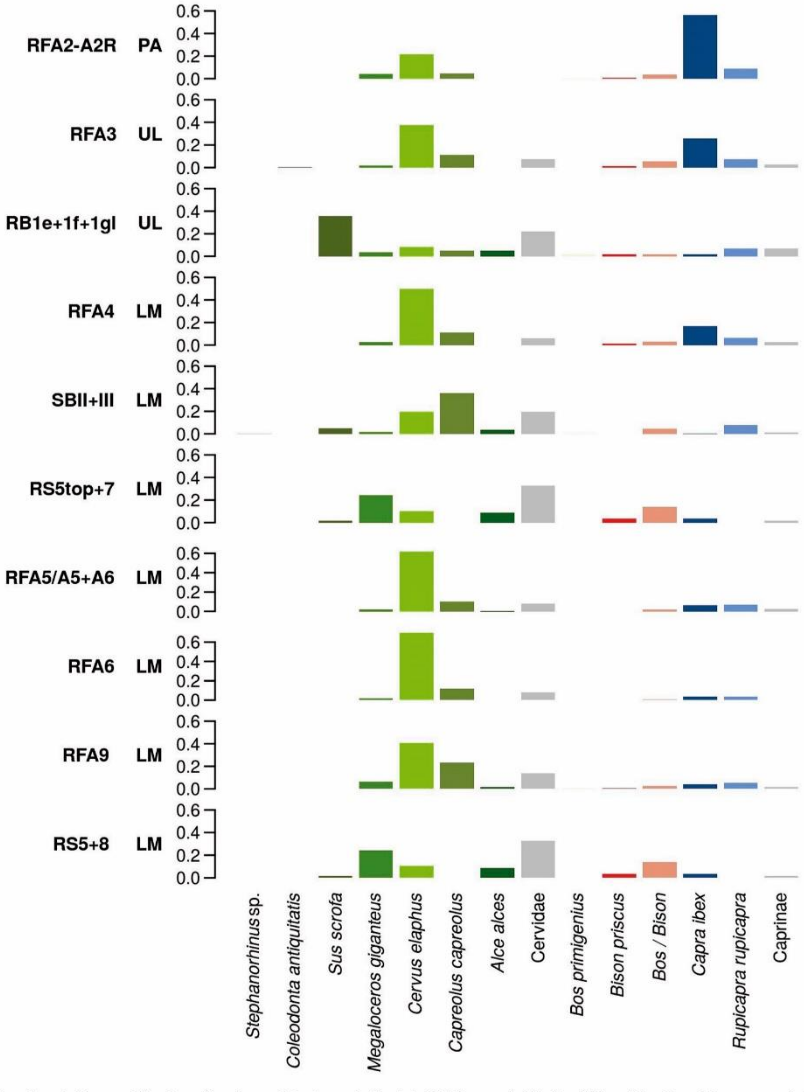


**Fig. 3.** Bar charts showing the relative contribution of each ungulate taxon to the total NISP recorded in the different levels and layers sampled in Northern Italy. The contexts are in chronological-cultural order (from bottom to top) based on the archaeological sequence of each site. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

Tagliacozzo et al., 2013; Romandini et al., 2016a, b; Gala et al., 2018; Fiore et al., 2004, 2016, 2019).

The bird species identified at Grotta di Fumane belong to the extant Italian avifauna (Table A.8) with the exception of the willow grouse (*L.* cf. *lagopus*), a boreal species which has historically never been observed in Italy. The parrot crossbill (*L. pytyopsittacus*) is another boreal species currently found in Northern Europe and considered a vagrant species in Italy (Brichetti and Fracasso, 2015). Taxa linked to open and rocky environments are the most abundant (Fig. 7). More specifically, bearded vulture (*G. barbatus*), golden eagle (*A. chrysaetos*), red-billed and yellow-billed chough (*P. pyrrhocorax* and *P. graculus*), common raven (*C. corax*), Eurasian crag martin (*P. rupestris*) and white-winged snowfinch (*M. nivalis*) indicate the presence of rocky cliffs, while treeless terrain with rocky outcrops is indicated by rock partridge (*A. graeca*) and rock ptarmigan (*L. muta*). On the other hand, the presence of wooded areas in the surroundings of the cave is indicated by the black grouse (*L. tetrix*), stock dove (*C. oenas*), common woodpigeon (*C. palumbus*), Boreal owl (*A. funereus*), tawny owl (*S. aluco*), white-backed woodpecker (*D. leucotos,* currently reduced to small populations in the Central Apennines but once more widespread; Pavia, 1999; Brichetti

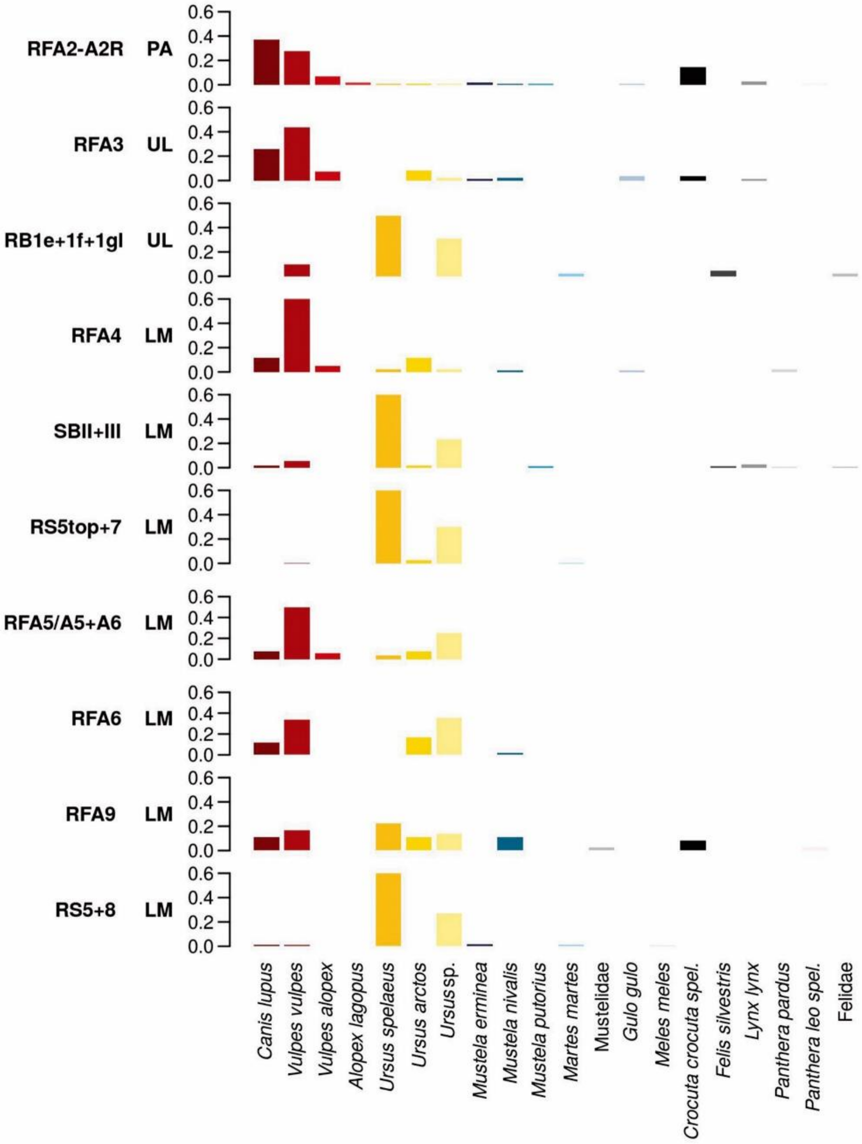


**Fig. 4.** Bar charts showing the relative contribution of each carnivore taxon to the total NISP recorded in the different levels and layers sampled in Northern Italy. The contexts are in chronological-cultural order (from bottom to top) based on the archaeological sequence of each site. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

and Fracasso, 2007) Eurasian jay (*G. glandarius*), and Eurasian bullfinch (*P. pyrrhula*). The presence of the northern nutcracker (*N. caryocatactes*) and parrot crossbill (*L. pytyopsittacus*) also point to the presence of coniferous forests. Additionally, open grasslands and wet meadows are indicated by common quail (*C. coturnix*), grey partridge (*P. perdix*), corncrake (*C. crex*, which was breeding in the surroundings of the cave, as attested by the finding of juvenile bones) and northern lapwing (*V. vanellus*), while willow grouse (*L.* cf. *lagopus*) is an indicative of tundra-like open areas such as moors and peatlands. Finally, the presence of two duck species (*A. platyrhynchos* and *A.* cf. *crecca*) and two Rallidae (*R. aquaticus* and cf. *G. chloropus*) suggests nearby wetlands or slow-flowing water courses (Cramp, 1998).

As a whole the bird assemblage at Fumane points to an Alpine ecological setting with forests and open areas. Several identified bird species (rock ptarmigan, black grouse, Boreal owl, bearded vulture, white-backed woodpecker, red and yellow-billed chough, Northern nutcracker and white-winged snowfinch) currently live in Italy at considerably higher altitudes than Fumane. The presence of their fossil remains at 350 m asl suggests the downward shifting of the vegetational zones during MIS 3 due to a decrease in climate value parameters. The presence of remains probably belonging to willow grouse in layer A6 and to parrot crossbill in layers A1 + A2 during two of the harsher climatic phases (Heinrich Event 5 and Heinrich Event 4 respectively) (López-García et al., 2015) might be an example of two boreal species seeking a *refugium* in Mediterranean Europe (Tyrberg, 1991; Carrera et al., 2018a,b).

The relative frequency of species related to forest, open, rocky and water environments calculated for each layer (Fig. 7) suggests the presence of temperate conditions for layer A9, followed by a colder climate in A6. The species linked to open environments decline sharply in layer A4 (attributed to the GI12 interstadial) before increasing anew in layer A3, marking the beginning of Heinrich Event 4 that lasts until

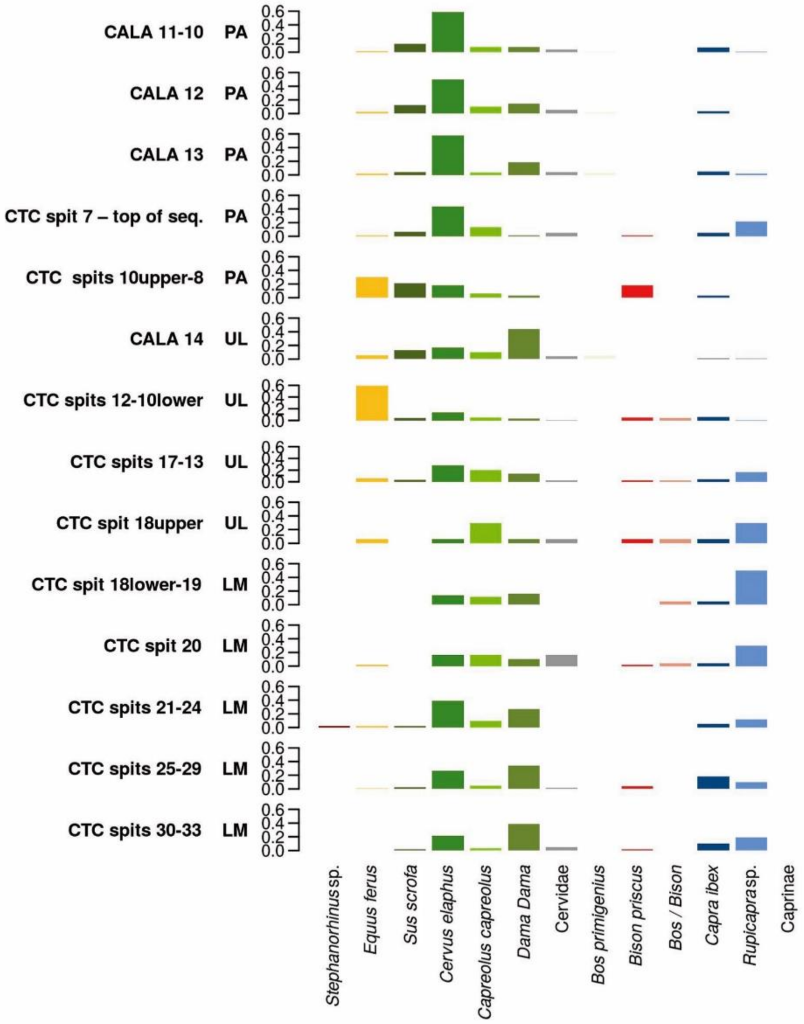


**Fig. 5.** Bar charts showing the relative contribution of each ungulate taxon to the total NISP recorded in the different levels and layers sampled in Southwestern Italy (Tyrrhenian Area). Contexts are presented in chronological-cultural order (from bottom to top) based on the archaeological sequence of each site. CTC = Grotta di Castelcivita; CALA = Grotta della Cala. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

the end of the sequence (López-García et al., 2015). Heinrich Event 4, however, did not prevent the persistence of open forests, as attested by the bird taxa found in A1 + A2 and A3. The apparent increase of forest bird taxa in the layers corresponding to Heinrich Event 4 could be explained by a switch from anthropic to natural accumulation in the Protoaurignacian, as suggested by the lack of anthropic marks on bird bones.

Turning to Grotta di Castelcivita, while the bird remains have been the object of a recent taphonomic revision (Fiore et al., 2019), the data discussed here are drawn from Cassoli and Tagliacozzo (1997). All identified taxa belong to the extant Italian avifauna (Table A.8 and Fig. 8, Cassoli and Tagliacozzo, 1997; Brichetti and Fracasso, 2015; Gala et al., 2018). In terms of NISP, the vast majority are from open and rocky environments. The presence of extensive wetlands and marshes near the cave is suggested by several duck, wader and gull species (*A. nyroca*, *S. querquedula*, *M. strepera*, *M. penelope*, *A. platyrhynchos*, *A. crecca*, *P. squatarola*, *N. phaeopus*, *L. limosa*, *A. interpres*, *C. pugnax*, *G. media*, *L. ridibundus*). The red-billed chough (*P. pyrrhocorax*), yellow-billed chough (*P. graculus*) and Eurasian crag martin (*P. rupestris*) are indicative of rocky cliffs, while rock partridge (*A. graeca*) attests to the presence of treeless rocky terrain. Open areas such as grasslands, steppe and shrublands were also present, as indicated by the common quail (*C. coturnix*), grey partridge (*P. perdix*), Eurasian thick-knee (*B. oedicnemus*), and little owl (*A. noctua*). The stock dove (*C. oenas*) and tawny owl (*S. aluco*) are associated with wooded areas, while the presence of the northern nutcracker (*N. caryocatactes*) suggests the presence of coniferous forests (Cramp, 1998) and confirms that, in the past, this species was distributed across a much broader area than today (Gala and Tagliacozzo, 2010; Brichetti and Fracasso, 2011). The surroundings of Castelcivita were therefore characterised during MIS 3 by extensive wetlands in plain areas, and by drier environments (such as grasslands, bare terrains and cliffs) intermingled with conifer or mixed forests at higher elevations. The presence at about 100 m asl of species that currently live at higher altitudes (rock partridge, choughs and northern nutcracker), suggests colder and harsher conditions during the whole sequence. In the Uluzzian layer rpi, the number of bird taxa related to open environments increases and point to an expansion of grasslands linked to colder and more arid conditions possibly corresponding to the beginning of Heinrich Event 4 (or a preceding stadial), based on currently available dates (Fig. 8). In the Protoaurignacian layers, the riparian taxa slightly increase, as do those of forest environments in layer ars, probably indicating a climatic amelioration at the top of the sequence (Cassoli and Tagliacozzo, 1997; Gala et al., 2018). All phases provided evidence of human exploitation of at least some bird species (Fiore et al., 2019).

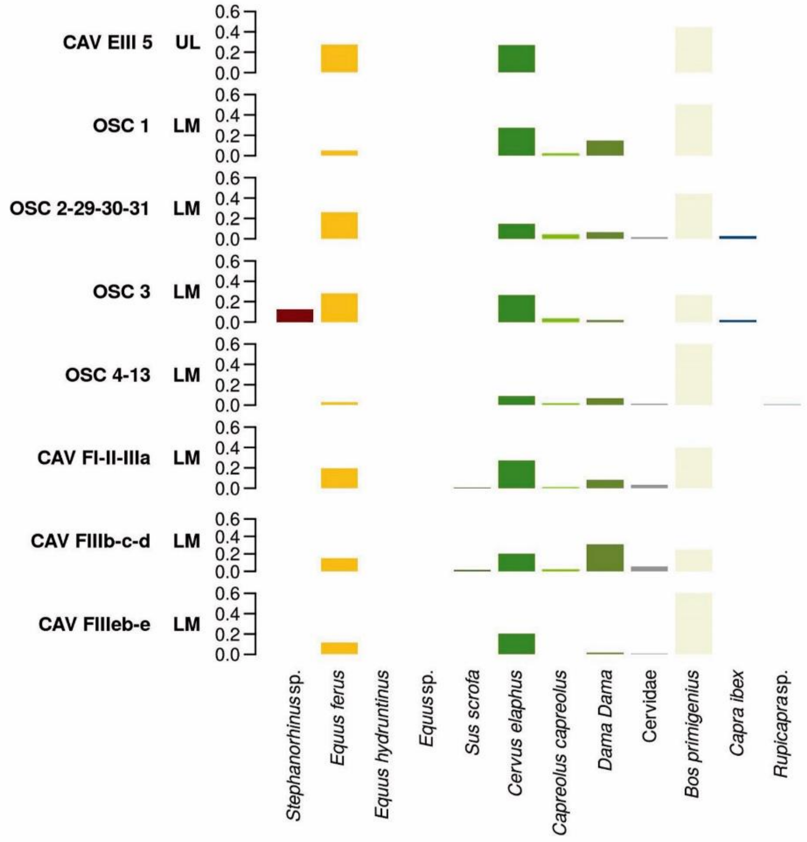


**Fig. 6.** Bar charts showing the relative contribution of each ungulate taxon to the total NISP recorded in the different levels and layers sampled in Southeastern Italy (Ionian-Adriatic area). Contexts are presented in chronological-cultural order (from bottom to top) based on the archaeological sequence of each site. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

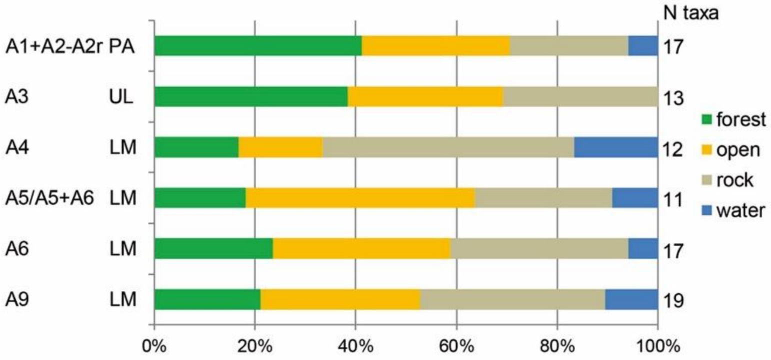


**Fig. 7.** % share of the bird taxa of different environments (see legend) in the various layers of Grotta di Fumane, calculated on the total number of bird taxa of each layer. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

### 4.3. Aoristic analysis

As far as estimated relative frequencies of ungulates are concerned, the resulting graph exhibits trends of change over time (Fig. 9 B). The estimates of *Capreolus* relative abundance are high at 47.6 ky while they decrease after ~45 ky. After ~45 ky the estimated remains of *Cervus elaphus* start becoming more abundant than in previous bins and reach their maximum between 45-44 ky. In bins following that date the presence of red deer starts declining in favour of *Capra ibex* and *Rupicapra rupicapra*. In the same time interval *Bos* and *Bison* show a quick unimodal trend. The apparent stability that emerges after ~40.5 ky it is due to the assumed uniform probability distribution in the absence of additional information on layer chronology. This trend, which can be noticed for all taxa, could be an artefact of uneven chronological sampling, and underscores the great temporal uncertainty associated with Protoaurignacian assemblages.

The distribution of relative carnivore estimates (Fig. 10) shows a marked increase in the presence of Ursidae between ~45 and ~43.6 ky. The relative frequency of wolves becomes higher than that of Ursidae between ~44.1 and 43.6 ky and becomes the highest value from 41.1 ky onwards. Foxes become most frequent when Ursidae increase and exhibit a inverse trend to that of wolf. From both an environmental and taphonomic point of view, it is interesting to note that after 41.6 ky the estimated relative frequency of *Crocuta crocuta spelaea* is considerably higher than in previous bins, including bins that record its presence between 47.6-46.6 ka.

Birds adapted to rocky environments are the most frequent at Fumane for the entire study sequence (Fig. 11). At 44.1 ky they exhibit a much lower estimate, while the percentage of avifaunal specimens linked to wooded/forested environments is higher than it was at the beginning of the sequence.

Rates of change based on simulated dates for ungulates (Figs. 9 and 11) add interesting elements and support this emerging scenario. When trends for ungulates are plotted against dummy sets based on estimated absolute frequencies of carnivores (i.e. of species with no particular links to change in environmental conditions), simulated 95% confidence envelopes exceed the expectations of the dummy model confidence area between 47.6-45.6 ky for bovids (Fig. 12 C). Although median values of simulated rates of change for all three ungulate families never emerge from the 95% dummy confidence envelope – suggesting the lack of significant deviations from a null model of deposition which is supposedly not based on environmental change – boxplots consistently point to the same chronological bins as the interesting ones. More specifically, there is evidence of a possible absolute increase in the frequency of all ungulate families between ~45.6-45.1 ky, while a decrease could be hypothesis between 45.1-44.1 ky (see Fig. 12).

Aoristic sum and simulated frequency estimates of all ungulates as a whole (Fig. 9 A) further support the hypothesis that at Grotta di Fumane there was an intensification of the deposition of ungulates between ca 45 and 44 ky, coinciding with higher percentages of red deer

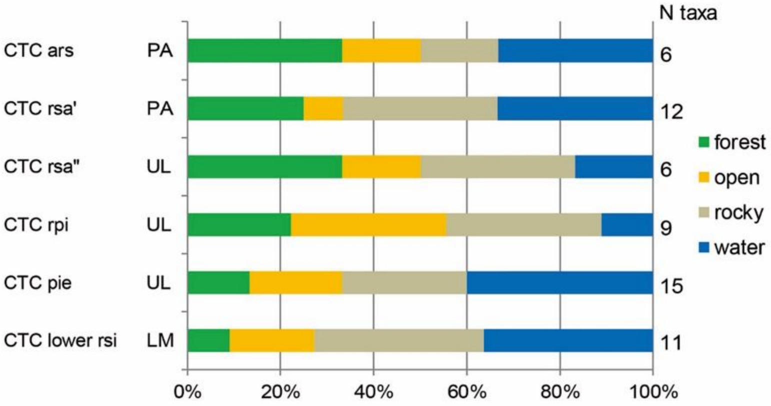


**Fig. 8.** % share of the bird taxa of different environments (see legend) in the various layers of Grotta di Castelcivita, calculated on the total number of bird taxa of each layer. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

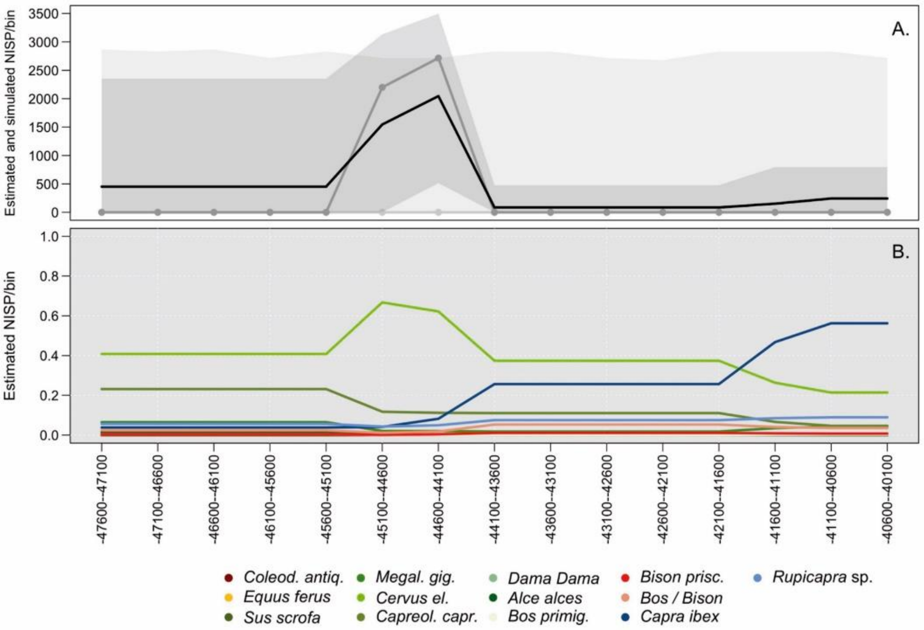


**Fig. 9.** A) Aoristic sum and estimated chronological frequency distribution of ungulates at Grotta di Fumane. The solid black line represents the aoristic sum, while the darker grey polygon indicates the simulated 95% confidence interval. The dark grey solid line-and-dots corresponds to simulated median values. The lighter grey envelope is instead the 95% confidence region of the null model based on uniform frequency distribution across the entire study period; B) Estimated diachronic relative frequency of each ungulate taxon based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP.

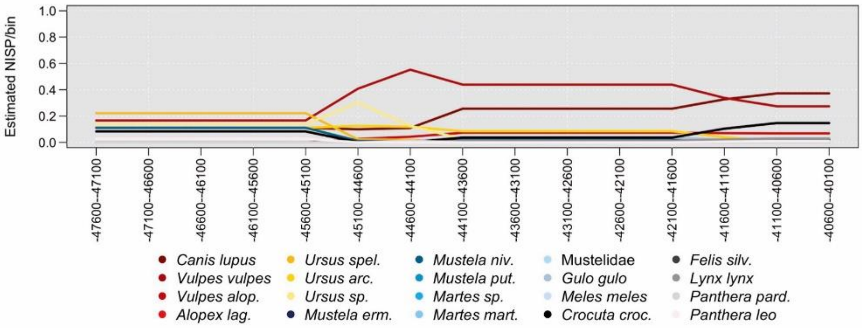


**Fig. 10.** Estimated diachronic relative frequency of each carnivore taxon at Grotta di Fumane, based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP.

in the assemblages. A second moment of more intense process could be identified between 41 and 39 ky, corresponding to higher percentages of *Capra ibex* and *Rupicapra rupicapra*. These trends confirm what emerged through the inspection of relative frequency estimates and of relative taxonomic abundance analysis, and hint at a potential change in environmental and climatic conditions in the region, but also point to a possible change in hunting and subsistence strategies, in particular by comparing ungulates, carnivores, and small preys from taxon abundance analysis.

### 4.4. Human exploitation of mammals

The vast majority of faunal remains uncovered in Northeastern Italy (up to 97% in some contexts) is highly fragmented, i.e. with length comprised between 0.1 and 3 cm. Intense fragmentation in Northeastern contexts may be imputed to the marrow extraction activity and the use of fire, also to trampling and a set of natural processes (Table 2 and A.13), but the potential influence of hyenas and other carnivores in specific layers (e.g. Grotta di Fumane USS A9-Mousterian, A3-Uluzzian, A2-Protoaurignacian; Table A.12) cannot be excluded, although, once estimated, it appears to be negligible. With the exception of Grotta del Rio Secco, burnt materials contribute to more than 50% of the total assemblage only in a few Late Mousterian contexts (Table 2). The proportion of calcined bones is higher in Uluzzian layers than in Late Mousterian ones. The frequency of butchering cut marks is also higher in the same temporal interval, while the frequency of percussion marks is lower across the MP-UP transition (Table 3). In the same timeframe, most contexts exhibit higher numbers of cranial bones

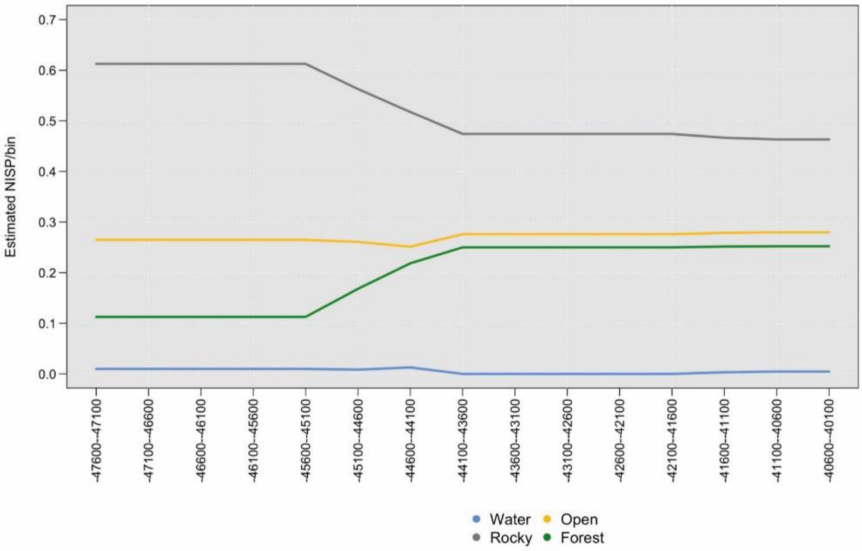


**Fig. 11.** Estimated diachronic relative frequency of avifaunal remains grouped by the relative environment, based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP.

and limb extremities, and lower frequency of long bone fragments (Table 4). In contrast, elements of the trunk are underrepresented in the whole sequence on all contexts (Table 4).

All ungulate species bear traces of human exploitation (Fig. 13), and anthropic modifications were aimed at obtaining skin, meat, and marrow. The density of wear traces is higher on tibias, femurs and metapodials, radii, and humeri from cervids (red deer, roe deer, and very large specimens of giant deer or moose), and to a lesser extent on the same portions of other ungulates, many of which were likely used as retouchers (Jéquier et al., 2018; Romandini et al., 2018a).

At the end of the Middle Palaeolithic (Fumane A6, A5 + A6; San Bernardino, Unit II), Ursidae (*Ursus spelaeus* and *Ursus arctos*) were heavily exploited for fur, meat and marrow, while red fox and beaver were hunted for their skins (Fig. 13). In the Uluzzian at Fumane (A3) there is clear evidence of skinning of foxes, *Canis lupus*, and *Ursus arctos*. (Tagliacozzo et al., 2013; Romandini, 2012; Romandini et al., 2014a, 2016a, 2018a, b). At the same site, the Protoaurignacian (A2) shows evidence of anthropic exploitation of all these carnivores (Fig. 13) with the addition of Eurasian lynx (*Lynx lynx*), while until now there is no evidence of exploitation of avifauna outside of the Mousterian and Uluzzian deposits (Peresani et al., 2011a; Tagliacozzo et al., 2013; Romandini et al., 2014b, 2016b; Fiore et al., 2004, 2016).

The southern Italian assemblages show the same high proportion of ungulates bearing traces of human exploitation as they do in northern Italy (Fig. 13). In addition, also in southern Italian contexts, the spectrum of hunted species mirrors coeval changes in climate and environment, and anthropic modifications are aimed at obtaining skins, meat, and marrow. It is interesting to note the low number of butchered small carnivores and lagomorph taxa, which are particularly concentrated in the Uluzzian and Protoaurignacian phases (Fig. 13). Grotta della Cala in southwestern/Tyrrhenian Italy exhibits increasingly higher percentages of phalanges and sesamoids across the Uluzzian, Protoaurignacian, Early Gravettian and Evolved Gravettian (Benini et al., 1997; Boscato et al., 1997; Boscato and Crezzini, 2006, 2012).

Taphonomic analysis was carried out on a sample of identified ungulate remains from the Late Mousterian (NISP = 67), Uluzzian (NISP = 251), and Protoaurignacian (NISP = 38) layers at Castelcivita (Southwestern Italy; Table 6). Specimens mostly consist of cranial and limb bones (especially metacarpals and metatarsals), while evidence of vertebral bones is limited. The frequency of small limb bones (phalanges, sesamoids, carpal, and tarsal) is higher in Uluzzian and Protoaurignacian layers than in Mousterian ones (Mousterian = 17.9%, Uluzzian = 20.3%, Protoaurignacian = 25%). The ratio of diaphysis/epiphysis fragments is lower in the Uluzzian and Protoaurignacian (4) than in the Late Mousterian (5.3). Anthropic marks were identified on 7.5% of remains in the Late Mousterian sample, on 10.6% of Uluzzian material, and have not been identified in the Protoaurignacian assemblage. Carnivore gnawing marks are fewer in the Protoaurignacian layers (2.6% of total material) and more abundant in the Late Mousterian (4.5%) and Uluzzian (7.7%) layers.

A sample of unidentified remains from the Mousterian levels of Castelcivita (n = 1920) is highly fragmented (91.9% falls in the class 1–3 cm) (Table 5). In this context diaphysis fragments are the most abundant (40.4%), followed by spongy bones (16%), rib fragments (14.7%), and epiphysis fragments (7.2%) (Tables A.10 and A.11). Anthropic marks are present on 2.8% of the unidentified material, while carnivores left traces on 1.5% of the remains (mostly vertebrae and epiphysis fragments).

As far as skeletal components of the most represented taxa are concerned (Table 7), results obtained at Castelcivita are consistent with what emerged from other southern contexts (Boscato and Crezzini, 2006, 2012), i.e. small limb bones (phalanges, sesamoids, carpals, and tarsals) and epiphyses are present with increasingly higher frequency across the archaeological sequence, while diaphysis fragments exhibit increasingly lower frequency (Tables 7, A.10 and A.11). Nevertheless, the estimate of the contribution of anthropic actions to the formation of faunal assemblages found at Castelcivita may be biased by the presence of spotted hyena (*Crocuta crocuta spelaea*).

Most unidentified specimens fall in the smallest dimensional category (1–3 cm), while the percentage of larger findings is higher in Uluzzian deposits (Table 5). Turning to Southeastern Italy, fragments of long bone diaphyses are abundant in the Mousterian assemblages of Riparo l'Oscurusciuto and Grotta del Cavallo whereas epiphysis fragments are rare. At Grotta del Cavallo, on the other hand, percentages of diaphysis fragments are lower in the Uluzzian than they are in the Late Mousterian ones (Table A.11; Boscato and Crezzini, 2006, 2012).

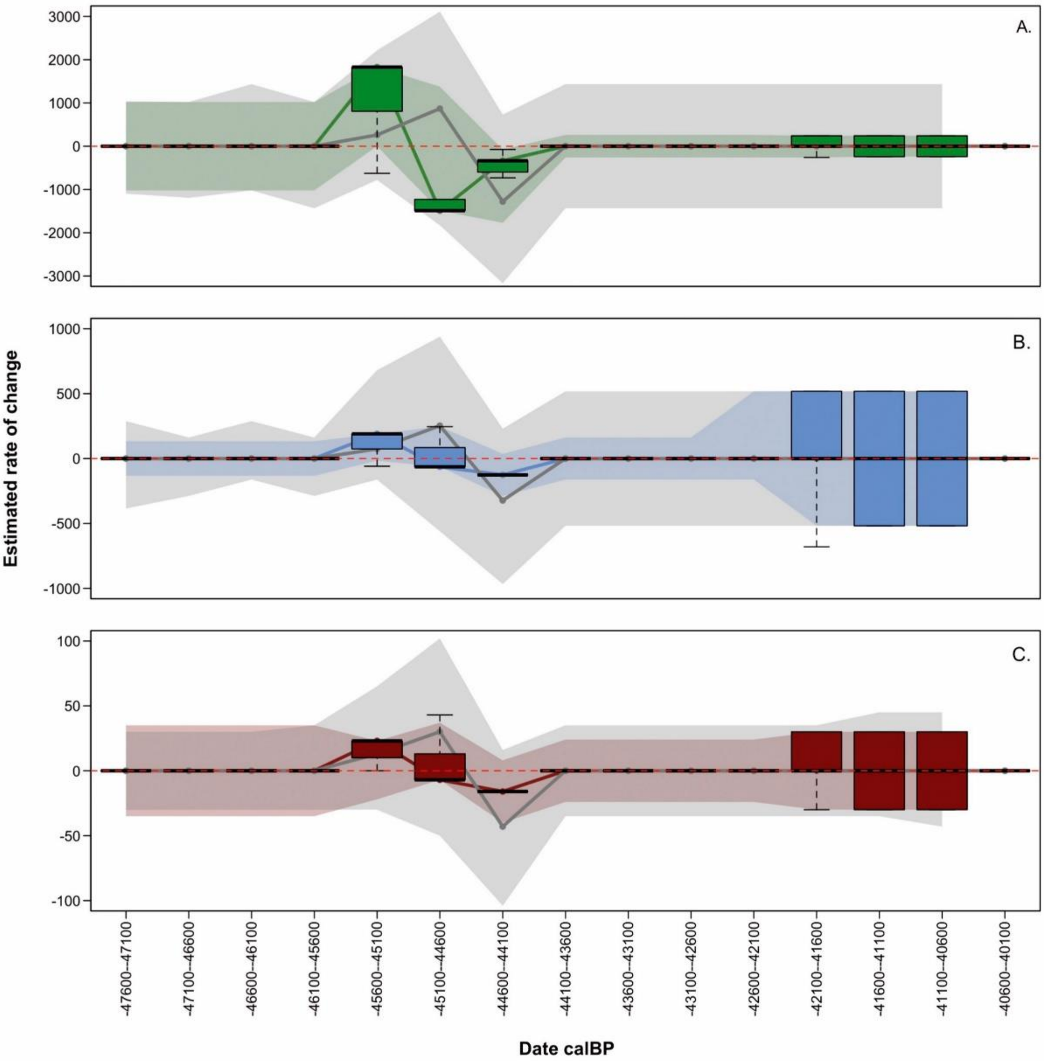


**Fig. 12.** Simulated diachronic rates of change computed for ungulate families at Grotta di Fumane. Box-plots and coloured polygons indicate the distribution of simulated rates of change based on observed family frequencies, while grey polygons represent 95% confidence regions for a null model based on the aoristic sums of carnivores uncovered at the same archaeological site. A (green): Cervidae; B (blue): Caprinae; C (red): Bovinae. Based on 5000 simulation runs and computed at 500-year bin resolution. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Considering Riparo Oscurusciuto and Grotta del Cavallo (where bone assemblages are not biased by the action of carnivores), the observed differences between the Late Mousterian and the Uluzzian in the proportion of diaphysis, spongy-bone and phalanges are statistically significant (Tables A.14, A.15, A.16 and A.17). As far as the degree of fragmentation is concerned, it is important not to directly compare any of the (preliminary) values currently available for Southern assemblages with those presented for the northern regions.

## 5. Discussion

### 5.1. *Comparison of taxon frequencies in macro-mammals between Northeastern, Southwestern, and Southeastern Italy*

Mammal assemblages show that the Middle to Upper Palaeolithic Transition in Northern Italy was associated with a shift to colder and arid climatic conditions, as previously observed by Fiore et al. (2004) and Holt et al. (2019). In Northeastern Italy, human groups used rock shelters in the prealpine fringe and in the alpine foreland and exploited closed forest environments. The surroundings of such shelters were characterised by open environments, alpine meadows and cliffs populated by herbaceous and shrubby species, while humans had to share

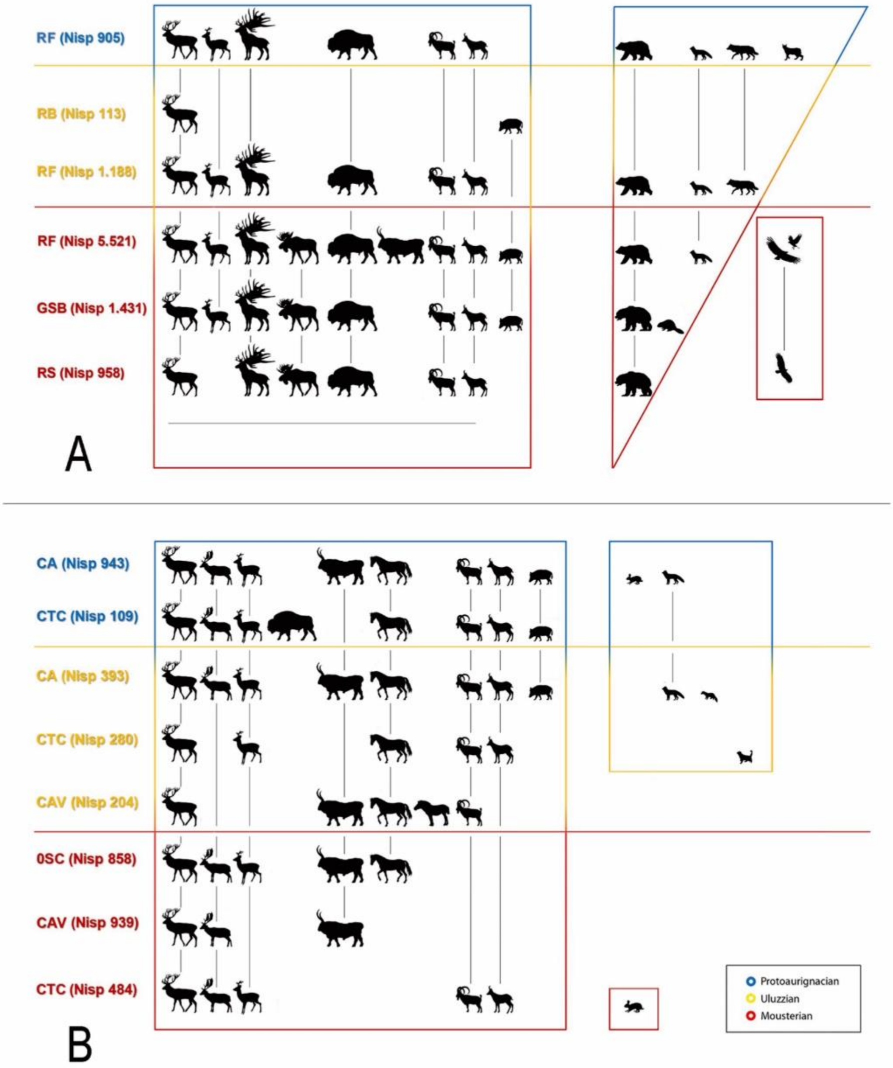


**Fig. 13.** Comparative summary of diachronic trends concerning the presence of taxa whose bones bear cut-marks, percussion marks and/or evidence of combustion. A) Northern Italy. RF = Grotta di Fumane; RB = Riparo del Broion; GSB = Grotta di San Bernardino; RS = Grotta del Rio Secco. B) Southern Italy. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto; CTC = Grotta di Castelcivita; CA = Grotta della Cala. Colors of temporal phases: Protoaurignacian = blue; Uluzzian = yellow; Late Mousterian = red (for interpreting the color coding in the figure legend the reader is referred to the Web version of this article).

and compete for their shelters with bears (Romandini et al., 2018a). At the end of Middle Palaeolithic, the examined faunal assemblages are dominated by cervidae while species adapted to open environments became considerably less abundant, suggesting a gradual change towards more temperate-humid climate which favoured the expansion of forests and wooded environments before the Uluzzian (such as in Fumane A4). Uluzzian and Protoaurignacian (e.g. Fumane A2) layers bear instead evidence of an abrupt shift to colder and arid conditions, which favoured the diffusion of steppic environments and alpine meadows. These observations are supported by the relative frequencies of cervids and caprids, both of which appear in higher percentages in moments of higher absolute intensity of deposition of ungulate remains. Caprids and bovids also show instances of increase and decrease that are not entirely predicted by the null model based on the distribution of carnivores (i.e. might actually be related to change in environmental conditions).

The aoristic analysis of Grotta di Fumane's zooarchaeological data confirm some of the trends observed by investigating taxon frequency across different sites of Northeastern Italy, especially in the first half of the study sequence. In addition, the comparison of simulated trends against null models based on constant deposition and on the aoristic sum of carnivores provides a means to more formally assess empirical patterns against explicit scenarios. This is particularly useful in a case study affected by small sample size and limited data comparability such as the present one. Most trends appear flattened in the aoristic sum graph, since the analysis explicitly incorporates the temporal uncertainty embedded in the present dataset. Nevertheless, the adoption of this approach paves the

**Table 3**
Number of remains (NR) and relative % with anthropic modifications identified in the MP/UP transition from Northern Italian sites (see Fig.1 - Area 1). RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. CM = Cut Marks; SCR. = Scrapings; IF = Impact Flakes; PM = Percussion Marks; BM = Butchering Marks.

| MODIF. | RS 5 + 8 LM | | RF A9 LM | | RF A6 LM | | RF A5 LM | | RS 5top + 7 LM | | SB II + III LM | | RF A4 LM | | RB 1e + 1f + 1g UL | | RF A3 UL | | RF A2 PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % |
| CM + SCR | 61 | 63.5 | 882 | 53.5 | 1003 | 37.8 | 399 | 35.5 | 76 | 67.3 | 92 | 54.8 | 626 | 68.9 | 16 | 59.3 | 289 | 53.4 | 348 | 64.7 |
| CM + IF/CM + PM | 10 | 10.4 | 143 | 8.7 | 171 | 6.5 | 50 | 4.4 | 20 | 17.7 | 14 | 8.3 | 128 | 14.1 | | | 106 | 19.6 | 30 | 5.6 |
| IF + PM | 25 | 26 | 623 | 37.8 | 1477 | 55.7 | 676 | 60.1 | 17 | 15 | 62 | 36.9 | 154 | 17 | 11 | 40.7 | 146 | 27 | 160 | 29.7 |
| TOTAL BM | 96 | | 1648 | | 2651 | | 1125 | | 113 | | 168 | | 908 | | 27 | | 541 | | 538 | |

ground for future direct comparisons between northern and southern contexts by highlighting long-term processes that can be directly compared against palaeoecological and palaeoclimatic data collected from a variety of archives, so that future inferences on change in adaptive strategies can be more objective. Additional dates and more detailed information on taphonomy and post-depositional processes will also help shed light on the mechanisms actually underlying the potential diachronic change for Protoaurignacian contexts.

In southern Italy, Late Mousterian deposits exhibit evidence of generally temperate conditions. In this phase, cervids are the most common ungulates in the Tyrrhenian region, while *Bos primigenius* is the most represented species in Ionian contexts. At Grotta di Castelcivita, this phase is characterised by the same palaeoenvironmental trend documented at Fumane.

The Uluzzian phases at Grotta del Cavallo and Grotta di Castelcivita show data compatible with the establishment of a colder climate, while human groups active at Grotta della Cala experienced more temperate conditions. During MIS 3, the Tyrrhenian side appears to be still characterised by temperate and humid conditions favouring forests and wooded environments, while the Ionian areas were marked by steppic environments and wooded steppe.

Outside of the Italian Peninsula, the only possible comparisons in terms of temporal span and of an archaeological sequence comprising Late Mousterian – Uluzzian – Protoaurignacian (only Aurignacian in Greece) It's represented by Kephalari and Klissoura Cave, Peloponnese, Greece (Starkovich, 2012; Starkovich and Ntinou, 2017; Starkovich et al., 2018). Especially at the latter site, the MIS 3 was highly variable, as suggested by evidence of variation between forested environments, mixed forest-steppe (with red deer, roe deer, chamois and ibex), and drier intervals with steppe species (such as European wild ass, aurochs, ibex and great bustard). The Uluzzian (V) and Aurignacian (IV) layers yielded evidence of fallow deer and small game, in addition to species adapted to both open and forested environments. Plants indicate a mixture of forest and steppe, although taxonomic evenness suggests that conditions were slightly wetter in the Uluzzian layers than during the final MP occupations.

If we exclude Upper Palaeolithic layers of both Kephalari and Klissoura Cave, the exploitation of small game across the transition between Middle and Upper Palaeolithic could be linked to coeval environmental change and a change in resource availability, as it is suggested by the remains of tortoise and hare identified at Klissoura Cave1 in assemblages associated with Neandertals (Starkovich, 2012, 2017, Starkovich et al., 2018). The range of hunted taxa in this region therefore seems to be stable across the Middle and Upper Palaeolithic, and trends can be ascribed to species availability dictated by environmental and climatic change, rather than to convergence in hunting strategies with the Italian Peninsula (Starkovich et al., 2018; Stiner and Munro, 2011). At present a more detailed comparison between the exploitation of animal remains documented in Italy and Greece is not yet possible as research on the subject is still in progress and additional data are required. Nevertheless, trends emerging from taxon abundance analysis are broadly comparable to those identified for Southwestern and Southeastern Italy and documented in the present work. On the other hand, preliminary results presented here suggest in Middle to UP transition a more intensive exploitation of small game in Northeastern Italy than in Southern contexts and the Peloponnese. This finding might be particularly relevant for interpreting regional patterns of change in subsistence/adaptive strategies, considering that large game is generally considered a higher-rank resource than small game.

### 5.2. Comparison of avifaunal remains between Fumane and Castelcivita

The avifaunal assemblages of Grotta di Fumane and Grotta di Castelcivita provide relevant insights on the paleoenvironmental and palaeoclimatic framework of both deposits. The surroundings of Fumane were characterised by mixed and conifer forests, grasslands and alpine meadows with rocky outcrops, cliffs and slow-flowing water

**Table 4**
Number of remains and relative % of the specific anatomical elements, referring to the most represented mammals species present in the layers and levels analysed in MP/UP transition Northern Italian sites (see Fig. 1 – Area 1). The subtotals of the different anatomical compartments are reported at the bottom of the table. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

| TECHNOCOMPLEX | LM | | LM | | LM | | LM | | LM | | LM | | LM | | LM | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE - US/Lev. | RS 5+8 | | RF A9 | | RF A9 | | RF A6 | | RF A6 | | RF A5 | | RF A5 | | RS 5top+7 | |
| *Taxa* | *Ursus* sp. | | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *C. capreolus* | | *Ursus* sp. | |
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| Cranium | 14 | 6.4 | 23 | 4.6 | 7 | 2.5 | 43 | 3.8 | 6 | 3.3 | 10 | 3.2 | 1 | 2 | 18 | 8.3 |
| Emimandible | 21 | 9.6 | 35 | 7.1 | 16 | 5.7 | 64 | 5.6 | 6 | 3.3 | 19 | 6.1 | 7 | 14 | 13 | 6 |
| Tooth indet. | 14 | 6.4 | 14 | 2.8 | 6 | 2.1 | 17 | 1.5 | 1 | 0.5 | 1 | 0.3 | | | 2 | 0.9 |
| Hioyd | 6 | 2.8 | | | | | 1 | | | | 2 | 0.6 | | | 2 | 0.9 |
| Atlas-axis | 2 | 0.9 | | | | | 1 | 0.1 | | | | | | | 3 | 1.4 |
| Vertebra | 21 | 9.6 | 3 | 0.6 | 2 | 0.7 | 7 | 0.6 | 1 | 0.5 | 2 | 0.6 | | | 12 | 5.6 |
| Rib | 39 | 17.9 | 4 | 0.8 | 2 | 0.7 | 7 | 0.6 | | | 1 | 0.3 | | | 54 | 25 |
| Clavicle | | | | | | | | | | | | | | | 1 | 0.5 |
| Baculum | 1 | 1.6 | | | | | | | | | | | | | 2 | 0.9 |
| Scapula | 3 | 6.1 | | | | | 4 | 0.4 | 1 | 0.5 | | | | | 3 | 1.4 |
| Humerus | 2 | 0.9 | 27 | 5.5 | 12 | 4.3 | 89 | 7.8 | 5 | 2.7 | 24 | 7.7 | 1 | 6.25 | 3 | 1.4 |
| Radius/Ulna | | | | | | | 3 | | | | 1 | 0.3 | | | | |
| Radius | 3 | 1.4 | 29 | 5.9 | 10 | 3.6 | 69 | 6.1 | 6 | 3.3 | 14 | 4.5 | 1 | 2 | 15 | 6.9 |
| Ulna | 6 | 2.8 | 4 | 0.8 | 1 | 0.4 | 26 | 2.3 | 3 | 1.6 | 3 | 1 | | | 4 | 1.9 |
| Carpals | 6 | 2.8 | | | 6 | 2.1 | 8 | 0.7 | 5 | 2.7 | 1 | 0.3 | | | 7 | 3.2 |
| Metacarpal | 4 | 1.8 | 55 | 11.1 | 32 | 11.4 | 123 | 10.8 | 19 | 10.4 | 40 | 12.9 | 11 | 22 | 12 | 5.6 |
| Metacarpal rud. | | | | | 4 | 1.4 | 6 | 0.5 | 1 | 0.5 | | | 1 | 2 | | |
| Coxal | | | 4 | 0.8 | | | 5 | 0.4 | 2 | 1.1 | 1 | 0.3 | | | | |
| Femur | 28 | 12.8 | 44 | 8.9 | 17 | 6 | 117 | 10.3 | 11 | 6 | 27 | 8.7 | 3 | 6 | 24 | 11.1 |
| Patella | 1 | 0.5 | | | 1 | 0.4 | | | | | 1 | 0.3 | 1 | 2 | | |
| Tibia | 10 | 4.6 | 96 | 19.4 | 38 | 13.5 | 181 | 15.9 | 15 | 8.2 | 49 | 15.8 | | | 8 | 3.7 |
| Fibula | 4 | 1.8 | | | | | | | | | | | | | 4 | 1.9 |
| Malleolar bone | | | | | | | 2 | 0.2 | 2 | 1.1 | | | | | | |
| Calcaneum | | | 1 | 0.2 | | | | | 1 | 0.5 | | | | | 2 | 0.9 |
| Astragalus | | | | | | | 1 | 0.1 | 2 | 1.1 | | | | | 1 | 0.5 |
| Tarsals | 1 | 0.5 | 2 | 0.4 | 1 | 0.4 | 3 | 0.3 | 2 | 1.1 | 2 | 0.6 | | | 3 | 1.4 |
| Metatarsal | 5 | 2.3 | 76 | 15.4 | 59 | 21 | 131 | 11.5 | 29 | 15.9 | 54 | 17.4 | 8 | 16 | 1 | 0.5 |
| Metapodial | 2 | 0.9 | 25 | 5.1 | 11 | 3.9 | 45 | 3.9 | 6 | 3.3 | 13 | 4.2 | 1 | 2 | | |
| First phal. | 11 | 5 | 11 | 2.2 | 21 | 7.5 | 28 | 2.5 | 7 | 3.8 | 10 | 3.2 | 1 | 2 | 8 | 3.7 |
| Second phal. | 6 | 2.8 | 12 | 2.4 | 9 | 3.2 | 50 | 4.4 | 15 | 8.2 | 16 | 5.1 | 6 | 12 | 8 | 3.7 |
| Third phal. | 6 | 2.8 | 4 | 0.8 | 4 | 1.4 | 28 | 2.5 | 1 | 0.5 | 6 | 1.9 | 2 | 4 | 6 | 2.8 |
| First phal. rud. | | | 3 | 0.6 | 4 | 1.4 | 9 | 0.8 | 4 | 2.2 | | | | | | |
| Sec. phal. rud. | | | 5 | 1 | 4 | 1.4 | 14 | 1.2 | 7 | 3.8 | 3 | 1 | 2 | 4 | | |
| Th. phal. rud. | | | 4 | 0.8 | 7 | 2.5 | 9 | 0.8 | 3 | 1.6 | 3 | 1 | | | | |
| Sesamoid | 2 | 0.9 | 14 | 2.8 | 7 | 2.5 | 49 | 4.3 | 21 | 11.5 | 8 | 2.6 | 4 | 8 | | |
| TOTAL | 218 | | 495 | | 281 | | 1140 | | 182 | | 311 | | 50 | | 216 | |
| Tot Cranium + - tooth | 55 | 25.2 | 72 | 14.5 | 29 | 10.3 | 125 | 11 | 13 | 7.1 | 32 | 10.3 | 8 | 16 | 35 | 16.2 |
| Tot trunk | *63* | *28.9* | *7* | *1.4* | *4* | *1.4* | *15* | *1.3* | *1* | *0.5* | *3* | *1* | | | *72* | *33.3* |

(continued on next page)

**Table 4** (*continued*)

| TECHNOCOMPLEX | LM | | LM | | LM | | LM | | LM | | LM | | LM | | LM | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE - US/Lev. | RS 5 + 8 | | RF A9 | | RF A9 | | RF A6 | | RF A6 | | RF A5 | | RF A5 | | RS 5top + 7 | |
| *Taxa* | *Ursus* sp. | | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *C. capreolus* | | *Ursus* sp. | |
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| Tot long limb bones | *68* | *35.9* | *360* | *72.9* | *185* | *65.8* | *799* | *70.1* | *98* | *56.6* | *227* | *73* | *27* | *58.3* | *74* | *35.6* |
| Carpal + tarsal | *7* | *3.2* | *3* | *0.4* | *7* | *2.5* | *14* | *1* | *12* | *3.8* | *3* | *1* | | | *13* | *4.6* |
| Phalan + sesamoides | *25* | *11.5* | *53* | *10.7* | *56* | *19.9* | *187* | *16.4* | *58* | *31.9* | *46* | *14.8* | *15* | *30* | *22* | *10.2* |

| TECHNOCOMPLEX | LM | | LM | | LM | | LM | | UL | | UL | | UL | | PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE - US/Lev. | SB II + III | | SB II + III | | RF A4 | | RF A4 | | RB 1f + 1g | | RF A3 | | RF A3 | | RF A2 | |
| *Taxa* | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *Capra ibex* | | *Sus scrofa* | | *C. elaphus* | | *Capra ibex* | | *Capra ibex* | |
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| Cranium | 15 | 11.3 | 18 | 7.5 | 10 | 4.6 | 7 | 9.5 | 1 | 4.2 | 7 | 3.8 | 15 | 12.9 | 6 | 4.6 |
| Emimandible | 32 | 24.1 | 36 | 15.1 | 14 | 6.4 | 15 | 20.3 | 1 | 4.2 | 10 | 5.5 | 22 | 19 | 13 | 10 |
| Tooth indet. | | | 8 | 3.3 | 13 | 6 | 3 | 4.1 | 3 | 12.5 | 24 | 13.2 | 3 | 2.6 | 7 | 5.4 |
| Hioyd | 1 | 0.8 | | | | | | | | | 2 | 1.1 | | | 1 | 0.8 |
| Atlas-axis | | | | | | | | | | | | | | | | |
| Vertebra | | | | | 2 | 0.9 | | | | | 2 | 1.1 | 1 | 0.9 | 3 | 2.3 |
| Rib | 1 | 0.8 | | | 1 | 0.5 | | | | | | | | | | |
| Clavicle | | | | | | | | | | | | | | | | |
| Baculum | | | | | | | | | | | | | | | | |
| Scapula | | | | | | | 1 | 1.4 | | | 3 | 1.6 | | 0 | 2 | 1.5 |
| Humerus | 5 | 3.8 | 2 | 0.8 | 6 | 2.8 | 4 | 5.4 | | | 9 | 4.9 | 4 | 3.4 | 6 | 4.6 |
| Radius/Ulna | 3 | 2.3 | | | | | 2 | 2.7 | | | | | 1 | 0.9 | | |
| Radius | 3 | 2.3 | 2 | 0.8 | 10 | 4.6 | 2 | 2.7 | 1 | 4.2 | 5 | 2.7 | 3 | 2.6 | 6 | 4.6 |
| Ulna | 4 | 3 | 2 | 0.8 | 6 | 2.8 | | | | | 2 | 1.1 | 1 | 0.9 | 2 | 1.5 |
| Carpals | 1 | 0.8 | 1 | 0.4 | 1 | 0.5 | 4 | 5.4 | | | 1 | 0.5 | 9 | 7.8 | 3 | 2.3 |
| Metacarpal | 6 | 4.5 | 12 | 5 | 19 | 8.7 | 2 | 2.7 | 1 | 4.2 | 16 | 8.8 | 6 | 5.2 | 4 | 3.1 |
| Metacarpal rud. | | | 5 | 2.1 | | | | | | | | | | | 4 | 3.1 |
| Coxal | 1 | 0.8 | | | 1 | 0.5 | 2 | 2.7 | | | 2 | 1.1 | 3 | 2.6 | | |
| Femur | 6 | 4.5 | 3 | 1.3 | 17 | 7.8 | 2 | 2.7 | | | 9 | 4.9 | 10 | 8.6 | 5 | 3.8 |
| Patella | | | 1 | 0.4 | | | | | | | | | | | | |
| Tibia | 8 | 6 | 3 | 1.3 | 16 | 7.3 | 4 | 5.4 | | | 18 | 9.9 | 5 | 4.3 | 6 | 4.6 |
| Fibula | | | | | | | | | | | | | | | | |
| Malleolar bone | | | | | 2 | 0.9 | 1 | 1.4 | | | | | | | 1 | 0.8 |
| Calcaneum | | | 1 | 0.4 | 1 | 0.5 | | | | | | | | | 1 | 0.8 |

(continued on next page)

**Table 4** (*continued*)

| TECHNOCOMPLEX | LM | | LM | | LM | | LM | | UL | | UL | | UL | | PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE - US/Lev. | SB II + III | | SB II + III | | RF A4 | | RF A4 | | RB 1f +1g | | RF A3 | | RF A3 | | RF A2 | |
| *Taxa* | *C. elaphus* | | *C. capreolus* | | *C. elaphus* | | *Capra ibex* | | *Sus scrofa* | | *C. elaphus* | | *Capra ibex* | | *Capra ibex* | |
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| Astragalus | 1 | 0.8 | 1 | 0.4 | | | | | | | 1 | 0.5 | | | 3 | 2,3 |
| Tarsals | 2 | 1.5 | 1 | 0.4 | | | 2 | 2.7 | | | | | 1 | 0.9 | 4 | 3.1 |
| Metatarsal | 12 | 9 | 28 | 11.7 | 41 | 18.8 | 2 | 2.7 | 3 | 12.5 | 29 | 15.9 | 4 | 3.4 | 3 | 2.3 |
| Metapodial | 2 | 1.5 | 9 | 3.8 | 9 | 4.1 | | | 3 | | 10 | 5.5 | 4 | 3.4 | 2 | 1.5 |
| First phal. | 8 | 6 | 35 | 14.6 | 7 | 3.2 | 8 | 10.8 | 3 | 12.5 | 4 | 2.2 | 4 | 3.4 | 12 | 9.2 |
| Second phal. | 9 | 6.8 | 24 | 10 | 15 | 6.9 | 3 | 4.1 | 3 | 12.5 | 10 | 5.5 | 3 | 2.6 | 9 | 6.9 |
| Third phal. | 3 | 2.3 | 13 | 5.4 | 4 | 1.8 | 1 | 1.4 | 1 | 4.2 | 5 | 2.7 | 2 | 1.7 | 6 | 4.6 |
| First phal. rud. | 1 | 0.8 | 4 | 1.7 | 2 | 0.9 | | | 3 | 12.5 | 2 | 1.1 | | | | |
| Sec. phal. rud. | | | 7 | 2.9 | 8 | 3.7 | | | | | 4 | 2.2 | | | | |
| Th. phal. rud. | 3 | 2.3 | 4 | 1.7 | 2 | 0.9 | | | | | 3 | 1.6 | | | | |
| Sesamoid | 6 | 4.5 | 19 | 7.9 | 11 | 5 | 9 | 12.2 | 1 | 4.2 | 4 | 2.2 | 15 | 12.9 | 21 | 16.2 |
| TOTAL | 133 | | 239 | | 218 | | 74 | | 24 | | 182 | | 116 | | 130 | |
| Tot Cranium + - tooth | 48 | 36.1 | 62 | 25.9 | 37 | 17 | 25 | 33.8 | 5 | 20.8 | 43 | 23.6 | 40 | 34.5 | 27 | 20.8 |
| Tot trunk | *1* | *0.8* | | | *3* | *1.4* | | | | | *2* | *1.1* | *1* | *0.9* | *3* | *2.3* |
| Tot long limb bones | *50* | *38.3* | *67* | *28.9* | *125* | *58.7* | *21* | *29.7* | *8* | *20.8* | *103* | *57.1* | *41* | *35.3* | *40* | *34.6* |
| Carpal + tarsal | *4* | *2.3* | *4* | *0.8* | *4* | *0.5* | *7* | *8.1* | | | *2* | *0.5* | *10* | *8.6* | *12* | *5.4* |
| Phalan + sesamoides | *30* | *22.6* | *106* | *44.4* | *49* | *22.5* | *21* | *28.4* | *11* | *45.8* | *32* | *17.6* | *24* | *20.7* | *48* | *36.9* |

**Table 5**

Size classes of mammals bones and relative frequency of burnt remains identified in the LM and UL layers sampled in Southern Italian sites (see Fig. 1 – Area 2 + 3). CAV = Grotta del Cavallo; CTC = Grotta di Castelcivita; OSC = Grotta l'Oscurusciuto.

| SITE<br>US - Levels | Technocomplex | 1–3 cm | % | > 3 cm | % | TOTAL Rem. | Burn. + Calc. | % |
|---|---|---|---|---|---|---|---|---|
| CAV EIII | UL | 4201 | 79.9 | 984 | 20.1 | 5185 | 3452 | 82.2 |
| CTC LM | LM | 1764 | 91.9 | 156 | 8.1 | 1920 | Not avail. | Not avail. |
| CAV FII | LM | 9836 | 87.7 | 1378 | 12.3 | 11214 | 1744 | 17.7 |
| OSC US 4/1 | LM | 17472 | 97.4 | 449 | 2.6 | 17921 | 12137 | 67.7 |

**Table 6**

Number (NR) and relative frequency (%) of remains with identified anthropic modification documented in the MP/UP transitional contexts from the sampled Southern Italian sites (see Fig. 1 – Area 2 + 3). CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto; CTC = Grotta di Castelcivita. CM = Cut Marks; SCR. = Scrapings; IF = Impact Flakes; PM = Percussion Marks; BM = Butchering Marks.

| MODIF. | CTC LM | | CAV FII LM | | OSC US 4 LM | | CAV EII5 UL | | CTC UL | | CTC PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NR | % | NR | % | NR | % | NR | % | NR | % | NR | % |
| CM + SCR | 9 | 0.4 | 63 | 67 | 1 | 3.3 | 75 | 80.6 | 16 | 89 | 5 | 17.2 |
| CM + IF/CM + PM | 43 | 45.3 | 13 | 13.8 | 26 | 83.9 | 11 | 11.8 | 1 | 5.5 | 12 | 41.4 |
| IF + PM | 43 | 45.3 | 18 | 19.2 | 4 | 2.8 | 7 | 0.6 | 1 | 5.5 | 12 | 41.4 |
| TOTAL BM | 95 | | 94 | | 31 | | 93 | | 18 | | 29 | |

bodies. The environmental framework of Grotta di Castelcivita was instead characterised by wetlands in the plains in front of the cave and by drier habitats like grasslands, rocky terrains and rock walls, alternated to conifer or mixed forests at higher altitudes.

Bird taxa across Italy indicate the presence of a consistently colder climate than the present one. Nevertheless, in the southwestern/Tyrrhenian area (Fig. 1, Area 2) climate seems milder and more temperate than in the Adriatic area, as suggested by the absence of boreal bird species and by a lower proportion of high altitude bird taxa in the former. Once again, faunal assemblages mirror climatic differences between Tyrrhenian and Ionian/Adriatic regions mostly due to the effect of the Balkanic influence on the latter. The Middle Paleolithic assemblages from both sites provide evidence of temperate-cool climate, where the species of open and rocky habitats prevail. The Late Mousterian Layer A6 at Fumane hints at a possible cold oscillation, however, and the Uluzzian at both sites (A3 at Grotta di Fumane, and CTC rsi at Grotta di Castelcivita) shows higher percentages of bird taxa typical of open habitats possibly due to colder conditions linked to Heinrich Event 4 (Higham et al., 2009; Moroni et al., 2018; Lopéz-García et al., 2015). Protoaurignacian deposits provide evidence for the persistence of harsh conditions which characterized previous phases (Cassoli and Tagliacozzo, 1994a). In spite of the low NISP, one exception seems to be represented by the latest Protoaurignacian layers of Castelcivita (gic-ars; referring here particularly to the layer ars, as the bird bone sample of the layer gic was too small to include it in the analysis), that yielded evidence for climatic shift toward more humid conditions (Cassoli and Tagliacozzo, 1997; Gala et al., 2018).

### 5.3. *Taphonomy*

Despite the facts that taphonomic data are still only partially investigated in most of the sampled contexts and that the majority of identified patterns cannot be proven to be statistically significant because of small sample size, interesting preliminary trends emerge. Although future studies may alter the pattern detected so far, at present, the percentage of calcined remains during the Uluzzian and Protoaurignacian levels in Northeastern Italian contexts is higher than the frequency of the same items in previous phases, and hints at a possible behavioural change linked to the use of fire: greater intensity and duration of use of the hearths, differentiation of fuel and/or cooking of animal resources. Cut-marks are also more frequent across the transition, while the degree of bone fragmentation for marrow extraction is higher in Mousterian layers than in later deposits. In the Early Upper Palaeolithic overall (i.e., Uluzzian and Protoaurignacian) there are higher percentages of cranial bones and limb extremities, with a consequent lower proportion of long bones. This trend may be imputed partly to human selection and partly to the use of the cave by hyenas and other carnivores. The remains of the most frequently hunted large (Cervidae, Bovinae) and medium-sized (Caprinae) ungulates show cut- and percussion-marks, all of which point to skinning, butchering, and marrow extraction. Over the same timespan, bears and middle- and small-sized carnivores appear to be more frequently exploited, suggesting a broadening in the range of species hunted for skin and fur (Collard et al., 2016).

Avifaunal assemblages provide evidence of human consumption of birds and contribute to an understanding of the role of avifaunal resources in the subsistence strategies of Middle Palaeolithic hominins (Peresani et al., 2011a; Romandini, 2012; Tagliacozzo et al., 2013; Fiore et al in this issue; Romandini et al., 2014b, 2016a, b; Gala et al., 2018; Fiore et al., 2004, 2016). The exploitation of these resources is testified by recognizable taphonomic indicators such as evidence for the exploitation of feathers from various raptors and other birds.

In the same way, evidence of Neandertal reliance on small mammal prey increased over the past 10 years due to the reassessment of faunal assemblages from a new taphonomic perspective (Romandini et al., 2018b; Morin et al., 2019).

In Ionian contexts, Late Mousterian assemblages exhibit a lack (or at least a scarcity) of long-bone epiphyses, carpal and tarsal bones, phalanges and sesamoides. In the analysed Late Mousterian samples from Grotta del Cavallo and Riparo l'Oscurusciuto, this evidence cannot be attributed to carnivores, differential bone density and other post-depositional processes (Boscato and Crezzini, 2006, 2012). The frequency of different anatomical parts (% of Minimum Animal Units, Binford, 1984) of *Bos primigenius* and the modal species in US 4 at Riparo l'Oscurusciuto were compared against Emerson's utility indices related to present-day *Bison bison* (Emerson, 1990, 1993). Previous results suggest a relationship between bone frequency and their content in marrow and fat, which was probably crucial in

**Table 7**
Number of remains and relative % of specific anatomical elements referable to the most represented mammal species documented in the MP/UP transition layers and levels of Southern Italian sites (see Fig. 1 – Area 2 + 3). The subtotals of the different anatomical compartments are reported at the bottom of the table. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto; CTC = Grotta di Castelcivita; CALA = Grotta della Cala.

| TECHNOCOMPLEX | LM | | LM | | LM | | UL | | UL | | UL | | PA | | PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE - US/Lev. | OSC | | CTC | | CAV (all lev.) | | CAV EIII5 | | CTC | | CALA 14 | | CTC ars-gic | | CALA 13-10 | |
| TAXA | *Bos primig.* | | *Dama dama* | | *Bos primig.* | | *Bos primig.* | | *C. elaphus* | | *Dama dama* | | *C. elaphus* | | *C. elaphus* | |
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| Antler/Horn | | | | | | | | | 3 | 3.2 | | | | | 1 | 0.2 |
| Cranium | 13 | 2.6 | 4 | 2.8 | 3 | 0.8 | 2 | 2.3 | 1 | 1 | 5 | 3.4 | | | 17 | 3.5 |
| Emimandible | 43 | 8.7 | 9 | 6.3 | 12 | 3 | | | 4 | 4.4 | 13 | 8.7 | 1 | 4.3 | 42 | 8.8 |
| Decidous teeth | 8 | 1.6 | 9 | 6.3 | 49 | 12.4 | 1 | 1.2 | 2 | 2.1 | | | 2 | 8.7 | | |
| Permanent teeth | 202 | 40.6 | 60 | 41.7 | 201 | 51 | 10 | 11.6 | 7 | 7.5 | | | 8 | 34.8 | | |
| Perm. + Deciduos teeth | 11 | 2.2 | | | | | | | | | 46 | 30.9 | | | 133 | 27.8 |
| Tooth indet. | 47 | 9.5 | 10 | 6.9 | 21 | 5.3 | 5 | 5.8 | | | 2 | 1.3 | 2 | 8.7 | 7 | 1.5 |
| Hioyd | | | | | 7 | 1.8 | 1 | 1.2 | | | | | | | | |
| Atlas-axis | | | | | | | | | | | | | | | | |
| Vertebra | | | | | | | | | 3 | 3.3 | 1 | 0.7 | | | 2 | 0.4 |
| Rib | | | | | | | | | 1 | 1 | | | | | | |
| Clavicle | | | | | | | | | | | | | | | | |
| Scapula | | | | | | | | | | | | | | | 1 | 0.2 |
| Humerus | 10 | 2 | 3 | 2.1 | | | 4 | 4.7 | 5 | 5.5 | 2 | 1.3 | | | 9 | 1.9 |
| Radius/Ulna | 5 | 1 | | | | | 2 | 2.3 | 1 | 1 | | | | | | |
| Radius | 10 | 2 | 5 | 3.5 | 9 | 2.3 | 1 | 1.2 | 4 | 4.4 | 6 | 4 | | | 12 | 2.5 |
| Ulna | 4 | 0.8 | | | 4 | 1 | 1 | 1.2 | | | 1 | 0.7 | | | 6 | 1.3 |
| Carpals | | | 2 | 1.4 | | | 4 | 4.7 | 8 | 8.7 | 3 | 2 | | | 15 | 3.1 |
| Metacarpal | 12 | 2.4 | 3 | 2.1 | 8 | 2 | 2 | 2.3 | 16 | 17.2 | | | 3 | 13 | 38 | 7.9 |
| Metacarpal rud. | | | | | | | | | | | | | | | | |
| Coxal | | | | | | | | | | | | | | | 1 | 0.2 |
| Femur | 5 | 1 | 4 | 2.8 | | | | | 4 | 4.4 | | | | | 2 | 0.4 |
| Patella | | | | | | | | | 1 | 1 | 1 | 0.7 | | | 1 | 0.2 |
| Tibia | 51 | 10.3 | | | 3 | 0.8 | 3 | 3.5 | 9 | 9.7 | 4 | 2.7 | | | 5 | 1 |
| Fibula | | | | | | | | | | | | | | | | |
| Malleolar bone | | | | | | | 1 | 1.2 | | | | | | | 3 | 0.6 |
| Calcaneum | | | | | | | | | | | | | | | | |
| Astragalus | | | | | | | | | | | | | | | | |
| Tarsals | 7 | 1.4 | 2 | 1.4 | 6 | 1.5 | 6 | 7 | | | 14 | 9.4 | | | 14 | 2.9 |
| Metatarsal | 38 | 7.6 | 12 | 8.3 | 21 | 5.3 | 5 | 5.8 | 14 | 15 | 22 | 14.7 | 3 | 13.2 | 78 | 16.3 |
| Metapodial | 4 | 0.8 | 3 | 2.1 | 16 | 4.1 | 2 | 2.3 | | | 8 | 5.4 | 2 | 8.7 | 24 | 5 |
| First phal. | 13 | 2.6 | 6 | 4.2 | 15 | 3.8 | 16 | 18.6 | 7 | 7.5 | 12 | 8.1 | 1 | 4.3 | 29 | 6.1 |
| Second phal. | 6 | 1.2 | 9 | 6.3 | 4 | 1 | 8 | 9.3 | 2 | 2.1 | 6 | 4 | 1 | 4.3 | 21 | 4.4 |
| Third phal. | 1 | 0.2 | 2 | 1.4 | 1 | 0.3 | 1 | 1.2 | | | | | | | 9 | 1.9 |
| First phal. rud. | | | | | | | | | | | | | | | | |
| Sec. phal. rud. | | | | | | | | | | | | | | | | |
| Th. phal. rud. | | | | | | | | | | | | | | | | |
| Sesamoid | 7 | 1.5 | 1 | 0.4 | 14 | 3.6 | 11 | 12.6 | 1 | 1 | 3 | 2 | | | 9 | 1.9 |
| TOTAL | 497 | | 144 | | 394 | | 86 | | 93 | | 149 | | 23 | | 479 | |
| Tot Cranium + tooth | 324 | 65.2 | 92 | 63.8 | 293 | 74.4 | 19 | 22.1 | 17 | 18.3 | 66 | 44.3 | 13 | 56.5 | 200 | 41.7 |
| Tot trunk | | | | | | | | | *4* | *4.3* | *1* | *0.7* | | | *4* | *0.9* |
| Tot long limb bones | *146* | *29.4* | *30* | *20.8* | *61* | *15.5* | *21* | *24.4* | *53* | *57* | *44* | *29.5* | *8* | *34.8* | *178* | *37.2* |
| Carpal + tarsal | | | *5* | *3.6* | *6* | *1.5* | *10* | *11.6* | *8* | *8.6* | *17* | *11.4* | | | *29* | *6* |
| Phal. + sesamoides | *27* | *5.4* | *17* | *11.8* | *34* | *8.6* | *36* | *41.9* | *11* | *11.8* | *21* | *14.1* | *2* | *8.7* | *68* | *14.2* |

the choice to select specific anatomical parts and to carry them back to camps/sites (Boscato and Crezzini, 2006, 2012). Recent studies demonstrated that at least at Riparo l'Oscurusciuto spongy bones were not systematically used as fuel in hearths (Spagnolo et al., 2016), suggesting their possible use as food (Costamagno and Rigaud, 2014). In southern Italy, Upper Palaeolithic assemblages indicate a different manner of exploiting ungulate bones (Boscato and Crezzini, 2006, 2012). A large amount of long-bone epiphyses and spongy elements (including carpal and tarsal bones) were not destroyed and can be found in these assemblages. Unlike Neandertals, who were evidently not interested in phalanges and probably left them at the kill sites, modern humans usually transported these small skeletal parts to their campsites where they fragmented them to recover the particular fat they contained: Morin (2006) underlines that, although the phalanges contain a low quantity of marrow, it is qualitatively different than the marrow contained in long bones, due to its higher percentage of oleic acid. These data suggest a change in processing hard animal tissues by Upper Palaeolithic people across southern Italy, a change that is already visible in Uluzzian assemblages, a documented by the case of Layer EIII5 at Grotta del Cavallo (Boscato and Crezzini, 2006, 2012).

## 6. Conclusions

The data collected and analysed show that human adaptive strategies changed over time to cope with variability in local topographic and ecological conditions, as well as with uncertainty in resource availability. Uncertainty and bias are critically embedded in the procurement and exploitation of animal resources, especially in such a fragmented and small-scale scenario as the Italian Peninsula. A sample of key sites from both southern and northern Italy offers evidence of how groups of Neandertals and modern humans occupied the Tyrrhenian and Ionian areas, as well as through the area between the great alluvial plain of the river Po and the Pre-Alpine mountains. In this context, a thorough and detailed zooarchaeological approach offers a unique perspective on palaeoenvironmental and palaeoecological settings, as well as on hunting and subsistence strategies. In the present study, we presented state-of-the-art evidence on the differential presence of large mammals and avifauna across Late Mousterian, Uluzzian, and Protoaurignacian assemblages from Italy. Incorporating an aoristic analysis further allows us to explicitly address the amount of temporal uncertainty embedded in one of the zooarchaeological assemblages of interest. While losing detail on individual archaeological layers, this method offers a practical solution to help overcome the effects of time-averaging and of the lack of information on layer-specific accumulation rates. At the same time, aoristic sums for ungulates, rates of change based on simulated data, and the comparison with null models depict a conservative scenario useful for inferring instances of *absolute* increase or decline of given taxa or families over time. The analysis of environmentally-informative bird taxa added significant detail to the environmental trends provided by mammal remains, improving our understanding of the climatic framework of the Middle-Upper Paleolithic transition. The future addition of micromammals to the analysis will make it possible to add detail on local biotopes, and to further test inferences on palaeoclimatic change in the different contexts. Interesting hypotheses on human behavioural ecology also emerge from the examined archaeological assemblages, although additional evidence is still clearly required for objectively test inferences about Uluzzian and Protoaurignacian contexts. In particular, differences seem to emerge in the use of fire (especially in terms of temperatures and bone processing) between Late Mousterian layers and the subsequent phases. More substantial data on the distribution of ungulate limb elements suggest a marked change in prey exploitation between the Late Mousterian and the Early Upper Palaeolithic in southern Italy, while northern sites show that a higher variety of processing techniques was already present in the Late Mousterian. As concerns differences in hunting strategies, traces of an increasing preference for small- and medium-sized mammals (carnivores, rodents, lagomorphs) can be already documented for the transition to Protoaurignacian, although presently available evidence is exclusively qualitative. Future research will ascertain if this difference can be ascribed to a forced expansion of niche breadth due to economic and technological competition between Neandertals and modern humans (Hockett and Haws, 2005).

The above mentioned hypotheses cannot yet be tested because of small sample size in all the analysed classes, and the emerging trends may or may not be confirmed by adding evidence on the same sites as well as on other, currently underrepresented areas of the Italian Peninsula to the analyses presented here. Over the next three years, the project ERC n. 724046 – SUCCESS will build on the results presented here by acquiring novel zooarchaeological and chronological evidence on all the mentioned contexts (Fig. 1), by directly comparing faunal time series to palaeoenvironmental and palaeoclimatic data, and by relying on innovative methods (Pothier Bouchard et al., 2019; Pothier Bouchard et al. in this issue) such as ZooMS (ZooArchaeology by Mass Spectrometry). This evidence will contribute to helping resolve or at least clarify longstanding debates surrounding strategic and technological shifts which occurred during the Middle-Upper Paleolithic transition and will help situate the questions concerning contacts between Neandertals and modern humans in Italy (and the eventual replacement of the former by the latter) in the broader framework of complex adaptive strategies and long-term human-environment interactions.

## Data availability

Datasets, scripts and related commands used to generate all of the results described in the paper are available at (http://doi.org/10.6092/unibo/amsacta/6209).

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## Appendices

Table A.1
Total Nisp and relative frequency of Ungulata documented in levels and layers of Northern Italy (Area 1) presented in chronological-cultural order. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

| *Taxa* | RS 5 + 8 - LM | | RF A9 - LM | | RF A6 - LM | | RF A5/A5+A6 - LM | | RS 5top+7 - LM | | SB II + III - LM | | RF A4 - LM | | RB 1f-1g - UL | | RF A3 - UL | | RF A2-A2R - PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| *Stephanorhinus* sp. | | | | | | | | | | | 2 | 0.3 | | | | | | | | |
| *Coelodonta antiquitatis* | | | | | | | | | | | | | | | | | 1 | 0.2 | | |
| *Sus scrofa* | 2 | 4.8 | 2 | 0.2 | 2 | 0.1 | | | 1 | 1.7 | 36 | 5.2 | | | 21 | 35.6 | | | | |
| *Megaloceros giganteus* | 5 | 11.9 | 79 | 6.5 | 28 | 1.8 | 10 | 2.1 | 14 | 24.1 | 12 | 1.7 | 12 | 2.5 | 2 | 3.4 | 8 | 1.8 | 34 | 4.3 |
| *Cervus elaphus* | 7 | 16.7 | 495 | 40.8 | 1095 | 69.7 | 297 | 62 | 6 | 10.3 | 136 | 19.6 | 242 | 50 | 5 | 8.5 | 169 | 37.4 | 170 | 21.4 |
| *Capreolus capreolus* | 1 | 2.4 | 281 | 23.1 | 182 | 11.6 | 48 | 10 | | | 251 | 36.2 | 54 | 11.2 | 3 | 5.1 | 50 | 11.1 | 37 | 4.7 |
| *Alces alces* | 2 | 4.8 | 17 | 1.4 | 4 | 0.3 | 1 | 0.2 | 5 | 8.6 | 24 | 3.5 | | | 3 | 5.1 | | | | |
| Cervidae | 6 | 14.3 | 166 | 13.7 | 128 | 8.2 | 39 | 8.1 | 19 | 32.8 | 135 | 19.5 | 29 | 6 | 13 | 22 | 33 | 7.3 | | |
| *Bos primigenius* | | | 6 | 0.5 | | | | | | | 1 | 0.1 | | | 1 | 1.7 | | | 2 | 0.3 |
| *Bison priscus* | 1 | 2.4 | 6 | 0.5 | 2 | 0.1 | | | 2 | 3.4 | | | 5 | 1 | 1 | 1.7 | 5 | 1.1 | 6 | 0.8 |
| *Bos/Bison* | 10 | 23.8 | 29 | 2.4 | 13 | 0.8 | 10 | 2.1 | 8 | 13.8 | 33 | 4.8 | 16 | 3.3 | 1 | 1.7 | 24 | 5.3 | 28 | 3.5 |
| *Capra ibex* | 5 | 11.9 | 46 | 3.8 | 54 | 3.4 | 30 | 6.3 | 2 | 3.4 | 3 | 0.4 | 82 | 16.9 | 1 | 1.7 | 116 | 25.7 | 447 | 56.2 |
| *Rupicapra rupicapra* | 3 | 7.1 | 68 | 5.6 | 55 | 3.5 | 32 | 6.7 | | | 53 | 7.6 | 31 | 6.4 | 4 | 6.8 | 34 | 7.5 | 71 | 8.9 |
| Caprinae | | | 19 | 1.6 | 7 | 0.4 | 12 | 2.5 | 1 | 1.7 | 8 | 1.2 | 13 | 2.7 | 4 | 6.8 | 12 | 2.7 | | |
| Total Ungulata | 42 | | 1214 | | 1570 | | 479 | | 58 | | 694 | | 484 | | 59 | | 452 | | 795 | |

Table A.2
Total Nisp and relative frequency of Carnivora documented in levels and layers of Northern Italy (Area 1 in Fig.1) presented in chronological-cultural order. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

| *Taxa* | RS 5 + 8 - LM | | RF A9 - LM | | RF A6 - LM | | RF A5/A5+A6 - LM | | RS 5top+7 - LM | | SB II + III - LM | | RF A4 - LM | | RB 1e+1f+1g - UL | | RF A3 - UL | | RF A2-A2R - PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| *Canis lupus* | 3 | 1.3 | 4 | 11.1 | 7 | 11.9 | 4 | 7.7 | | | 3 | 1.8 | 11 | 11.5 | | | 21 | 25.6 | 38 | 37.3 |
| *Vulpes vulpes* | 3 | 1.3 | 6 | 16.7 | 20 | 33.9 | 26 | 50 | 1 | 0.5 | 9 | 5.5 | 61 | 63.5 | 4 | 9.5 | 36 | 43.9 | 28 | 27.5 |
| *Vulpes/alopex* | | | | | | | 3 | 5.8 | | | | | 5 | 5.2 | | | 6 | 7.3 | 7 | 6.9 |
| *Alopex lagopus* | | | | | | | | | | | | | | | | | | | 2 | 2 |
| *Ursus spelaeus* | 157 | 66.2 | 8 | 22.2 | | | 2 | 3.8 | 148 | 66.7 | 100 | 61.3 | 2 | 2.1 | 21 | 50 | | | 1 | 1 |
| *Ursus arctos* | 1 | 0.4 | 4 | 11.1 | 10 | 16.9 | 4 | 7.7 | 6 | 2.7 | 3 | 1.8 | 11 | 11.5 | | | 7 | 8.5 | 1 | 1 |
| *Ursus* sp. | 64 | 27 | 5 | 13.9 | 21 | 35.6 | 13 | 25 | 66 | 29.7 | 38 | 23.3 | 2 | 2.1 | 13 | 31 | 2 | 2.4 | 1 | 1 |
| *Mustela erminea* | 4 | 1.7 | | | | | | | | | | | | | | | 1 | 1.2 | 2 | 2 |
| *Mustela nivalis* | | | 4 | 11.1 | 1 | 1.7 | | | | | | | 1 | 1 | | | 2 | 2.4 | 1 | 1 |
| *Mustela putorius* | | | | | | | | | | | 2 | 1.2 | | | | | | | 1 | 1 |
| *Martes martes* | 3 | 1.3 | | | | | | | 1 | 0.5 | | | | | 1 | 2.4 | | | | |
| Mustelidae | | | 1 | 2. | | | | | | | | | | | | | | | | |
| *Gulo gulo* | | | | | | | | | | | | | 1 | 1 | | | 3 | 3.7 | 1 | 1 |
| *Meles meles* | 2 | 0.8 | | | | | | | | | | | | | | | | | | |
| *Crocuta crocuta spelaea* | | | 3 | 8.3 | | | | | | | | | | | | | 3 | 3.7 | 15 | 14.7 |
| *Felis silvestris* | | | | | | | | | | | 2 | 1.2 | | | 2 | 4.8 | | | | |
| *Lynx lynx* | | | | | | | | | | | 4 | 2.5 | | | | | 1 | 1.2 | 3 | 2.9 |
| *Panthera pardus* | | | | | | | | | | | 1 | 0.6 | 2 | 2.1 | | | | | | |
| *Panthera leo spelaea* | | | 1 | 2.8 | | | | | | | | | | | | | | | 1 | 1 |
| Felidae | | | | | | | | | | | 1 | 0.6 | | | 1 | 2.4 | | | | |
| Total Carnivora | 237 | | 36 | | 59 | | 52 | | 222 | | 163 | | 96 | | 42 | | 82 | | 102 | |

Table A.3
Total Nisp and relative frequency of Rodentia and Lagomorpha documented in levels and layers of Northern Italy (Area 1 in Fig.1) presented in chronological-cultural order. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

| *Taxa* | RS 5 + 8 - LM | RF A9 - LM | RF A6 - LM | RF A5/A5+A6 - LM | RS 5top+7 - LM | SB II + III - LM | RF A4 - LM | RB 1e+1f+1g - UL | RF A3 - UL | RF A2-A2R - PA |
|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp |
| *Marmota marmota* | | 8 | 1 | | | 18 | | 3 | 2 | 2 |
| *Lepus* cfr. *timidus* | | | | | | | | 2 | | 4 |
| *Lepus* sp. | 1 | | | 1 | | 3 | | | 3 | 1 |
| *Castor fiber* | | | | | | 27 | | 1 | | 1 |
| Total Lagomorpha and Rodentia | 1 | 8 | 1 | 1 | 0 | 48 | 0 | 6 | 5 | 8 |

Table A.4
Total Nisp and relative frequency of Ungulata documented in levels and layers of Southwestern-Tyrrhenian italy (Area 2 in Fig.1) presented in chronological-cultural order. CTC = Grotta di Castelcivita; CALA = Grotta della Cala.

| *Taxa* | CTC spits 30–33 LM | | CTC spits 25–29 LM | | CTC spits 21–24 LM | | CTC spit 20 LM | | CTC 18lower-19 LM | | CTC spit 18upper UL | | CTC spit 17-13 UL | | CTC spits 12-10 lower UL | | CALA 14 UL | | CTC spits 10 upper-8 PA | | CTC spit 7 – top of seq.PA | | CALA 13 PA | | CALA 12 PA | | CALA 11-10 PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| *Stephanorhinus* sp. | | | | | 1 | 2.4 | | | | | | | | | | | 1 | 0.3 | | | | | | | | | | |
| *Equus ferus* | | | 1 | 0.5 | 1 | 2.4 | 1 | 2 | | | 1 | 5.9 | 7 | 6 | 65 | 59.1 | 18 | 5.2 | 10 | 30.3 | 1 | 1.7 | 5 | 2.2 | 10 | 2.3 | 4 | 1.8 |
| *Sus scrofa* | 2 | 1.5 | 4 | 2.1 | 1 | 2.4 | | | | | | | 4 | 3.4 | 4 | 3.6 | 46 | 13.3 | 7 | 21.2 | 4 | 6.7 | 10 | 4.3 | 52 | 12.1 | 28 | 12.3 |
| *Cervs elaphus* | 28 | 21.4 | 49 | 26.2 | 16 | 39 | 8 | 16 | 6 | 13.6 | 1 | 5.9 | 33 | 28.2 | 15 | 13.6 | 58 | 16.7 | 6 | 18.2 | 26 | 43.3 | 132 | 57.4 | 213 | 49.8 | 134 | 58.8 |
| *Capreolus capreolus* | 4 | 3.1 | 8 | 4.3 | 4 | 9.8 | 8 | 16 | 5 | 11.4 | 5 | 29.4 | 24 | 20.5 | 5 | 4.5 | 34 | 9.8 | 2 | 6.1 | 8 | 13.3 | 8 | 3.5 | 44 | 10.3 | 17 | 7.5 |
| *Dama dama* | 51 | 38.9 | 63 | 33.7 | 11 | 26.8 | 5 | 10 | 7 | 15.9 | 1 | 5.9 | 16 | 13.7 | 3 | 2.7 | 152 | 43.8 | 1 | 3 | 1 | 1.7 | 42 | 18.3 | 62 | 14.5 | 18 | 7.9 |
| Cervidae indet. | 6 | 4.6 | 3 | 1.6 | | | 8 | 16 | | | 1 | 5.9 | 3 | 2.6 | 1 | 0.9 | 13 | 3.7 | | | 3 | 5 | 10 | 4.3 | 22 | 5.1 | 9 | 3.9 |
| *Bos primigenus* | | | | | | | | | | | | | | | | | 16 | 4.6 | | | | | 7 | 3 | 8 | 1.9 | 2 | 0.9 |
| *Bison priscus* | 2 | 1.5 | 7 | 3.7 | | | 1 | 2 | | | 1 | 5.9 | 3 | 2.6 | 5 | 4.5 | | | 6 | 18.2 | 1 | 1.7 | | | | | | |
| *Bos/Bison* | | | | | | | 2 | 4 | 2 | 4.5 | 1 | 5.9 | 3 | 2.6 | 4 | 3.6 | | | | | | | | | | | | |
| *Capra ibex* | 13 | 9.9 | 34 | 18.2 | 2 | 4.9 | 2 | 4 | 2 | 4.5 | 1 | 5.9 | 5 | 4.3 | 6 | 5.5 | 3 | 0.9 | 1 | 3 | 3 | 5 | 12 | 5.2 | 14 | 3.3 | 15 | 6.6 |
| *Rupicapra* sp | 25 | 19.1 | 18 | 9.6 | 5 | 12.2 | 15 | 30 | 22 | 50 | 5 | 29.4 | 19 | 16.2 | 1 | 0.9 | 4 | 1.2 | | | 13 | 21.7 | 4 | 1.7 | 2 | 0.5 | 1 | 0.4 |
| Caprinae | | | | | | | | | | | | | | | | | 2 | 0.6 | | | | | | | 1 | 0.2 | | |
| Total Ungulata | 131 | | 187 | | 41 | | 50 | | 44 | | 17 | | 117 | | 110 | | 347 | | 33 | | 60 | | 230 | | 428 | | 228 | |

Table A.5
Total Nisp and relative frequency of Carnivora documented in levels and layers of Southwestern-Tyrrhenian italy (Area 2 in Fig.1) presented in chronological-cultural order. CTC = Grotta di Castelcivita; CALA = Grotta della Cala.

| *Taxa* | CTC gar LM | CTC lower rsi LM | CTC spit 18 upper UL | CTC spits 17 -13 UL | CTC spits 12–10 lower UL | CALA 14 UL | CTC PA | CALA 13 PA | CALA 12 PA | CALA 11 PA | CALA 10 PA |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp |
| *Canis lupus* | | | | | 1 | | 2 | 2 | 1 | | |
| *Vulpes vulpes* | | | | 2 | 2 | 9 | | 2 | 1 | | |
| *Ursus spelaeus* | | 1 | | | 1 | | | | | | |
| *Ursus arctos* | | | | 4 | | 7 | | | 2 | 1 | |
| *Mustela nivalis* | 1 | | | 1 | 2 | | | | | | |
| *Martes* sp. | | | | | | 14 | | | 1 | | |
| Mustelidae | | | | 2 | | | | | | | |
| *Meles meles* | | | | 2 | | | | | | | |
| *Crocuta crocuta spelaea* | 11 | | | 1 | 6 | | 1 | | | | |
| *Felis silvestris* | | | | 2 | 3 | 5 | | 2 | | | |
| *Panthera pardus* | 3 | 1 | | 3 | 2 | 17 | | 4 | 6 | 3 | |
| *Panthera leo spel.* | | | | | | | | | | | |
| Carnivora indet. | 6 | 5 | 1 | 7 | 1 | 3 | 2 | 1 | 1 | 1 | |
| Total Carnivora | 21 | 7 | 1 | 24 | 18 | 55 | 5 | 11 | 12 | 5 | 0 |

Table A.6
Total Nisp and relative frequency of Ungulata documented in levels and layers of Southeastern (Ionian-Adriatic) Italy (Area 3 in Fig.1) presented in chronological-cultural order. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto.

| > *Taxa* | CAV FIIIeb-e LM | | CAV FIIIb-c-d LM | | CAV FI-II-IIIa LM | | OSC 4–13 LM | | OSC 3 LM | | OSC 2-29-30-31 LM | | OSC 1 LM | | CAV EIII 5 UL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % | Nisp | % |
| *Stephanorhinus* sp. | | | | | | | 1 | 0.2 | 7 | 12.3 | | | | | | |
| *Equus ferus* | 40 | 11.5 | 40 | 14.9 | 50 | 19.8 | 17 | 3 | 16 | 28.1 | 48 | 25.9 | 2 | 5 | 53 | 27.3 |
| *Equus hydruntinus* | | | | | | | | | | | | | | | 1 | 0.5 |
| *Equus* sp. | | | | | | | | | | | | | | | 1 | 0.5 |
| *Sus scrofa* | 1 | 0.3 | 4 | 1.5 | 2 | 0.8 | 1 | 0.2 | | | | | | | 1 | 0.5 |
| *Cervus elaphus* | 72 | 20.6 | 54 | 20.1 | 69 | 27.3 | 51 | 8.9 | 15 | 26.3 | 27 | 14.6 | 11 | 27.5 | 52 | 26.8 |
| *Capreolus capreolus* | | | 6 | 2.2 | 3 | 1.2 | 11 | 1.9 | 2 | 3.5 | 8 | 4.3 | 1 | 2.5 | | |
| *Dama dama* | 7 | 2 | 83 | 31 | 20 | 7.9 | 38 | 6.6 | 1 | 1.8 | 12 | 6.5 | 6 | 15 | | |
| *Cervidae indet.* | 2 | 0.6 | 15 | 5.6 | 8 | 3.2 | 6 | 1 | | | 3 | 1.6 | | | | |
| *Bos primigenus* | 227 | 65 | 66 | 24.6 | 101 | 39.9 | 445 | 77.5 | 15 | 26.3 | 82 | 44.3 | 20 | 50 | 86 | 44.3 |
| *Capra ibex* | | | | | | | 1 | 0.2 | 1 | 1.8 | 5 | 2.7 | | | | |
| *Rupicapra* sp. | | | | | | | 3 | 0.5 | | | | | | | | |
| Total Nisp | 349 | | 268 | | 253 | | 574 | | 57 | | 185 | | 40 | | 194 | |

Table A.7
Total Nisp and relative frequency of Carnivora documented in levels and layers of Southeastern (Ionian-Adriatic) Italy (Area 3 in Fig.1) presented in chronological-cultural order. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto.

| *Taxa* | CAV FIII LM | CAV F II LM | OSC US 4–13 LM | OSC US 3 LM | OSC US 2-29-31 LM | OSC US 1 LM | CAV EIII5 UL |
|---|---|---|---|---|---|---|---|
| | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp | Nisp |
| *Canis lupus* | | | 1 | | | | 2 |
| *Vulpes vulpes* | 42 | 13 | | | | | 4 |
| *Ursus spelaeus* | | | | | | | |
| *Ursus arctos* | | | | | | | |
| *Mustela nivalis* | | | | | | | |
| *Martes* sp. | | | | | | | |
| Mustelidae | | | | | | | |
| *Meles meles* | | | | | | | |
| *Crocuta crocuta spelaea* | | | | | | | 1 |
| *Felis silvestris* | 2 | | | | | | |
| *Panthera pardus* | | | | | | | |
| *Panthera leo spelaea* | | | | | 1 | | |
| Carnivora indet. | 2 | | | | | | |
| Total Carnivora | 46 | 13 | 1 | 0 | 1 | 0 | 7 |

Table A.8
Nisp and relative frequency of avifaunal taxa recovered in different levels and layers of Grotta di Fumane and Grotta di Castelcivita, in chronological-cultural order. For taxonomic order, 2016.

| | FUMANE | | | | | | | | | | | | CASTELCIVITA | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A9 – LM | | A6 – LM | | A5/A5 + A6 – LM | | A4 - LM | | A3 - UL | | A1-2 PA | | rsi lower - LM | | pie -UL | | rpi - UL | | rsa" - UL | | rsa' - PA | | gic – PA | | ars – PA | |
| | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % |
| *Coturnix coturnix* | 3 | 0.6 | 1 | 0.9 | 1 | 0.6 | | | 2 | 1.6 | | | 1 | 2.3 | 5 | 3.3 | 2 | 2.4 | | | | | 2 | 25 | | |
| *Alectoris graeca* | 2 | 0.4 | | | | | 1 | 0.7 | | | | | 5 | 11.6 | 24 | 15.8 | 20 | 23.5 | 6 | 23.1 | 19 | 24.4 | 1 | 12.5 | 10 | 43.5 |
| *Perdix perdix* | 2 | 0.4 | | | | | 3 | 2.1 | 1 | 0.8 | 1 | 0.4 | 5 | 11.6 | 45 | 29.6 | 30 | 35.3 | 11 | 42.3 | 11 | 14.1 | 1 | 12.5 | 5 | 21.7 |
| *Lagopus* cf. *lagopus* | | | 1 | 0.9 | | | | | | | | | | | | | | | | | | | | | | |
| *Lagopus muta* | | | 1 | 0.9 | | | | | 1 | 0.8 | 3 | 1.2 | | | | | | | | | | | | | | |
| *T. urogal./L. tetrix* | 2 | 0.4 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Lyrurus tetrix* | 24 | 5.1 | 8 | 6.9 | 22 | 12.5 | 28 | 19.4 | 24 | 18.9 | 45 | 18.3 | | | | | | | | | | | | | | |
| cf. *Lyrurus tetrix* | | | 3 | 2.6 | 6 | 3.4 | 2 | 1.4 | 2 | 1.6 | | | | | | | | | | | | | | | | |
| Galliformes unid. | 1 | 0.2 | | | 3 | 1.7 | | | | | | | | | | | | | | | | | | | | |
| *Aythya nyroca* | | | | | | | | | | | | | | | 2 | 1.3 | | | 2 | 7.7 | | | | | | |
| *Spatula querquedula* | | | | | | | | | | | | | 1 | 2.3 | 13 | 8.6 | | | | | | | | | | |
| *Mareca strepera* | | | | | | | | | | | | | 5 | 11.6 | | | | | | | 1 | 1.3 | | | | |
| *Mareca penelope* | | | | | | | | | | | | | 1 | 2.3 | | | | | | | | | | | | |
| *Anas platyrhynchos* | | | | | | | 1 | 0.7 | | | | | | | 1 | 0.7 | | | | | | | | | | |
| *Anas crecca* | | | | | | | | | | | | | | | | | | | | | 2 | 2.6 | | | 1 | 4.3 |
| *Anas* cf. *crecca* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Columba livia/oenas* | 2 | 0.4 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Columba oenas* | | | | | | | | | | | 1 | 0.4 | 2 | 4.7 | 11 | 7.2 | 9 | 10.6 | 1 | 3.8 | 6 | 7.7 | | | 2 | 8.7 |
| *Columba palumbus* | | | 1 | 0.9 | | | | | | | | | | | | | | | | | | | | | | |
| *Caprimulgus europaeus* | | | | | | | | | | | | | | | | | | | | | | | 1 | 12.5 | | |
| *Rallus aquaticus* | 2 | 0.4 | | | 1 | 0.6 | 1 | 0.7 | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Crex crex* | 70 | 14.7 | 16 | 13.8 | 24 | 13.6 | 24 | 16.7 | 25 | 19.7 | 53 | 21.5 | | | 4 | 2.6 | 2 | 2.4 | | | 2 | 2.6 | | | 1 | 4.3 |
| cf. *Crex crex* | | | 1 | 0.9 | 6 | 3.4 | | | | | | | | | | | | | | | | | | | | |
| cf. *Gallinula chloropus* | | | 1 | 0.9 | | | | | | | | | | | | | | | | | | | | | | |
| Rallidae unid. | 13 | 2.7 | 2 | 1.7 | 1 | 0.6 | | | | | | | | | | | | | | | | | | | | |
| *Burhinus oedicnemus* | | | | | | | | | | | | | | | | | 1 | 1.2 | | | | | | | | |
| *Pluvialis squatarola* | | | | | | | | | | | | | | | | | | | | | 4 | 5.1 | | | | |
| *Vanellus vanellus* | | | | | 1 | 0.6 | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Numenius phaeopus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.3 | | | | |
| *Limosa limosa* | | | | | | | | | | | | | 2 | 4.7 | | | | | | | | | | | | |
| *Arenaria interpres* | | | | | | | | | | | | | | | 1 | 0.7 | | | | | | | | | | |
| *Calidris pugnax* | | | | | | | | | | | | | | | | | 1 | 1.2 | | | | | | | | |
| *Scolopax rusticola* | | | | | 1 | 0.6 | 1 | 0.7 | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Gallinago media* | | | | | | | | | | | | | | | 1 | 0.7 | | | | | | | | | | |
| *Larus ridibundus* | | | | | | | | | | | | | | | 1 | 0.7 | | | | | | | 1 | 12.5 | 1 | 4.3 |
| *Athene noctua* | | | | | | | | | | | | | | | 1 | 0.7 | | | | | | | | | | |
| *Aegolius funereus* | | | 2 | 1.7 | | | | | | | | | | | | | | | | | | | | | | |
| *Otus scops* | | | | | | | | | | | | | | | | | 1 | 1.2 | | | | | | | | |
| *Asio otus* | 5 | 1.1 | 1 | 0.9 | 3 | 1.7 | 6 | 4.2 | 1 | 0.8 | 10 | 4.1 | 1 | 2.3 | 6 | 3.9 | 4 | 4.7 | | | | | | | | |
| *Asio flammeus* | | | | | | | 2 | 1.4 | 2 | 1.6 | | | | | | | | | | | | | | | | |
| *Asio* cf. *flammeus* | 3 | 0.6 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Asio* sp. | 1 | 0.2 | 1 | 0.9 | 1 | 0.6 | 2 | 1.4 | 2 | 1.6 | | | | | | | | | | | | | | | | |
| *Strix aluco* | | | | | | | | | | | 2 | 0.8 | | | | | 1 | 1.2 | | | 4 | 5.1 | | | 2 | 8.7 |
| cf. *Strix aluco* | | | | | | | | | 1 | 0.8 | | | | | | | | | | | | | | | | |
| *Gypaetus barbatus* | | | 1 | 0.9 | | | | | | | | | | | | | | | | | | | | | | |
| cf. *Gypaetus barbatus* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Aegypius monachus* | 1 | 0.2 | 1 | 0.9 | | | | | | | | | | | | | | | | | | | | | | |
| cf. *Aegypius monachus* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Clanga clanga* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |

| | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aquila chrysaetos* | | | | | | | 1 | 0.7 | | | | | | | | | | | | | | | | | | |
| *Buteo lagopus* | | | | | | | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Buteo buteo* | | | | | | | | | | | | | | | | | | | | | 1 | 1.3 | | | | |
| *Coracias garrulus* | | | | | | | | | | | | | | | 2 | 1.3 | 2 | 2.4 | | | | | | | | |
| *Dendrocopos leucotos* | | | | | | | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Falco naumanni* | | | | | | | | | | | | | | | | | | | 1 | 3.8 | | | | | | |
| *Falco tinnunculus* | | | 4 | 3.4 | 7 | 4 | | | 4 | 3.1 | 6 | 2.4 | | | | | | | | | | | | | | |
| *Falco* cf. *tinnunculus* | 3 | 0.6 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Falco vespertinus* | 2 | 0.4 | 1 | 0.9 | 4 | 2.3 | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Falco vespert./columb.* | 3 | 0.6 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Falco columbarius* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Falco subbuteo* | | | 1 | 0.9 | 3 | 1.7 | 1 | 0.7 | 1 | 0.8 | 6 | 2.4 | | | 2 | 1.3 | 2 | 2.4 | 2 | 7.7 | | | | | | |
| *Falco* sp. | | | | | | | 1 | 0.7 | | | | | | | | | | | | | | | | | | |
| *Pyrrhocorax pyrrhoc.* | 1 | 0.2 | | | | | 1 | 0.7 | | | | | 5 | 11.6 | 3 | 2 | | | 1 | 3.8 | 4 | 5.1 | | | | |
| *Pyrrhocorax graculus* | 166 | 34.9 | 39 | 33.6 | 64 | 36.4 | 44 | 30.6 | 48 | 37.8 | 96 | 39 | 11 | 25.6 | 17 | 11.2 | 7 | 8.2 | | | 14 | 17.9 | | | | |
| cf. *Pyrrhocorax grac.* | | | 6 | 5.2 | 21 | 11.9 | 5 | 3.5 | 5 | 3.9 | | | 1 | 2.3 | | | | | | | | | | | | |
| *P.graculus/C.monedula* | 6 | 1.3 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pyrrhocorax* sp. | 10 | 2.1 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Garrulus glandarius* | 5 | 1.1 | | | | | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Pica pica* | 2 | 0.4 | | | 3 | 1.7 | 2 | 1.4 | 1 | 0.8 | 4 | 1.6 | | | | | | | | | | | | | | |
| *Nucifraga caryocatac.* | | | | | | | | | 1 | 0.8 | 1 | 0.4 | | | 5 | 3.3 | | | 1 | 3.8 | 1 | 1.3 | | | | |
| *Corvus monedula* | 2 | 0.4 | | | | | 1 | 0.7 | | | 2 | 0.8 | | | | | | | | | | | | | | |
| *Corvus corax* | | | | | 1 | 0.6 | | | | | | | | | | | | | | | | | | | | |
| *Corvus* cf. *corax* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Corvus corone* | | | | | | | 1 | 0.7 | | | | | | | | | | | | | | | | | | |
| *Corvus* cf. *corone* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| Corvidae unid. | 11 | 2.3 | 4 | 3.4 | 3 | 1.7 | 3 | 2.1 | 1 | 0.8 | | | | | | | | | | | | | | | | |
| *Lullula arborea* | | | | | | | | | | | 1 | 0.4 | | | | | | | | | | | | | | |
| *Delichon urbicum* | | | | | | | | | | | | | 1 | 2.3 | | | | | | | 5 | 6.4 | | | | |
| *Ptyonoprogne rupes.* | 4 | 0.8 | 1 | 0.9 | | | 1 | 0.7 | | | 1 | 0.4 | | | 4 | 2.6 | 1 | 1.2 | | | 3 | 3.8 | | | | |
| *Turdus viscivorus* | 2 | 0.4 | | | | | | | | | 1 | 0.4 | 2 | 4.7 | 2 | 1.3 | 2 | 2.4 | 1 | 3.8 | | | 2 | 25 | 1 | 4.3 |
| *Turdus visciv./pilaris* | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Turdus iliacus* | | | | | | | | | | | | | | | 2 | 1.3 | | | | | | | | | | |
| *Turdus pilaris* | 1 | 0.2 | | | | | | | | | 2 | 0.8 | | | | | | | | | | | | | | |
| *Turdus* sp. | 1 | 0.2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Montifringilla nivalis* | | | 1 | 0.9 | | | | | 1 | 0.8 | 1 | 0.4 | | | | | | | | | | | | | | |
| *Pyrrhula pyrrhula* | 3 | 0.6 | | | | | | | 1 | 0.8 | | | | | | | | | | | | | | | | |
| *Linaria cannabina* | | | | | | | 1 | 0.7 | | | | | | | | | | | | | | | | | | |
| *Loxia pytyopsittacus* | | | | | | | | | | | 3 | 1.2 | | | | | | | | | | | | | | |
| Passeriformes unid. | 114 | 24 | 18 | 15.5 | | | 11 | 7.6 | 3 | 2.4 | | | | | | | | | | | | | | | | |
| Total Nisp | 475 | | 116 | | 176 | | 144 | | 127 | | 246 | | 43 | | 152 | | 85 | | 26 | | 78 | | 8 | | 23 | |

Table A.9
The most recently available dates for the context of interest used in the present work.

| | site | Code(s) | Material | Method | Level | Detailed level | Technocomplex | 14CAge | sd | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Fumane | OxA-11347 | Charcoal | ABA14C | A2 | A2; sq. 97d | Protoaurignacian | 30650 | 260 | Higham et al., (2009); Higham (2011) |
| 2 | Fumane | OxA-17569 | Charcoal | ABOx-SC_14C | A2 | A2; sq. 97d | Protoaurignacian | 35640 | 220 | Higham et al., (2009); Higham (2011) |
| 3 | Fumane | OxA-11360 | Charcoal | ABA14C | A2 | A2; sq. 107i | Protoaurignacian | 31830 | 260 | Higham et al., (2009); Higham (2011) |
| 4 | Fumane | OxA-17570 | Charcoal | ABOx-SC_14C | A2 | A2; sq. 107i | Protoaurignacian | 35180 | 220 | Higham et al., (2009); Higham (2011) |
| 5 | Fumane | OxA-19411 | Charcoal | ABA14C | A2 | A2/struc.17 | Protoaurignacian | 32530 | 240 | Higham et al., (2009); Higham (2011) |
| 6 | Fumane | OxA-19413 | Charcoal | ABA14C | A2 | A2/struc.16/lev.B | Protoaurignacian | 32120 | 240 | Higham et al., (2009); Higham (2011) |
| 7 | Fumane | OxA-19414 | Charcoal | ABOx-SC_14C | A2 | A2/struc.16/lev.Ba | Protoaurignacian | 34180 | 270 | Higham et al., (2009); Higham (2011) |
| 8 | Fumane | OxA-19412 | Charcoal | ABOx-SC_14C | A2 | A2/struc.17a | Protoaurignacian | 34940 | 280 | Higham et al., (2009); Higham (2011) |
| 9 | Fumane | OxA-19525 | Charcoal | ABA14C | A2 | A2/struc.18 | Protoaurignacian | 33380 | 210 | Higham et al., (2009); Higham (2011) |
| 10 | Fumane | OxA-19584 | Charcoal | ABOx-SC_14C | A2 | A2/struc.18 | Protoaurignacian | 35850 | 310 | Higham et al., (2009); Higham (2011) |
| 11 | Fumane | Oxa-21736 | Mammal Bone | 14C-ultrafiltration | A3 | A3 | Uluzzian | 39100 | 1000 | Douka et al. (2014) |
| 12 | Fumane | Oxa-X-2295-52 | Mammal Bone | 14C-ultrafiltration | A3 | A3 | Uluzzian | 41300 | 1300 | Douka et al. (2014) |
| 13 | Fumane | Oxa-21735 | Mammal Bone | 14C-ultrafiltration | A4 | A4/struct. II/744 | Late Mousterian | 42000 | 1700 | Douka et al. (2014) |
| 14 | Fumane | Oxa-21733 | Mammal Bone | 14C-ultrafiltration | A4 | A4II | Late Mousterian | 41000 | 1300 | Douka et al. (2014) |
| 15 | Fumane | Oxa-21734 | Mammal Bone | 14C-ultrafiltration | A4 | A4II | Late Mousterian | 42000 | 1400 | Douka et al. (2014) |
| 16 | Fumane | OxA-17566 | Charcoal | ABOx-SC_14C | A5 | A5 + A6, sq.90 | Late Mousterian | 40460 | 360 | Higham et al., (2009); Higham (2011) |
| 17 | Fumane | OxA-17567 | Charcoal | ABA14C | A5 | A5 + A6, sq.90 | Late Mousterian | 39500 | 330 | Higham et al., (2009); Higham (2011) |
| 18 | Fumane | OxA-17568 | Charcoal | ABA14C | A5 | A5 + A6, sq.90 | Late Mousterian | 39490 | 350 | Higham et al., (2009); Higham (2011) |
| 19 | Fumane | OxA-8022 | Charcoal | ABA14C | A5 | A5 + A6, sq.90 | Late Mousterian | 38800 | 750 | Higham et al., (2009); Higham (2011) |
| 20 | Fumane | OxA-8023 | Charcoal | ABA14C | A5 | A5 + A6, sq.90 | Late Mousterian | 38250 | 700 | Higham et al., (2009); Higham (2011) |
| 21 | Fumane | OxA-19410 | Charcoal | ABA14C | A5 | A5 sq. 88i,3789/struc.III | Late Mousterian | 34500 | 270 | Higham et al., (2009); Higham (2011) |
| 22 | Fumane | OxA-X-2275-45 | Charcoal | ABOx-SC_14C | A5 | A5 sq. 88i,3789/struc.III | Late Mousterian | 41650 | 650 | Higham et al., (2009); Higham (2011) |
| 23 | Fumane | OxA-17980 | Charcoal | ABOx-SC_14C | A5 | A5, sqs. 85,86,95,96 | Late Mousterian | 40150 | 350 | Higham et al., (2009); Higham (2011) |
| 24 | Fumane | OxA-18199 | Charcoal | ABA14C | A5 | A5, sqs. 85,86,95,96 | Late Mousterian | 36860 | 700 | Higham et al., (2009); Higham (2011) |
| 25 | Fumane | OxA-6463 | Charcoal | ABA14C | A5 | A5, sqs. 85,86,95,96 | Late Mousterian | 33700 | 600 | Higham et al., (2009); Higham (2011) |
| 26 | Fumane | OxA-21796 | Bone | 14C-ultrafiltration | A2 | | Protoaurignacian | 35400 | 750 | Higham (2011) |
| 27 | Fumane | OxA-21712 | Bone | 14C-ultrafiltration | A5 | | Late Mousterian | 40000 | 1100 | Higham (2011) |
| 28 | Fumane | OxA-21809 | Bone | 14C-ultrafiltration | A5 | A5 + A6 | Late Mousterian | 40200 | 1200 | Higham (2011) |
| 29 | Fumane | OxA-21758 | Bone | 14C-ultrafiltration | A5 | A5 + A6 | Late Mousterian | 41100 | 1300 | Higham (2011) |
| 30 | Fumane | OxA-21757 | Bone | 14C-ultrafiltration | A5 | A5 + A6 | Late Mousterian | 41500 | 1500 | Higham (2011) |
| 31 | R. Broion | OxA-35527 | Bone | 14C | 1g | 1g | Uluzzian | 38900 | 1000 | Peresani et al. (2019) |
| 32 | Rio Secco | S-EVA25353/MAMS15230 | Bone with cutmarks | 14C | 5 top | I14 b | Mousterian | 44100 | 660 | Talamo et al. (2014) |
| 33 | Rio Secco | S-EVA25355/MAMS15231 | Bone with cutmarks | 14C | 5 top I | G14III | Mousterian | 45695 | 790 | Talamo et al. (2014) |
| 34 | Rio Secco | S-EVA25356/MAMS15232 | Bone | 14C | 5 top II | H14IV | Mousterian | 43210 | 600 | Talamo et al. (2014) |
| 35 | Rio Secco | S-EVA25357/MAMS15233 | Bone with cutmarks | 14C | 5 top I | I14II | Mousterian | 45740 | 800 | Talamo et al. (2014) |
| 36 | Rio Secco | S-EVA25359/MAMS15235 | Bone | 14C | 7 | H14h | Mousterian | 46320 | 1430 | Talamo et al. (2014) |
| 37 | Rio Secco | S-EVA25361/MAMS15236 | Bone with cutmarks | 14C | 7 | H13IV | Mousterian | > 49000 | | Talamo et al. (2014) |
| 38 | Rio Secco | S-EVA25362/MAMS15237 | Bone with cutmarks | 14C | 7 | H13IV | Mousterian | 44560 | 1150 | Talamo et al. (2014) |
| 39 | Rio Secco | S-EVA25363/MAMS15238 | Bone with cutmarks | 14C | 7 | H14g | Mousterian | 44770 | 1180 | Talamo et al. (2014) |
| 40 | Rio Secco | OxA-25359 | Charcoal | 14C | 8 | sq.H11IV n.17 | Mousterian | 42000 | 900 | Peresani et al. (2014); Talamo et al. (2014) |
| 41 | Rio Secco | LTL429A | Bone | 14C | 5 top II | GRSI | Mousterian | 37790 | 360 | Peresani et al. (2014); Talamo et al. (2014) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 42 | S.Bernardino | | | U/Th ESR | II | | Mousterian | 52000 | 5000 | |
| 43 | S.Bernardino | | | U/Th ESR | II | | Mousterian | 38000 | 5000 | Gruppioni (2003); López-García (2017) Peresani et al. (2015) |
| 44 | S.Bernardino | | | U/Th ESR | II | | Mousterian | 35000 | 4000 | Gruppioni (2003); López-García et al. (2017) |
| 45 | S.Bernardino | | | U/Th ESR | II | | Mousterian | 49000 | 5000 | |
| 46 | S.Bernardino | | | U/Th ESR | II | | Mousterian | 54000 | 5000 | |
| 47 | Castelcivita | GrN-13984 | Charcoal | 14C | cgr | spits 29-30 | Late Mousterian | 42700 | 900 | Gambassini (1997) |
| 48 | Castelcivita | GrN-13982 | Charcoal | 14C | cgr | spits 29-30 | Late Mousterian | 39100 | 1300 | Gambassini (1997) |
| 49 | Castelcivita | Oxa-22622 | Charcoal | ABOx-SC_14C | rsa" | spit 11 | Uluzzian | 36120 | 360 | Wood et al. (2012) |
| 50 | Oscurusciuto | Beta 181165 | Mammal bone | 14C | 1 | 1 | Late Mousterian | 38500 | 900 | Marciani et al. (2016) |
| 51 | Oscurusciuto | | Tephra | Ar$^{40}$/Ar$^{39}$ | 14 | 1-TM19 | Mousterian | ~55000 | | Spagnolo et al. (2016) |
| 57 | Cavallo | Oxa-19254 | Shell | 14C | D1 = DIb | | Uluzzian | 35080 | 230 | Benazzi et al. (2011) |
| 58 | Cavallo | Oxa-19255 | Shell | 14C | D2 = DIb | | Uluzzian | 36260 | 250 | Benazzi et al. (2011) |
| 59 | Cavallo | Oxa-20631 | Shell | 14C | DII | | Uluzzian | 36780 | 310 | Benazzi et al. (2011) |
| 60 | Cavallo | Oxa-19257 | Shell | 14C | D3 = DII | | Uluzzian | 42360 | 400 | Benazzi et al. (2011) |
| 61 | Cavallo | Oxa-19258 | Shell | 14C | D8 = DII? | | Uluzzian | 36000 | 400 | Benazzi et al. (2011) |
| 62 | Cavallo | Oxa-19256 | Shell | 14C | E1 = E-D | | Uluzzian | 39060 | 310 | Benazzi et al. (2011) |
| 63 | Cavallo | Oxa-X2280-16 | Shell | 14C | E1 = E-D | | Uluzzian | 38300 | 400 | Benazzi et al. (2011) |
| 64 | Cavallo | Oxa-19242 | Shell | 14C | E4 = EII-I | | Uluzzian | 39990 | 340 | Benazzi et al. (2011) |
| 65 | Cavallo | Fi0822 | Charcoal | ABA14C | FII | | Mousterian | 42000 | 2400 | Fabbri et al. (2016) |
| 66 | Cavallo | Fi0824 | Charcoal | ABA14C | FII | | Mousterian | 39300 | 1900 | Fabbri et al. (2016) |
| 67 | Cavallo | | Tephra | Ar$^{40}$/Ar$^{39}$ | Fa-Y6 | | | 45500 | 1000 | Zanchetta et al. (2018) |
| 68 | Cavallo | | Tephra | Ar$^{40}$/Ar$^{39}$ | CII–Y5 | | | 39850 | 140 | Zanchetta et al. (2018) |

Most recent available absolute datings for the sampled archaeological sites.

Table A.10

Number and % of single teeth and small limb bones of Ungulata uncovered in different levels of the Late Mousterian, Uluzzian and Protoaurignacian sites of Southern Italy. CALA = Grotta della Cala; CTC = Grotta di Castelcivita; CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto.

| Sites levels - US | Single teeth | | Carpal and tarsal bones | | Phalanges + sesamoides | | Total ungulates |
|---|---|---|---|---|---|---|---|
| | NR | % | NR | % | NR | % | Nisp |
| CALA PA | 299 | 35.4 | 188 | 22.3 | 115 | 13.6 | 844 |
| CTC PA | 2 | 5.6 | 4 | 11.1 | 5 | 13.9 | 38 |
| CALA UL | 137 | 41.5 | 31 | 9.4 | 41 | 12.4 | 331 |
| CAV EIII5 UL | 46 | 23.5 | 30 | 15.3 | 59 | 30.1 | 196 |
| CTC UL | 38 | 15.1 | 13 | 5.2 | 38 | 15.1 | 233 |
| OSC US 2 LM | 128 | 69.2 | 3 | 1.6 | 5 | 2.7 | 185 |
| CAV str. F LM | 552 | 65.3 | 12 | 1.4 | 67 | 7.9 | 845 |
| CTC LM | 6 | 9 | 3 | 4.5 | 9 | 13.4 | 67 |

Table A.11

Percentages of determinated skeletal parts in the taxonomically indeterminate remains recovered from the different Late Mousterian and Uluzzian layers and levels sampled in Southern Italy. OSC = Riparo l'Oscurusciuto; CAV = Grotta del Cavallo; CTC = Grotta di Castelcivita.

| Elements | OSC US 4/1 LM | CAV FII LM | CTC LM | CAV EIII5 UL |
|---|---|---|---|---|
| | % | % | % | % |
| Antler/Horn | 0.4 | 0.3 | | 3.5 |
| Skull | 4.3 | 4.8 | 4.9 | 2.5 |
| Mandible | 0.4 | 0.4 | 2 | 0.7 |
| Teeth | 18.4 | 14.9 | 3.6 | 7.9 |
| Vertebrae | | 3 | 4.6 | 3.3 |
| Ribs | 3.5 | 11.2 | 15.7 | 13.4 |
| Scapula | | 2.3 | | 0.4 |
| Sternum | | | 0.7 | 0.7 |
| Pelvis | 0.4 | | 0.3 | 0.2 |
| Metapodials | | | 0.8 | |
| Diaphysis | 45.3 | 41.3 | 41.4 | 18.6 |
| Epiphysis | 5.6 | 8.2 | 8,2 | 12,9 |
| Spongy bones | 21.8 | 11.6 | 12 | 31.9 |
| Total remains | 5747 | 9574 | 1920 | 5185 |

Table A.12
Detail and percentages of remains that present with evidence of digestion and/or gnawing by carnivores documented in the levels and layers of Northern Italy (Adriatic Area 1 in Fig. 1). Contexts are presented in chronological-cultural order. GM: gnawing marks; TOT CM: total carnivore marks; D: digested.

| Sites | US/levels | GM | (D)igested | TOT.Car.M | TOT % | TOT. NR |
|---|---|---|---|---|---|---|
| RS-Rio Secco | 5 + 8 | 53 | 2 | 55 | 1.3 | 4301 |
| RF-Fumane | A9 | 100 | 1 | 101 | 0.09 | 111841 |
| RF-Fumane | A6 | 24 | 16 | 40 | 0.03 | 111044 |
| RF-Fumane | A5/A5 + A6 | 20 | 9 | 29 | 0.04 | 67083 |
| RS-Rio Secco | 5top + 7 | 31 | – | 31 | 5.9 | 524 |
| SB-S. Bernardino | II + III | 61 | 1 | 62 | 0.6 | 9217 |
| RF-Fumane | A4 | 51 | 17 | 68 | 0.3 | 19955 |
| RB-Broion | 1e + 1f + 1g | 3 | 1 | 4 | 0.01 | 37390 |
| RF-Fumane | A3 | 53 | 36 | 89 | 0.5 | 16989 |
| RF-Fumane | A2-A2R | 17 | 9 | 26 | 0.1 | 19829 |

Table A.13
Results of Mann-Whitney test for assessing significant differences in the distribution of fragment size classes and the proportion of burned and calcinated remains across Uluzzian and Late Mousterian layers of Northern Italy. The test was run on arcsine-transformed proportions.

| | Mann-Whitney W | P-value |
|---|---|---|
| 1–3 cm LM – UL Northern Italy | 7 | 1 |
| > 3 cm LM – UL Northern Italy | 4 | 0.5 |
| Burn. + Calc LM – UL Northern Italy | 5 | 0.86 |

Table A.14
Results of test for differences in proportion of fragment size classes between Uluzzian and Late Mousterian layers of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with relative effect size and statistical power.

| | X-squared | df | P-value | Effect size (Cohen's h) | Power |
|---|---|---|---|---|---|
| 1–3 cm CAV UL – CAV LM | 128.7 | 1 | < 0.001 | −0.19 | 1 |
| 1–3 cm CAV UL – OSC LM | 1875.8 | 1 | < 0.001 | −0.55 | 1 |
| > 3 cm CAV UL – CAV LM | 128.7 | 1 | < 0.001 | 0.19 | 1 |
| > 3 cm CAV UL – OSC LM | 1875.8 | 1 | < 0.001 | 0.58 | 1 |
| Burn + Calc CAV UL – CAV LM | 4264.7 | 1 | < 0.001 | 1.1 | 1 |
| Burn + Calc CAV UL – OSC LM | 2.4161 | 1 | 0.12 | −0.04 | 0.72 |

Table A.15
Results of test for differences in proportion of carpal/tarsal and phalanges/sesamoides of *Bos primigenius* between Uluzzian and Late Mousterian layers of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with the relative effect size and statistical power.

| | X-squared | df | P-value | Effect size (Cohen's h) | Power |
|---|---|---|---|---|---|
| Carpal + tarsal CAV UL – CAV LM | 19.344 | 1 | < 0.001 | 0.45 | 0.965 |
| Carpal + tarsal CAV UL – OSC LM | 52.104 | 1 | < 0.001 | 0.69 | 0.999 |
| Phalang. + Sesamoides CAV UL – CAV LM | 59.942 | 1 | < 0.001 | 0.81 | 0.999 |
| Phalang. + Sesamoides CAV UL – OSC LM | 97.192 | 1 | < 0.001 | 0.93 | 1 |

Table A.16
Results of test for differences in proportion of carpal/tarsal and phalanges/sesamoides across all ungulates between Uluzzian and Late Mousterian layers of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with the relative effect size and statistical power.

| | X-squared | df | P-value | Effect size (Cohen's h) | Power |
|---|---|---|---|---|---|
| Carpal + tarsal CAV UL – CAV LM | 79.232 | 1 | < 0.001 | 0.57 | 0.999 |
| Carpal + tarsal CAV UL – OSC LM | 20.831 | 1 | < 0.001 | 0.55 | 0.999 |
| Phalanges + Sesamoides CAV UL – CAV LM | 73.523 | 1 | < 0.001 | 0.59 | 0.999 |
| Phalanges + Sesamoides CAV UL – OSC LM | 51.12 | 1 | < 0.001 | 0.83 | 1 |

Table A.17
Results of test for differences in proportion of diaphysis, epiphysis, and spongy bones between Uluzzian and Late Mousterian layers of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with the relative effect size and statistical power.

| | X-squared | df | P-value | Effect size (Cohen's h) | Power |
|---|---|---|---|---|---|
| Diaphysis CAV UL – CAV LM | 780.01 | 1 | < 0.001 | 0.5 | 1 |
| Diaphysis CAV UL – OSC LM | 883.87 | 1 | < 0.001 | 0.58 | 1 |
| Epiphysis CAV UL – CAV LM | 83.663 | 1 | < 0.001 | 0.15 | 1 |
| Epiphysis CAV UL – OSC LM | 176.26 | 1 | < 0.001 | 0.25 | 1 |
| Spongy bones CAV UL – CAV LM | 910.5 | 1 | < 0.001 | 0.55 | 1 |
| Spongy bones CAV UL – OSC LM | 142.45 | 1 | < 0.001 | 0.23 | 1 |

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# 5. Manuscript III

## Integrated multidisciplinary ecological analysis from the Uluzzian settlement at the Uluzzo C Rock Shelter, south-eastern Italy

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JQS Journal of Quaternary Science QRA Quaternary Research Association

# Integrated multidisciplinary ecological analysis from the Uluzzian settlement at the Uluzzo C Rock Shelter, south-eastern Italy

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ABSTRACT: The Middle to Upper Palaeolithic transition, between 50 000 and 40 000 years ago, is a period of important ecological and cultural changes. In this framework, the Rock Shelter of Uluzzo C (Apulia, southern Italy) represents an important site due to Late Mousterian and Uluzzian evidence preserved in its stratigraphic sequence. Here, we present the results of a multidisciplinary analysis performed on the materials collected between 2016 and 2018 from the Uluzzian stratigraphic units (SUs) 3, 15 and 17. The analysis involved lithic technology, use-wear, zooarchaeology, ancient DNA of sediments and palaeoproteomics, completed by quartz single-grain optically stimulated luminescence dating of the cave sediments. The lithic assemblage is characterized by a volumetric production and a debitage with no or little management of the convexities (by using the bipolar technique), with the objective to produce bladelets and flakelets. The zooarchaeological study found evidence of butchery activity and of the possible exploitation of marine resources, while drawing a picture of a patchy landscape, composed of open forests and dry open environments surrounding the shelter. Ancient mitochondrial DNA from two mammalian taxa were recovered from the sediments. Preliminary zooarchaeology by mass spectrometry results are consistent with ancient DNA and zooarchaeological taxonomic information, while further palaeoproteomics investigations are ongoing. Our new data from the re-discovery of the Uluzzo C Rock Shelter represent an important contribution to better understand the meaning of the Uluzzian in the context of the Middle/Upper Palaeolithic transition in south-eastern Italy. © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: ancient DNA of sediment; lithic technology; Uluzzian; zooarchaeology; ZooMS

## Introduction

The Middle to Upper Palaeolithic (MP/UP) transition corresponds to the period between around 50 000 and 40 000 years ago and is a key period of change in the prehistory of the Old World. This timespan covers the last millennia of Neanderthal presence in the fossil record, together with the appearance of Modern Human (MH) populations in Europe (Benazzi *et al.*, 2011a; Douka *et al.*, 2014; Higham *et al.*, 2014).

Mediterranean Europe, and in particular Italy, plays an essential role in the study of this period due to: (i) its geographical position and ecological variability; (ii) the presence of key archaeological sites dating back to the MP/UP transition; and (iii) the evidence of different techno-complexes – such as Late Mousterian, Uluzzian and Protoaurignacian – associated with human fossil remains. In the Palaeolithic context of Mediterranean Europe, Neanderthals are associated with Mousterian assemblages, while, according to Benazzi *et al.* (2011b, 2015) MHs are associated with Uluzzian and Protoaurignacian assemblages.

The Uluzzian is one of the first lithic assemblages related to the arrival of MHs in Europe. It is characterized by its own

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originality and coherence, observable in lithic technology (Riel-Salvatore, 2009, 2010; De Stefani *et al.*, 2012; Moroni *et al.*, 2013, 2018; Ronchitelli *et al.*, 2018; Villa *et al.*, 2018; Peresani *et al.*, 2019; Arrighi *et al.*, 2020a; Collina *et al.*, 2020; Marciani *et al.*, 2020a), manufacturing of formal bone tools (d'Errico *et al.*, 2012; Peresani *et al.*, 2016; Villa *et al.*, 2018; Peresani *et al.*, 2019; Arrighi *et al.*, 2020a) and ornaments (Arrighi *et al.*, 2020b, 2020c), which point towards the sharing of common behaviours among its social groups and group members.

From a technological point of view, the Uluzzian is in fact characterized by the following. (i) A specific conceptualization of production that consists in the application of a straightforward debitage method, which implies the collection of raw blocks presenting convexities, angles and guide ribs appropriate for knapping; the striking platform being either opened by a single or few removals, or not opened at all by using a natural or cortical plan; the debitage surfaces are roughly managed, and the production of blanks follows unidirectional, bidirectional or orthogonal directions. (ii) The deliberate selection of the bipolar technique (aiming at the production of small blades/bladelets and small flakes/flakelets). (iii) The idea of a 'simple' production for complex tools (the use of composite tools) (Riel-Salvatore, 2009, 2010; Moroni *et al.*, 2013, 2018; Sano *et al.*, 2019; Collina *et al.*, 2020; Marciani *et al.*, 2020a).

Among retouched tools we note the production of lunates (tools characterized by a curved backed side opposite to a rectilinear cutting edge), which at Grotta del Cavallo were used as armatures (Sano *et al.*, 2019), and the systematic production of end-scrapers (Palma di Cesnola, 1964, 1993, 2004; Gambassini, 1997).

Zooarchaeological data suggest that human adaptive strategies changed over time to cope with variations in the local topographic and ecological conditions, as well as to deal with the uncertainty of resource availability (Romandini *et al.*, 2020). However, while in southern Italy more substantial data on the distribution of ungulate limb elements might point to a marked change in ungulate exploitation between the Late Mousterian and the Early Upper Palaeolithic (Boscato and Crezzini, 2012; Romandini *et al.*, 2020), in northern sites a higher variety of processing techniques were already present at the beginning of the Late Mousterian (Romandini *et al.*, 2020). Accordingly, our understanding of the Uluzzian is far from exhaustive, and additional evidence is required to empirically test inferences regarding Late Mousterian, Uluzzian and Protoaurignacian contexts.

The Uluzzo C Rock Shelter provides another piece of evidence towards a better understanding of the role of the Uluzzian within the MP/UP transition in south-eastern Italy. The site is located in the Bay of Uluzzo, where numerous Uluzzian sites have already been reported (Moroni *et al.*, 2013, 2018; Marciani *et al.*, 2020a) – including Grotta del Cavallo – and where the Uluzzian was first discovered and described (Palma di Cesnola, 1964). Moreover, the site of Uluzzo C includes a long stratigraphic sequence composed of several levels, including Romanellian, Uluzzian and a long and rich Mousterian sequence. Here we report the results from our multidisciplinary investigation on the sediments from the cave entrance and the archaeological materials from Uluzzo C Rock Shelter, which were collected during previous and new excavations (i.e. in the 1960s and between 2016 and 2018). Our approach includes the analysis of lithic technology and use-wear, zooarchaeological remains, sedimentary DNA and palaeoproteomics to provide further insights into the lithic behaviour (as far as reduction sequences, goals and knapping techniques are concerned) and the hunting strategies of the human groups that inhabited Uluzzo C during the MP/UP transition. Moreover, we present palaeoecological evidence on the composition of the landscape surrounding the rock shelter during this period.

## Archaeological and chronological context

The Uluzzo C Rock Shelter is located in the Parco Naturale di Porto Selvaggio (Nardò, Lecce, southern Italy), on the western side of the Apulian Coast facing the Ionian Sea (40°9′27.84″N, 17°57′35.34″E) (Fig. 1). The Uluzzo C site was discovered during archaeological investigations carried out in the area in the 1960s by the Italian Institute of Prehistory and Protohistory and led by Borzatti von Löwenstern (Borzatti von Lowerstern, 1965; Borzatti von Löwenstern and Magaldi, 1966). During this first exploration, the stratified deposit of the cave yielded significant lithic assemblages that spanned from the Mousterian to the Bronze Age, including the Uluzzian technocomplex.

Today, the site is formed by a central hall with a smaller cavity on its right, whereas the stratigraphic sequence consists of 10 different layers (Borzatti von Lowerstern, 1965). From a cultural point of view, the stratigraphic sequence of Uluzzo C includes: a Romanellian layer (A); a sterile layer (B); two Uluzzian layers (C, D); a layer composed of a mixture of Upper Palaeolithic and Mousterian deposits (E); and a large sequence of Mousterian layers (F–L) (Borzatti von Lowerstern, 1965; Borzatti von Löwenstern and Magaldi, 1966; Spinapolice, 2018) (Fig. 2A). This sequence was confirmed by recent excavations, as well as by sedimentological and micromorphological analyses (for a detailed description see Spinapolice *et al.* in this special issue), which further detailed the sequence by identifying 22 stratigraphic units (SUs) within the layers originally identified by Borzatti.

In the new excavation, the site of Uluzzo C was divided into three sectors: A, B and C. Sectors A and B are located inside the rock shelter and correspond to the surface of the actual deposit (sector A) and to the bottom of Borzatti's trench (sector B) (Fig. 2B), whereas sector C is outside the rock shelter and has been explored to identify possible archaeological deposits on the terrace (Fiorini *et al.*, 2018, 2019). The recent investigations (2016–2018) focused on the area inside the rock shelter (sector A) and involved the stratigraphic excavation of the Uluzzian occupation (Borzatti's layer C), which in the new excavations corresponds to SUs 3, 15 and 17. Samples for sedimentological analysis and optically stimulated luminescence (OSL) dating, however, were not taken only from this layer, but from the entire stratigraphic succession accessible in sector A (i.e. Borzatti's layers B, C–L) (Fig. 2).

We performed specific investigations on sediments. The technical details of the sedimentological and micromorphological analyses and of the OSL dating campaign, as well as the individual OSL ages, are reported in Spinapolice *et al.* (this issue). Based on this single-grain OSL chronology, the grand weighted mean age for the Uluzzian occupations – layers C, D and E (OSL samples ULOC 3, 4 and 5) is 40.6 ± 1.4 ka (Fig. 2A). These OSL time constraints generated for the Uluzzian layers at Uluzzo C match the chronology of the main Uluzzian sequences of the region (e.g. Grotta del Cavallo). The Uluzzian occupation of Grotta del Cavallo (which probably corresponds to layers D and E at Uluzzo C) is constrained to between 45.5 ± 1.0 ka (Layer Fa/Y-6) and 39.85 ± 0.14 ka (CI) by Zanchetta *et al.* (2018). At Uluzzo C the Mousterian layer that underlies the Uluzzian complex (Layer G) has been OSL dated as well (i.e. 46 ± 4.0 ka, Layer G – OSL sample ULOC 1; Fig. 2A) (Spinapolice *et al.* in this special issue). Hence, despite the stratigraphic diversity and difficulties in matching the Uluzzian layers between Grotta del Cavallo and Uluzzo C, the chronological constraints for the end of the Mousterian appear to be congruent in the two caves: 45.5 ± 1.0 ka at Grotta del Cavallo (Zanchetta

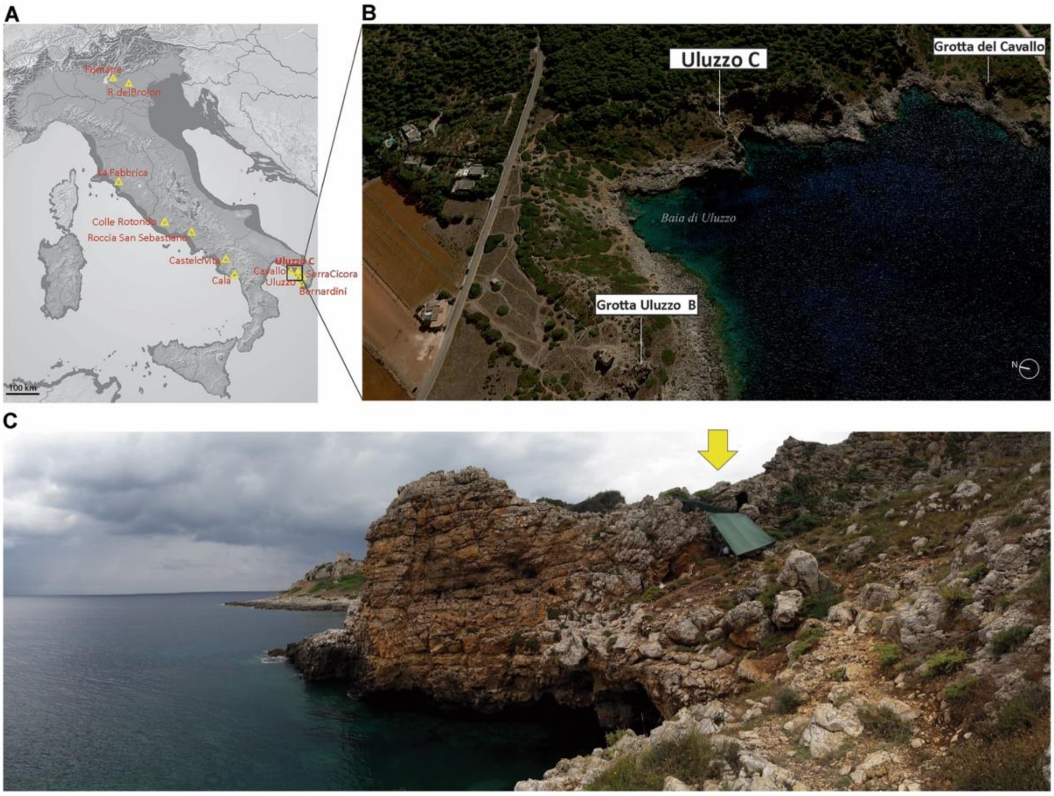


**Figure 1.** A. Uluzzian sites in Italy. B. Location of Uluzzo C in the bay of Uluzzo (Apulia, southern Italy) from Google Earth. C. General view of the site. [Color figure can be viewed at wileyonlinelibrary.com].

*et al.*, 2018) and OSL dated at 46 ± 4.0 ka at Uluzzo C (Layer G – ULOC 1) (Spinapolice *et al.* in this special issue).

## Materials and methods

This paper considers the archaeological finds (i.e. lithics and faunal remains) and sediment samples from the SUs 3, 15 and 17 of the new excavations (2016–2018), which correspond to Borzatti's layer C. In addition, it includes the lithics from layers C, D and E from the excavations carried out by Borzatti during the 1960s (Tables S1–S2). SUs 3, 15 and 17 are three components of the same level of occupation (Layer C) (Fig. 3).

The whole lithic assemblage was analysed by using a technological approach. Furthermore, traceological analysis, with both low- and high-power approaches, was performed on the six retouched items.

Taxonomic and taphonomic evaluations were performed on the macromammal, micromammal, avifaunal and malacofaunal remains. Moreover, DNA analysis of sediments and palaeoproteomics were used to corroborate the zooarchaeological studies.

### *Lithic technological analysis*

The technological analysis was carried out on the lithic materials coming from layers C, D and E of Borzatti's excavations and on the materials coming from SUs 3, 15, 17 of the new excavations.

We decided to include all the layers excavated by Borzatti because of the limited number of the items (i.e. layer C, corresponding to the SUs 3, 15 and 17 included only five lithic items).

Borzatti von Lowerstern and Magaldi (1966) report retrieving 145 lithic items from layers C, D and E. Currently, only 61 of these pieces are stored at the Museo della Preistoria di Nardò (MPN) (Table S1). A total of 339 pieces from SUs 3, 15 and 17 of the new excavations were here analysed (Table S2).

This lithic assemblage was analysed by using a technological approach: Geneste (1991) was used as a fundamental conceptual text on how to approach the reduction sequences; Inizan *et al.* (1999) was used for the definition of technological categories, whereas Boëda (2013) was used to approach lithic technology and, more precisely, regarding the description of the cores. All the archaeological material was sorted according to the lithology and texture of the raw material (chert, jasper, siliceous limestone, limestone and quartz sandstone), the colour of the cortex, the colour of the inner portion of each item, and the presence and type of post-depositional alteration (chemical, mechanical or thermal). Subsequently, items were divided into five dimensional classes (DC) (DC1: 0–50 $mm^2$, DC2: 50–100 $mm^2$, DC3: 100–150 $mm^2$, DC4: 150–200 $mm^2$, DC5: >200 $mm^2$) on the basis of the area covered by each specimen (Marciani *et al.*, 2020b; Spagnolo *et al.*, 2020). Complete items that were larger than the first DC were additionally measured according to both their technological and morphological axes.

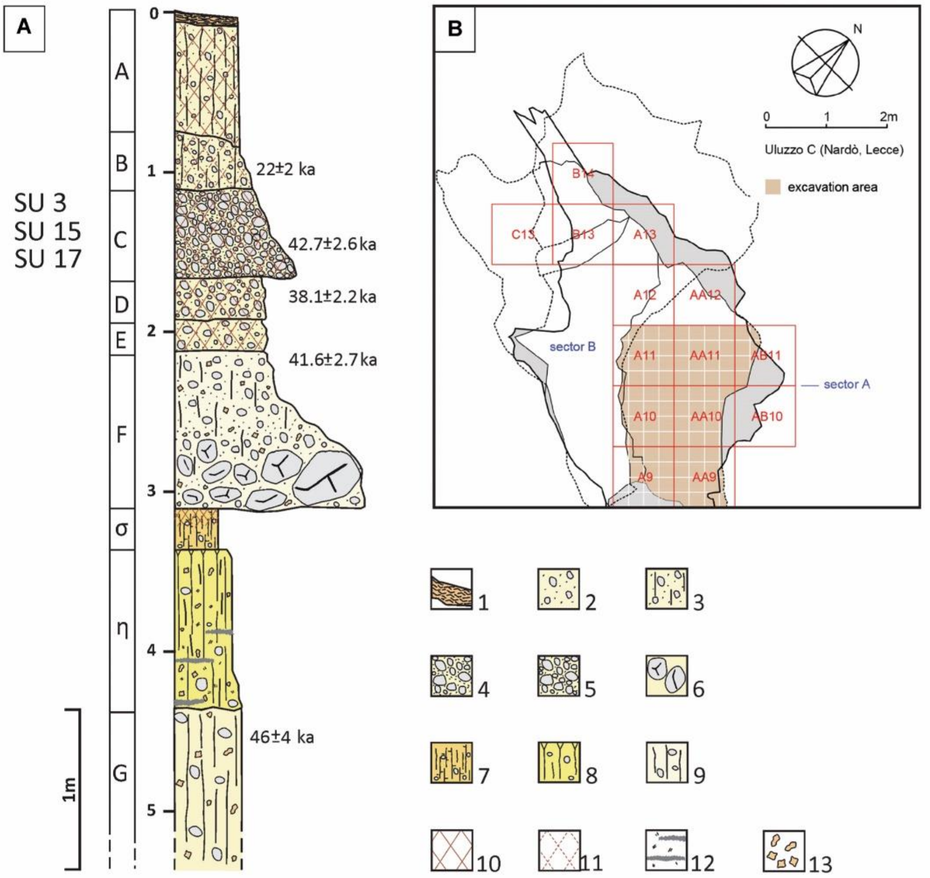


**Figure 2.** A. Log of the stratigraphic sequence of the deposit of the Uluzzo C Rock Shelter. For a full interpretation of the log the reader is referred to Spinapolice *et al.* (in this special issue). OSL dating results are indicated. Key: (1) flowstone; (2) sandy unit with rock fragments and bioturbation; (3) sandy unit with rock fragments and bioturbation; (4) clast-supported breccia displaying weak oblique lamination (sandy matrix); (5) matrix-supported breccia (sandy matrix); (6) large blocks due to roof collapse; (7) clay-rich deposit with scarce rock fragments; (8) slightly weathered silty deposit with scarce rock fragments; (9) silty deposit with scarce rock fragments; (10) $CaCO_3$-cemented deposit; (11) weakly $CaCO_3$-cemented deposit; (12) charcoal fragments and ash-rich lenses; (13) $CaCO_3$ nodules and/or concretions. B. New excavation in sector A. [Color figure can be viewed at wileyonlinelibrary.com].

As the material recorded at Uluzzo C is few in number, and the Uluzzian techno-complex is characterized by an absence of standardization of the categories, in particular regarding production (i.e. Collina *et al.*, 2020), we decided to define the categories of blank based on metric attributes.

Thus, we considered the following technological categories: flakes and blades based on the ratio between length and width, i.e. flakes (ratio length/width ratio $< 2$) and blades (length/width ratio $\geq 2$) (Laplace, 1966). This definition of flakes and blades was used for the Uluzzian layer EIII of Grotta del Cavallo (Moroni *et al.*, 2018). Moreover, flakes whose length is <2.5 cm are named flakelets (<2.5 cm), whereas blades whose length is <2.5 cm are named bladelets (<2.5 cm). The other technological classes are cores, pebbles, debris (items smaller than DC1) and indeterminates (fragmented pieces bigger than DC3, altered pieces, non-orientatable pieces).

For complete flakes, flakelets, blades and bladelets, we registered the localization and extension of the cortex. We identified the concept and methods of debitage and considered: volumetric aspects (morphology, symmetry, profile and section shape); the number and orientation of dorsal scars; the type of butt and bulb; and the position of the impact point (if present). Lastly, the occurrence, type and localization of the retouch or use-wear were also noted.

For each core we observed: the nature and morphology of the raw block; the volumetric conception of the exploitation; the hierarchy of surfaces; the type, location and preparation of the striking platform; the number and direction of the negatives on the surface of the debitage; the level of exhaustion and the possible reason for its abandonment.

Use of the bipolar technique on an anvil was evaluated on the basis of specific traits that characterized this kind of technique: rectilinear longitudinal profile of the ventral face, similar ventral and dorsal faces, pronounced ripple marks, shattered point-form or linear butts, diffused impact points, sheared bulbs of percussion, and the presence of a parasite scar (e.g. Guyodo and Marchand, 2005; Bietti *et al.*, 2010; Soriano *et al.*, 2010; Duke and Pargeter, 2015; de la Peña, 2015; Collina *et al.*, 2020).

## *Lithic use wear analysis*

To evaluate the functional potential of the lithic assemblage from Uluzzo C, a preliminary use-wear analysis was carried

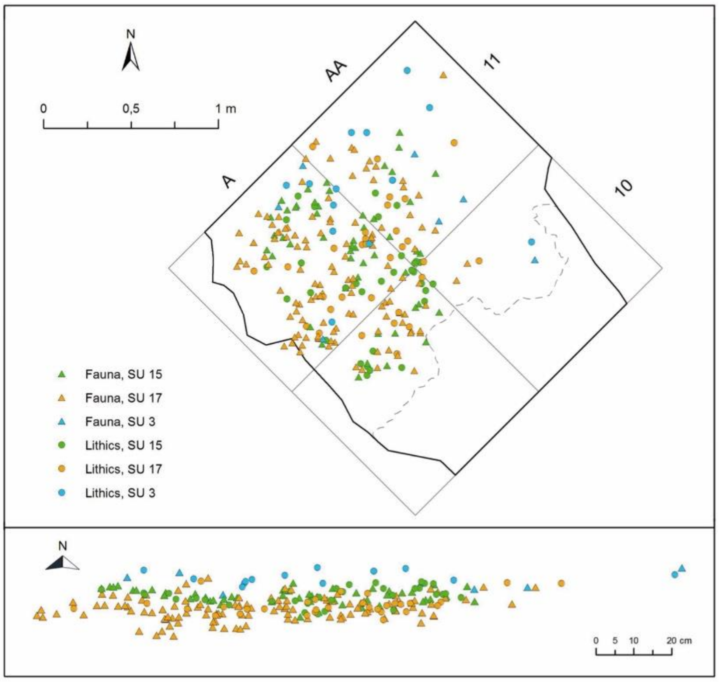


**Figure 3.** Vertical and horizontal distribution of lithic and faunal remains of SUs 3, 15 and 17 from Uluzzo C Rock Shelter. [Color figure can be viewed at wileyonlinelibrary.com].

out on the retouched items recovered during the 2016–2018 excavations (six specimens). Traceological analysis was undertaken following both the low-power approach (LPA) (Tringham *et al.*, 1974; Odell and Odell-Vereecken, 1980; Odell, 1981) and the high-power approach (HPA) (Keeley, 1980; Plisson, 1985; Van Gijn, 2010). Traces were observed by means of a Hirox KH-7700 3D digital microscope using an MX-G 5040Z body equipped with an AD-5040 Lows and an AD-5040HS lens working at low magnification (20–50×) to observe the macro-traces (fractures, edge damage, diagnostic impact fractures), and an MXG-10C body and an OL-140II lens (140–480×) used to analyse micro use-wear (polishes, abrasions and striations). Before examination with the microscope, the artefacts were washed in fresh water and subsequently cleaned with pure acetone to remove traces of soil and finger grease.

## Macromammal remains and zooarchaeological analysis

Identifications of both the skeletal element and the taxa were based on the reference collection stored at the Laboratory of Osteoarchaeology and Paleoanthropology (BONES Lab) of the Department of Cultural Heritage of the University of Bologna (Ravenna, Italy). Microscopic analysis of the bone surfaces was carried out using a Leica stereomicroscope. To identify the nature of the surface alterations on the bones, and to discriminate human from animal traces, trampling abrasion and modern mechanical modifications produced by excavation tools, a well-established taphonomic literature was used as a reference (Binford, 1981; Potts and Shipman, 1981; Shipman, 1981; Brain, 1983; Shipman and Rose, 1984; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Lyman, 1994; Blumenschine, 1995; Fisher, 1995). The degree of combustion was evaluated according to Stiner *et al.* (1995). Sex and age at death were estimated to reconstruct the exploitation strategies of the different species (Aitken, 1974; Mariezcurrena and Altuna, 1983; Vigal and Machordom, 1985; D'Errico and Vanhaeren, 2002; Fiore and Tagliacozzo, 2006). To evaluate species abundance, the number of identified specimens (NISP) was considered (Grayson, 1984).

## Micromammal sorting and palaeontological and taphonomic study

The few recovered micromammal fossil remains analysed in this study were disarticulated mandible fragments and isolated teeth (which were collected by water screening the sediments from the excavation of 2018 with a 0.5-mm mesh screen). The fragments were identified following the general criteria given by Galán-García (2019) for bats and rodents (Berto, 2013). The specific attribution of this material is based principally on the most diagnostic elements: mandible for the genus *Myotis*; and mandible and isolated teeth for the subfamily Arvicolinae and genus *Apodemus*. Moreover, the identified remains were grouped by using the minimum number of individuals (MNI) method, by which we determined the sample by counting the most represented diagnostic elements. Finally, a preliminary taphonomic study was performed to investigate the alterations caused by digestion, which were present in the first lower molars of the arvicoline rodent species (according to Andrews, 1990; Fernández-Jalvo *et al.*, 2016a), ultimately attesting to the action of predation.

## Avifaunal remains

The fossil avifauna from Uluzzo C analysed in this contribution consists of 12 bone remains. The bird remains were recovered after dry/wet sieving of the sediment, numbered with the acronym UC and subjected to taxonomic and taphonomic analyses. Bone identification was possible thanks to the comparison with modern skeletal specimens from two comparative collections: the Marco Pavia Osteological

Collection at the Department of Earth Sciences of the University of Torino and the collection at the Department of Humanities of the University of Ferrara. For identification of the remains, we also used osteology handbooks on particular bird families and orders (Janossy, 1983; Tomek and Bochenski, 2000). Taphonomic analysis was carried out with a 30× lens and a Leica S6D Verde Ough 0.75–70× stereomicroscope, available at the Laboratory of Archaeozoology and Taphonomy of the Prehistoric and Anthropological Sciences Section of the University of Ferrara.

### *Malacofaunal remains*

The classification and nomenclature used for taxonomic analysis of the malacofaunal remains were based on the updated datasets available online on the World Register of Marine Species (WoRMS). The NISP was used to define the number of specimens in the assemblage. The taphonomic study focused on three main groups of alterations (Claassen, 1998): pre-depositional alterations (e.g. marine abrasion, predation by other molluscs and bioerosion); intentional/unintentional anthropogenic alterations (e.g. thermic alterations, anthropic damage caused by consumption); and post-depositional transformations (e.g. fragmentation, abrasions, root marks, decalcification and excavation damage).

### *ZooMS*

We selected 12 unidentified bone samples (>1 cm in size) for zooarchaeology by mass spectrometry (ZooMS) analysis. We tested the protocol designed by Van Doorn *et al.* (2011) and used a warm (65 °C) ammonium bicarbonate buffer (50 mM) to leach bone collagen without acid digestion. Then, trypsin digestion was carried out for 18 h at 37 °C using 0.5 μL of sequencing-grade trypsin (Sigma). Enzymatic digestion was ended using 5 μL of 5% formic acid (FA), then the tryptic digests were purified and concentrated using C18 SpinTips (Thermo Scientific). Peptide elution was performed with 15 μL of 50% acetonitrile (ACN)/0.1% FA (v/v). Samples were dried overnight under a class 100 laminar flow hood. After re-suspension, each sample (1 μL) was spotted on a target steel plate, and mixed with 1 μL α-cyano-4-hydroxycinnamic acid (CHCA; Sigma) as matrix. The samples were then analysed in duplicate with MALDI-ToF (Bruker) over a mass-to-charge range of 700–3500 *m*/*z*. Spectra were manually inspected and averaged using mMass (Strohalm *et al.*, 2010), after setting a signal-to-noise ratio equal to 4. Taxonomic identification was performed comparing identified peptides with a database of peptide markers for all European, Pleistocene medium to large size mammals (Welker *et al.*, 2016).

### *Ancient DNA analysis*

A total of 14 sediment samples, which were collected from the site on two different occasions, were tested for the preservation of ancient faunal or hominin DNA. The first set consisted of 11 samples from squares A11 and AA11 in SU 15. The second set was composed of three samples collected from square A11 in SU 17 (Table S3). Subsamples of each sample, ranging between 42 and 100 mg, were used as input for DNA extraction using a silica-based protocol (Dabney *et al.*, 2013), which was performed either manually or using a liquid handling platform (Bravo NGS workstation, Agilent Technologies) as described by Rohland *et al.* (2018).

All subsequent laboratory procedures were performed on the liquid handling platform as described by Slon *et al.* (2017). A single-stranded DNA library was prepared from each DNA extract using the procedure described by Gansauge *et al.* (2017, 2020), the efficiency of which was assessed by quantitative PCR. The number of library molecules generated from sediment samples was higher than those prepared from associated negative controls (Table S3), which demonstrates that the library preparation procedures were successful (Gansauge and Meyer, 2013).

The number of molecules generated from a control oligonucleotide was similar between the sediment libraries and the controls, thus indicating that potential inhibitory substances that may have been co-extracted with the sediment were not interfering with the library preparation procedure to an appreciable extent (Glocke and Meyer, 2017).

Each library was then amplified to PCR plateau and tagged with two indices (Kircher *et al.*, 2012). Libraries originating from sample set 1 were enriched by hybridization capture for mammalian mitochondrial DNA (mtDNA) (Slon *et al.*, 2016), as well as specifically for human mtDNA (Maricic *et al.*, 2010; Fu *et al.*, 2013), while libraries from set 2 were only enriched for human mtDNA. Paired-end sequencing was performed on an Illumina MiSeq platform using 76 cycles. We note that all sample libraries were sequenced to an adequate depth, as indicated by the duplication rate observed (Table S3). Negative controls for the DNA extraction and library preparation procedures were carried along with the samples.

The processing of sequencing data was performed as described in detail by Slon *et al.* (2017). After removing PCR duplicates and fragments shorter than 35 bases, taxonomic identification at the family level was carried out for each sequenced DNA fragment by comparing it to a database of reference mammalian mtDNA genomes (Altschul *et al.*, 1990; Huson *et al.*, 2007). At least 10 fragments and at least 1% of identified fragments were required to be assigned to a family for it to be deemed present in a sample. For each identified family, we then tested whether the DNA fragments assigned to it displayed elevated frequencies (i.e. significantly higher than 10%, tested using an exact binomial test) of terminal cytosine (C) to thymine (T) nucleotide substitutions compared to a reference genome. These substitutions are a typical feature of ancient DNA and allow us to determine whether ancient DNA fragments are present in a sample (Briggs *et al.*, 2007). None of the negative controls tested positive for the preservation of ancient DNA (Table S3).

## Results

### *Lithic technology*

#### *Technological analysis: Borzatti's excavation*

The 61 lithic artefacts from Borzatti's excavation in 1964 (five items from layer C, six items from layer D, 50 items from layer E), which are stored at the Museo della Preistoria di Nardò (Lecce, Apulia), all have fresh margins, except for nine items with blunted edges. Moreover, 11 pieces show traces of a yellow or white patina, and traces of combustion are visible on four items. Generally, their state of preservation is coherent with the lithics coming from the current excavations. In all the layers there is a predominance of fine-grained chert, followed by siliceous limestone. Occasional limestone and jasper are attested to in layer E (Table 1). Most of the pieces, corresponding to 57.4% of the collection, pertain to DC 5 (corresponding to pieces >200 mm$^2$) (Tables 2 and 3). No lithics pertain to DC 1 (0–50 mm$^2$) and only seven pertain to DC 2 (50–100 mm$^2$) (Table 2). After comparison with the lithics from the more recent excavation (see below), it is evident that a selection bias must have affected the retrieval of

**Table 1.** Raw material (*Excavation Borzatti*)

| Raw material | Layer C | Layer D | Layer E | Total | % |
|---|---|---|---|---|---|
| Chert | 3 | 4 | 38 | 45 | 73.8 |
| Siliceous limestone | 2 | 2 | 7 | 11 | 18.0 |
| Limestone | 0 | 0 | 4 | 4 | 6.6 |
| Jasper | 0 | 0 | 1 | 1 | 1.6 |
| Total | **5** | **6** | **50** | **61** | **100** |

**Table 2.** Dimensional classes (*Excavation Borzatti*)

| Dimensional classes | Layer C | Layer D | Layer E | Total | % |
|---|---|---|---|---|---|
| DC 2 | 0 | 0 | 7 | 7 | 11.5 |
| DC 3 | 0 | 1 | 7 | 8 | 13.1 |
| DC 4 | 1 | 0 | 10 | 11 | 18.0 |
| DC 5 | 4 | 5 | 26 | 35 | 57.4 |
| Total | 5 | 6 | 50 | 61 | 100 |

the lithic artefacts in the 1960s, probably because researchers were more interested in large diagnostic items, such as retouched pieces. Given the biased composition of the collection and the high degree of the retouch, it was not possible to determine from which reduction sequence these items had come from.

Layer C is represented by only five items, and noteworthy is the presence of two cores that were reduced by the bipolar technique, one of which was then retouched (Fig. 4C). Layer D presents six items, among which there are two flakes and one bladelet. Layer E is the one with the most items (50), including one core, 16 flakelets, eight flakes and five blades. Complete cortex coverage is present in only two flakes, whereas three flakes present between 50 and 75%; all the other items present between 25% and 0 cortex coverage. The bipolar technique is attested to on 18 items in almost all the categories (Table 3).

The assemblage includes 20 retouched pieces made mainly on flakes, flake fragments and indeterminate fragments. Most of the retouched tools occurred on pieces with a length >3 cm. Typologically, there is a prevalence of scrapers ($n = 11$). Noteworthy is the presence of one end scraper and two lunates (Fig. 4A <B). The latter is the most representative retouched tool of the Uluzzian (Table 4).

From a diachronic point of view, chert is the prevailing raw material in all technological classes in the three layers. A greater variety of raw material and greater quantity of pieces is found in layer E. Layers C and D present very few entire pieces, in both cases the majority being retouched tools. Layer E displays a set of large retouched tools and a smaller component of flakelets (Fig. 5).

### *Technological analysis: 2016–2018 excavation*

The industry is not particularly affected by post-depositional alterations and there are no pieces presenting double patinas. All lithics have fresh margins, except for two pieces that present blunt edges, and only six pieces show traces of combustion.

Regarding the raw materials, we observe a selection of fine-grained raw materials of different nature: nine pieces were extracted from pebbles, four pieces from slabs of local siliceous limestone and 11 from local chert lists. Even without evident traces of cortex, it was still possible to associate the siliceous limestone with the local outcrops, used in the nearby sites throughout the Mousterian and the Uluzzian (Spinapolice, 2012, 2018; Moroni *et al.*, 2013; Spinapolice *et al.*, 2018). The chert, by contrast, is partly local (white and blue chert), coming from the same outcrops where the siliceous limestone was found, and partly (beige or very glassy grey chert) similar to the materials of the Apennines or of the Gargano area. We also noted the sporadic presence of jasper and quartzite (Table 5), probably coming from the Bradano River basin (Basilicata, southern Italy).

Most of the lithics, corresponding to 80.7% of the collection, are included in the first (71.4%) and second (11.5%) dimensional classes (Table 6). Most of them (250 items) are debris, which is the waste of the debitage and indicates that flaking activities were performed *in situ*. For these fragments, it is not possible to detect the concept of debitage. Among these artefacts, 26.2% (corresponding to 89 items) are the more diagnostic pieces, which are useful to infer information on the reduction sequences performed at the site. The initialization of the reduction sequence is attested to by only two semi-cortical flakes, and hence the first stage of debitage is not documented at the site (or at least in the portion of the site under investigation).

The phases of full debitage are mainly attested to by the production of flakelets (Fig. 6), blades and bladelets (Fig. 7) (Table 7). Also, a significant number of fragmented flakes and fragmented blade-bladelets are present (Table 7). The blanks show predominantly unidirectional scar patterns ($n = 43$). Some blanks show convergent ($n = 8$), orthogonal ($n = 8$) or bidirectional ($n = 5$) scar patterns. Most pieces exhibit a rectilinear profile ($n = 58$), but there are some that present a convex ($n = 7$), wavy ($n = 4$) or concave ($n = 2$) profile. The butts are mainly flat ($n = 15$), point-form ($n = 15$) or linear

**Table 3.** Technological categories: R indicates the retouched pieces, B indicates the pieces produced by the bipolar technique (*Excavation Borzatti*)

| | Layer C | | | Layer D | | | Layer E | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Technological category | Total | R | B | Total | R | B | Total | R | B | Total | R | B |
| Cortical flakes | | | | | | | 2 | | | 2 | | |
| Flakes | 1 | 1R | | 2 | 1R | | 8 | 3R | 1B | 11 | 5R | 1B |
| Flakelets <2.5 cm | | | | | | | 16 | 1R | 6B | 16 | 1R | 6B |
| Flakes fragmented | | | | 2 | 2R | | 7 | 2R | 2B | 9 | 4R | 2B |
| Blades | | | | | | | 5 | 3R | 4B | 5 | 3R | 4B |
| Bladelets <2.5 cm | 1 | | | 1 | 1R | 1B | | | | 2 | 1R | 1B |
| Cores | 2 | 1R | 2B | | | | 1 | 1R | | 3 | 2R | 2B |
| Indeterminate fragment >DC 3 | 1 | | | 1 | 1R | 1B | 7 | 3R | 1B | 9 | 4R | 2B |
| Debris DC 1–2 | | | | | | | 4 | | | 4 | | |
| Total | 5 | 2R | 2B | 6 | 5R | 2B | 50 | 13R | 14B | 61 | 20R | 18B |

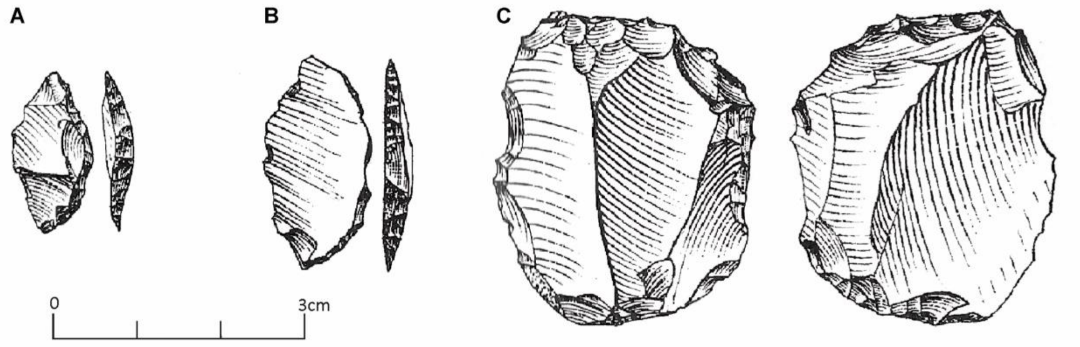


**Figure 4.** A. Lunates from layer E. B. Lunates from layer C. C. Splintered piece/core from layer C (modified from Borzatti, 1965).

**Table 4.** Retouched tools (*Excavation Borzatti*)

| Retouched tools | Layer C | Layer D | Layer E | Total |
|---|---|---|---|---|
| Unilateral scraper | 1 | 2 | 7 | 10 |
| Bilateral scraper | | | 1 | 1 |
| End scraper | | 1 | | 1 |
| Lunate | 1 | 1 | | 2 |
| Limace | | | 1 | 1 |
| Point | | 1 | 2 | 3 |
| Indeterminate retouched | | | 2 | 2 |
| Total | 2 | 5 | 13 | 20 |

**Table 5.** Raw material (*Excavation 2016–2018*)

| | SU 3 | | SU 15 | | SU 17 | | | |
|---|---|---|---|---|---|---|---|---|
| Raw material | *N* | % | *N* | % | *N* | % | Total | % |
| Chert | 25 | 78.1 | 56 | 74.7 | 170 | 73.3 | 251 | 74.0 |
| Siliceous limestone | 3 | 9.4 | 14 | 18.7 | 46 | 19.8 | 63 | 18.6 |
| Jasper | 1 | 3.1 | 4 | 5.3 | 4 | 1.7 | 9 | 2.7 |
| Quartz sandstone | | | 1 | 1.3 | 3 | 1.3 | 4 | 1.2 |
| Indeterminate | 3 | 9.4 | | | 9 | 3.9 | 12 | 3.5 |
| Total | 32 | 100 | 75 | 100 | 232 | 100 | 339 | 100 |

($n = 14$). The impact point is mainly central or diffused. The percussion bulb is mostly not prominent. The flat or linear butt, the non-prominent bulb, the diffused point of percussion and the linear profile, as well as the considerable variability in the debitage-objective's morphology (Figs. 6 and 7), are typical traits of the bipolar technique. This technique is found on 32 items, mainly flakelets, flake fragments, bladelets and the four cores.

The assemblage counts six retouched pieces made on flakelets, flake fragments and indeterminate fragments (Table 7). Typologically, there are four side scrapers and two transversal scrapers. Four are made from chert, one from jasper and one from siliceous limestone. These items pertain to DCs 4 and 5.

The four cores are characterized by: (i) an advanced state of exploitation and (ii) the use of the bipolar technique on an anvil (Fig. 8). Specifically, the raw blocks chosen to be flaked are flakes or fragments made of chert. The dimension of the natural supports is relatively small (length 22–16 mm; width 15–12 mm; thickness 11–6 mm). The striking platforms were used without any preparation and are orthogonal to the debitage surface. The scars on the surface of the debitage have mainly a bidirectional pattern. Due to the small dimensions of the cores, the extracted blanks are also very small: <2 cm. This size is compatible with the objective of the debitage.

To summarize: SU 3 is characterized by very few items, mainly made of chert; SU 15 is characterized by the most

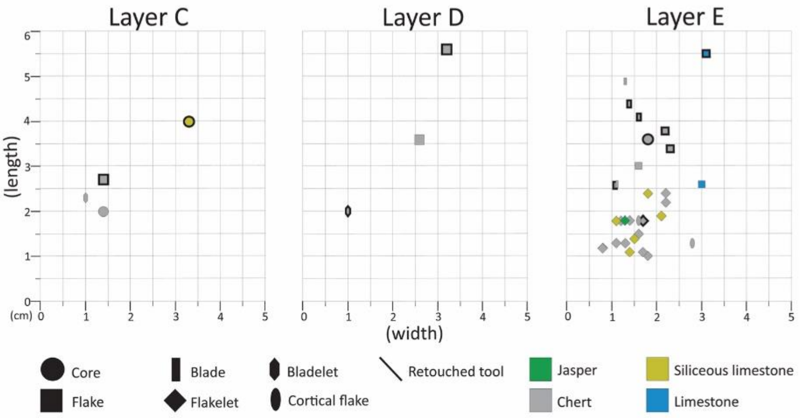


**Figure 5.** Scatter plot of the lithic items coming from Borzatti's excavation. The technological categories are shown with different symbols; the raw materials are shown with different colours. The items marked with a dark black line are the retouched tools. As the plot is based on length/width, only entire items were considered. [Color figure can be viewed at wileyonlinelibrary.com].

**Table 6.** Dimensional classes (*Excavation 2016-2018*)

| | SU 3 | | SU 15 | | SU 17 | | | |
|---|---|---|---|---|---|---|---|---|
| Dimensional class | *N* | % | *N* | % | *N* | % | Total | % |
| DC 1 | 19 | 59.4 | 39 | 52.0 | 184 | 79.3 | 242 | 71.4 |
| DC 2 | 4 | 12.5 | 10 | 13.3 | 25 | 10.8 | 39 | 11.5 |
| DC 3 | 1 | 3.1 | 7 | 9.3 | 11 | 4.7 | 19 | 5.6 |
| DC 4 | 2 | 6.3 | 9 | 12.0 | 5 | 2.2 | 16 | 4.7 |
| DC 5 | 6 | 18.8 | 10 | 13.3 | 7 | 3.0 | 23 | 6.8 |
| Total | 32 | 100 | 75 | 100 | 232 | 100 | 339 | 100 |

scattered distribution of pieces based on size and presents the most significant variety of raw material, i.e. mainly chert, but there is also a flake made in jasper and three pieces made in siliceous limestone. SU 17 is the one that has the most even distribution of items based on their dimensions, most of its blanks are flakelets and it is where the cores were found (Fig. 9). These three SUs represent an occupation palimpsest made up by at least two types of activities: (i) the small blanks made of chert are the result of *in situ* flaking; while (ii) the bigger items, the retouched tools and the blanks made of a raw material other than chert, come from reduction sequences that are not attested to in the excavated portion of the site.

## *Lithic use-wear analysis*

Within the sample of six retouched specimens, diagnostic use-wear was identified on only one transversal scraper (R76 – Fig. 10A). It exhibits a developed edge rounding and a weak polish with rough texture on the retouched portion (Fig. 10). The traces suggest the tool was used for hide-working activities by using a transversal motion (scraping). A few bright spots were also detected on the proximal edge which could indicate that the tool had been hafted.

The other transversal scraper (R54 – Fig. 10B) shows unclear traces on the retouched edge. The remaining four pieces did not reveal any traces at all.

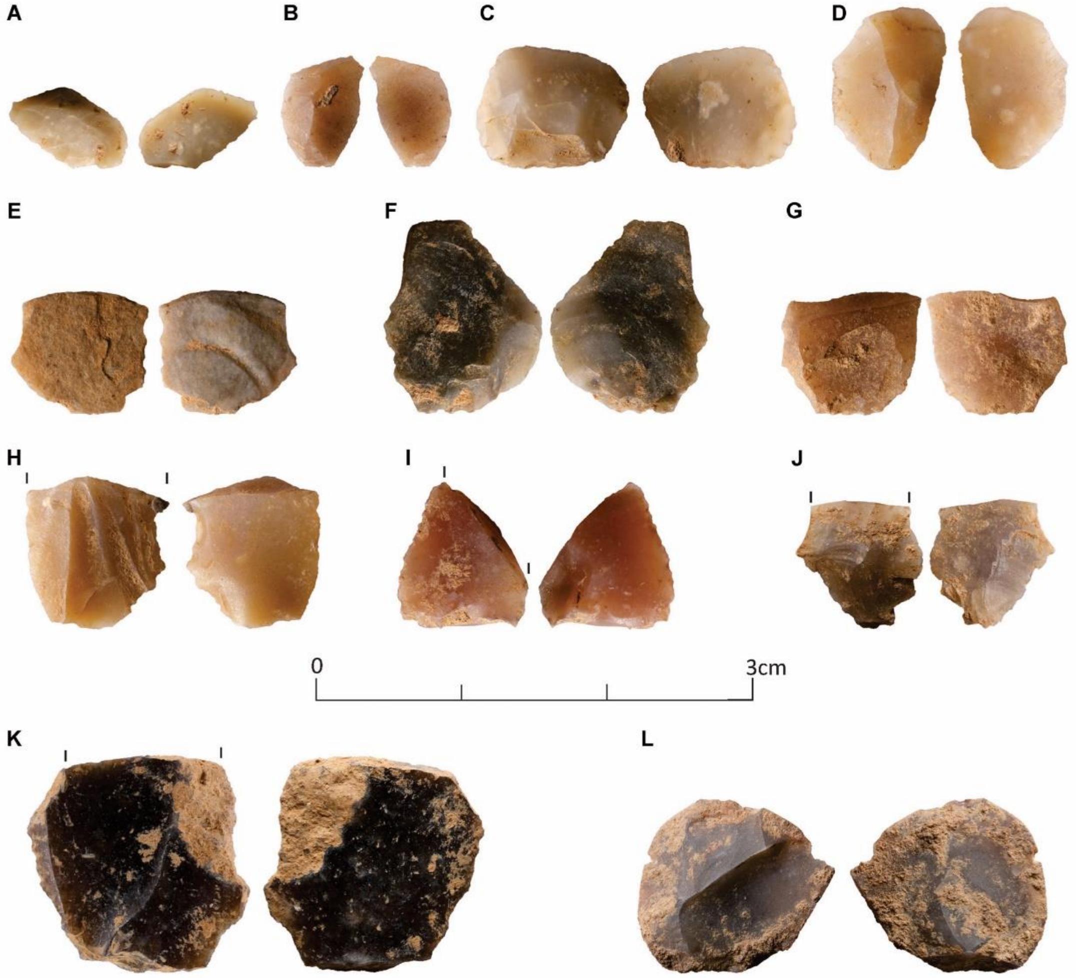


**Figure 6.** Flakelets (A–G, L) and fragmented flakes (H–K). Note the small size and the absence of a standardization in the shapes. Blanks produced by the bipolar technique on an anvil (B, D, E, F, H, I, J). Note that J has very similar ventral and dorsal face of the flake; E, F and H have ripple marks, and E, F and J have flat or smashed bulbs. [Color figure can be viewed at wileyonlinelibrary.com].

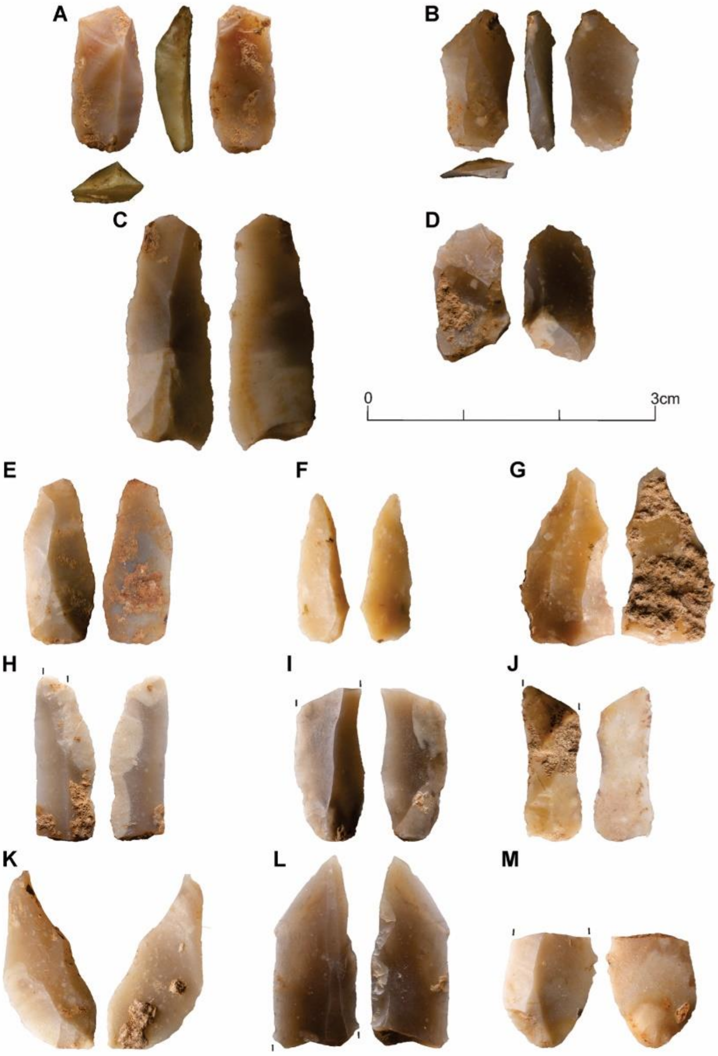
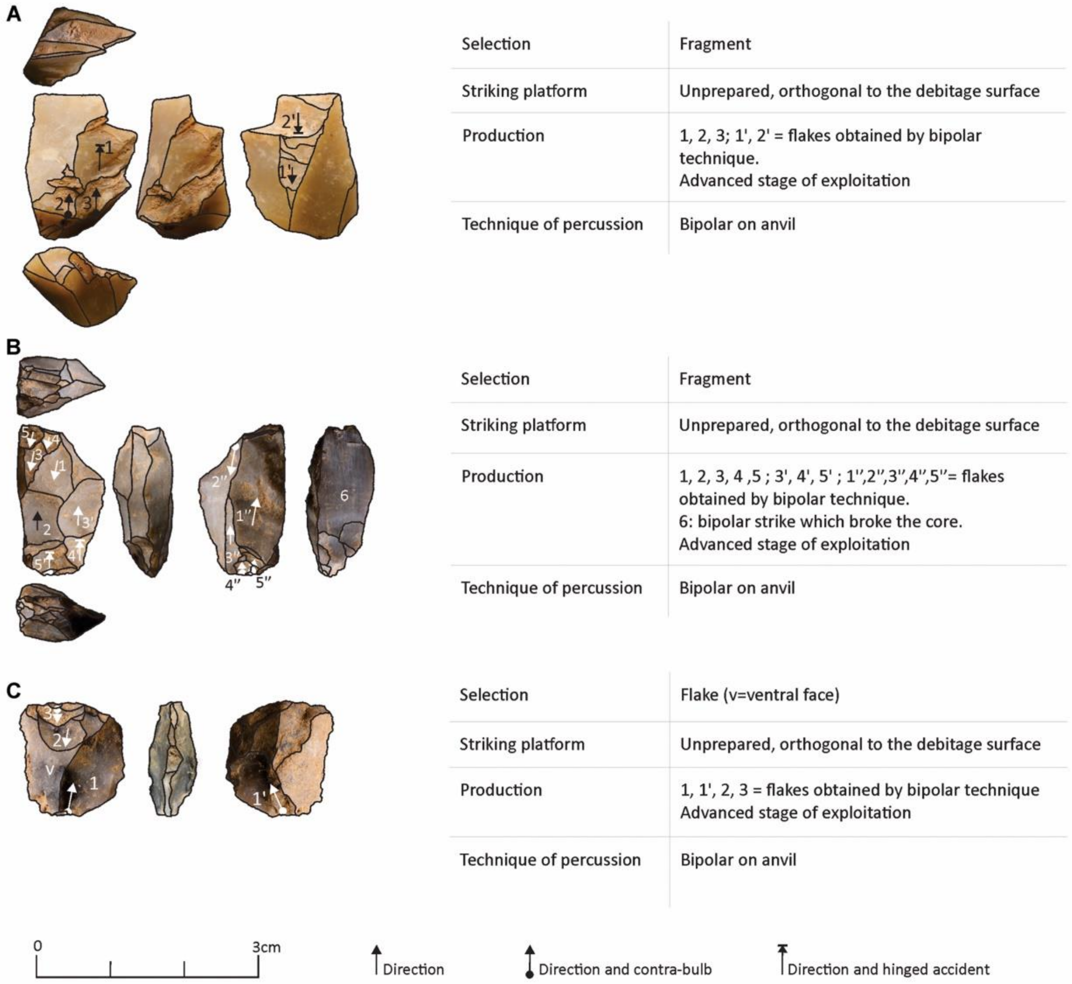


**Figure 7.** Bladelets (A, B, D, E, F, G), blade (C, K), fragmented blade-bladelets (H, I, J, L, M). Blanks produced by the bipolar technique on an anvil (A–D); blanks produced by direct percussion technique (E–M). Note that the raw material is fine-grained chert. [Color figure can be viewed at wileyonlinelibrary.com].

**Table 7.** Technological categories: R indicates the retouched pieces, B indicates the pieces produced by the bipolar technique (*Excavation 2016–2018*)

| | SU 3 | | | | SU 15 | | | | SU 17 | | | | Total | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Technological category | *N* | % | R | B | *N* | % | R | B | *N* | % | R | B | *N* | % | R | B |
| Flakes | | | | | 2 | 2.7 | | | | | | | 2 | 0.6 | | |
| Flakelets <2.5 cm | 4 | 12.5 | | 1B | 10 | 13.3 | 2R | 5B | 13 | 5.6 | | 5B | 27 | 8 | 2R | 11B |
| Flakes fragmented | 2 | 6.3 | | 1B | 6 | 8.0 | 1R | 1B | 17 | 7.3 | 2R | 6B | 25 | 7.4 | 3R | 8B |
| Blades | | | | | 4 | 5.3 | | 1B | | | | | 4 | 1.2 | | 1B |
| Bladelets <2.5 cm | | | | | 4 | 5.3 | | 1B | 3 | 1.3 | | 2B | 7 | 2.1 | | 3B |
| Blade–bladelets fragmented | 1 | 3.1 | | | 5 | 6.7 | | 1B | 6 | 2.6 | | 1B | 12 | 3.5 | | 2B |
| Cores | 1 | 3.1 | | 1B | | | | | 3 | 1.3 | | 3B | 4 | 1.2 | | 4B |
| Indeterminate fragments >DC 3 | 2 | 6.3 | | | 1 | 1.3 | 1R | | 5 | 2.2 | | 1B | 8 | 2.4 | 1R | 1B |
| Debris DC 1–2 | 22 | 68.8 | | | 43 | 57.3 | | 2B | 185 | 79.7 | | | 250 | 73.7 | | 2B |
| Total | 32 | 100 | 0R | 3B | 75 | 100 | 4R | 11B | 232 | 100 | 2R | 18B | 339 | 100 | 6R | 32B |
| Total (without debris) | 10 | | | | 32 | | | | 47 | | | | 89 | | | |



**A**

| | |
|---|---|
| Selection | Fragment |
| Striking platform | Unprepared, orthogonal to the debitage surface |
| Production | 1, 2, 3; 1', 2' = flakes obtained by bipolar technique.<br>Advanced stage of exploitation |
| Technique of percussion | Bipolar on anvil |

**B**

| | |
|---|---|
| Selection | Fragment |
| Striking platform | Unprepared, orthogonal to the debitage surface |
| Production | 1, 2, 3, 4 ,5 ; 3', 4', 5' ; 1'',2'',3'',4'',5''= flakes obtained by bipolar technique.<br>6: bipolar strike which broke the core.<br>Advanced stage of exploitation |
| Technique of percussion | Bipolar on anvil |

**C**

| | |
|---|---|
| Selection | Flake (v=ventral face) |
| Striking platform | Unprepared, orthogonal to the debitage surface |
| Production | 1, 1', 2, 3 = flakes obtained by bipolar technique<br>Advanced stage of exploitation |
| Technique of percussion | Bipolar on anvil |

**Figure 8.** Bipolar cores from SU 17 (A–C). [Color figure can be viewed at wileyonlinelibrary.com].

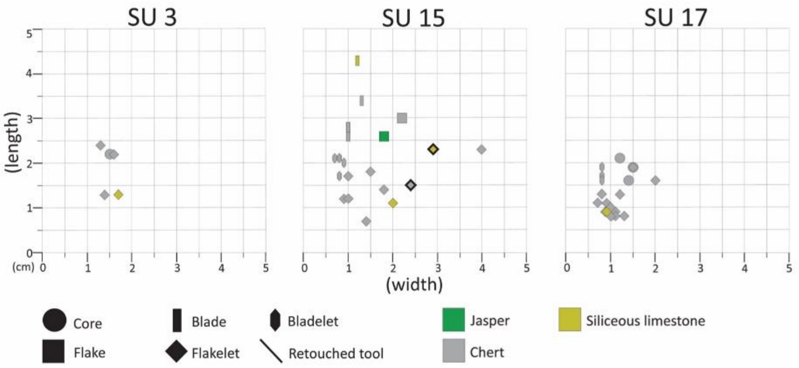


**Figure 9.** Scatter plot of the lithic items coming from the new excavation. The technological categories are shown with different symbols; the raw materials are shown with different colours. The items marked with a dark black line are the retouched tools. As the plot is based on length/width, only entire items were considered. [Color figure can be viewed at wileyonlinelibrary.com].

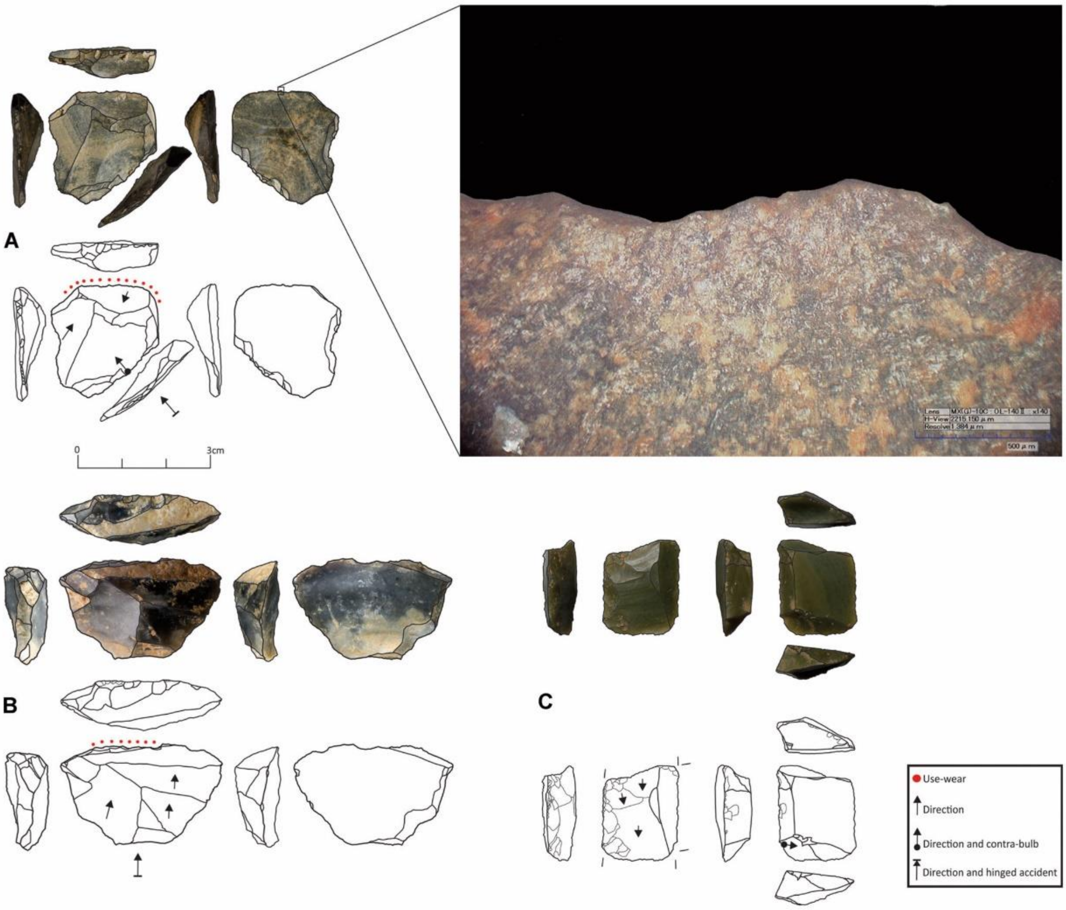


**Figure 10.** Retouched tools. The pointed line indicates the presence of use-wear. A, B: transverse scrapers, C: lateral scraper. [Color figure can be viewed at wileyonlinelibrary.com].

## *Zooarchaeological analysis*

### *Macromammal bone assemblage: Borzatti's excavation*

The composition of the faunal assemblage for all the stratigraphic sequence was analysed by Borzatti following his excavation (1964). The bone remains appeared fragmented and scarce, limiting the zooarchaeological considerations. However, in spite of this, he tried to infer information on the palaeoclimatic and palaeoenvironmental conditions at the Uluzzo C Rock Shelter. The faunal composition was characterized by the presence of *Equus caballus, Equus asinus hydruntinus, Cervus elaphus, Dama dama, Bos* sp., *Sus scrofa, Vulpes vulpes, Canis lupus, Lepus* sp., *Merula merula, Falco tinnunculus, Turdus musicus* and *Columba palumbus*.

In the stratigraphic sequence, considering the transition from Borzatti's layer D to C, it is important to highlight that the increase in the presence of equid remains (dry open environments) corresponds to the decrease of cervids (forest) and bovids (open humid landscape). Borzatti noted the change of a pivotal element in the stratigraphic sequence: the presence of humidity in different phases. For layer C, he observed an abundant presence of *Equus*, which indicates grassland habitats, and minor evidence regarding the presence of Cervidae and Bovidae compared to layer D (Borzatti von Lowerstern, 1965). He suggested that a fluctuation in the climatic conditions may have affected the extension or reduction of the forests and grasslands surrounding the site.

### *Macromammal bone assemblage: 2016–2018 excavation*

Only 119 out of 2304 bone remains from the 2016–2018 excavations (5.1% of the faunal assemblage) were identifiable to a taxonomic level (Table 8). Eleven genera and nine species belonging to four different orders of mammals (lagomorphs, carnivores, perissodactyls and artiodactyls) were recognized. Some of these mammals are represented by very few specimens (*Mustela nivalis, Martes* sp., *Meles meles, Capreolus capreolus, Rupicapra* sp.), while others are represented by a fair quantity of bone elements (*Vulpes vulpes, Cervus elaphus*). Among the layers that were considered, differences in faunal composition are minimal, with *Vulpes vulpes* and *Cervus elaphus* always present, while *Equus ferus, S. scrofa* and Caprinae present only in SUs 17 and 15 (Fig. 11).

However, in SU 17 the presence of red deer increases compared to SUs 15 and 3. Moreover, only in SU 17 is there the presence of hare, weasel, badger, marten, auroch or bison, roe deer and chamois, which suggests a low-temperate climate

**Table 8.** Mammal NISP (number of identified specimens) for SUs 3, 15 and 17

| Uluzzo C – Sector A | SU 3 NISP | SU15 NISP | SU 17 NISP | Total | % |
|---|---|---|---|---|---|
| *Lepus* sp. | 1 | | 5 | 6 | 5.0 |
| Total Rod. –Lagomorpha | 1 | | 5 | 6 | 5.0 |
| *Vulpes vulpes* | 1 | 3 | 6 | 10 | 8.4 |
| *Vulpes* sp. | | 2 | 1 | 3 | 2.5 |
| *Mustela nivalis* | | | 1 | 1 | 0.8 |
| *Meles meles* | | | 1 | 1 | 0.8 |
| *Martes* sp. | | | 1 | 1 | 0.8 |
| Carnivora indet. | | 2 | 4 | 6 | 5.0 |
| Total Carnivora | 1 | 7 | 14 | 22 | 18.4 |
| *Equus ferus* | | 5 | 5 | 10 | 8.4 |
| *Sus scrofa* | | 4 | 3 | 7 | 5.8 |
| *Cervus elaphus* | 1 | 2 | 10 | 13 | 10.9 |
| *Capreolus capreolus* | | | 1 | 1 | 0.8 |
| Cervidae | | 1 | 4 | 5 | 4.2 |
| *Bos/Bison* | | | 5 | 5 | 4.2 |
| *Rupicapra* sp. | | | 1 | 1 | 0.8 |
| Caprinae | | 2 | 3 | 5 | 4.2 |
| Ungulata | 1 | 5 | 38 | 44 | 36.9 |
| Total Ungulata | 2 | 19 | 70 | 91 | 76.4 |
| Total NISP | 4 | 26 | 89 | 119 | 100 |
| Small mammals | 1 | 1 | 12 | 14 | 0.64 |
| Small to medium-sized mammals | | 1 | 6 | 7 | 0.32 |
| Medium-sized mammals | 1 | 4 | 8 | 13 | 0.59 |
| Medium-large sized mammals | 1 | 7 | 30 | 38 | 1.7 |
| Large mammals | 3 | 7 | 24 | 34 | 1.5 |
| Indet. sized mammals | 94 | 269 | 1716 | 2079 | 95.1 |
| Total mammals indet. | 100 | 289 | 1796 | 2185 | 94.8 |
| Total NR | 104 | 315 | 1885 | 2304 | 100 |
| Fragm. burned | 15 | 24 | 108 | 147 | 96.7 |
| Fragm. calcined | 1 | 3 | 1 | 5 | 3.2 |
| Total burned | 16 | 27 | 109 | 152 | 6.5 |

with woodland covering and the presence of open environments.

Given the small number of determined elements and the preliminary state of the analysis of the faunal remains, the MNI was not calculated. Bones are mostly fragmented and over 98.3% of the specimens are smaller than 3 cm. Among the analysed remains, only 9% [number of remains (NR) = 209] are burned: over 97.6% (NR = 204) of these show a brown or black colour (indicating a burning temperature of ca. 200–400 °C) (Stiner *et al.*, 1995; Costamagno *et al.*, 2005) and only 2.3% (NR = 5) are small calcinated fragments (<2 cm). Among the analysed bones, 19.2% (NR = 444) have concretions, while 15.7% (NR = 362) are characterized by a manganese coating and a few other remains present root furrows.

Evidence of butchering activity is provided by three bone remains with cutmarks that are probably linked to defleshing activities. In detail, two of the three elements are diaphyseal fragments of ribs, one from a large ungulate and one from either *Bos primigenius* or *Bison priscus*. In both these remains, the butchering traces are located on the dorsal surface and are short, closely related, and oblique to the major axis of the anatomical element (Fig. 12). The third is a left medial proximal diaphyseal fragment of *Lepus* sp. with evident scraping-marks, probably associated with the removal of muscular mass and flesh (Fig. 12). Moreover, some bone fragments showed traces of acid corrosion from partial digestion.

Finally, we identified three percussion cones indicating the activity of bone fracturing for the extraction of marrow (Fig. 12).

### *Micromammals*

The micromammal assemblage consists of 25 identified specimens, corresponding to a minimum of 17 individuals, and representing only three taxa [*Myotis myotis*, *Microtus* (*Terricola*) *savii* and *Apodemus* (*Sylvaemus*) sp.] (Fig. 13; Table 9).

A total of 24 lower first molars of Savi's pine vole [*Microtus* (*Terricola*) *savii*] from the totality of the stratigraphic units were studied. All the observed teeth presented some degree of digestion (Table 10), indicating that the micromammal accumulation was caused by the action of predation. According to Andrews (1990) and Fernández-Jalvo *et al.* (2016a), predators from Categories 1 to 4 – which include a broad spectrum of nocturnal and diurnal birds of prey – could be responsible for such an accumulation of micromammal remains.

### *Avifauna*

Of 12 bird bone remains, 11 have been identified either at the species level or at the supraspecific level. The poor state of preservation of the remains, due to their fragmentary nature and the presence of concretions that concealed the bones' diagnostic features, allowed us to identify at a specific level only two remains, which luckily provided precise palaeoenvironmental indications. *Melanocorypha calandra* suggests the presence, in the surroundings of the cave, of open environments such as grasslands and steppes, with bare terrains and low vegetation, whereas *Pyrrhocorax pyrrhocorax* points to the presence of rocky cliffs and crags with grassland areas (Cramp, 1998).

The taphonomic analysis detected the presence of some natural modifications. The most abundant ones are manganese dioxide staining and sediment concretions, but we also have identified traces of root etching and trampling (Fernández-Jalvo and Andrews, 2016b). No modifications by carnivores, nocturnal raptors or humans have been found. The finding of Corvidae and *Falco* sp. remains, together with the *P. pyrrhocorax* remains, could be due to the natural death of birds living close to the rock shelter, which could have served as a nesting place for these species (Cramp, 1998).

### *Malacofauna*

The malacological assemblage includes 20 specimens belonging to *Patella* sp. and *Phorcus turbinatus* (Table 11). Moreover, a sea urchin fragment was discovered in SU 17. Six small fragments are the only invertebrate remains found in SU 15 and just one was identified as *Patella* sp. Moving down the stratigraphic sequence (SU 17), the amount of invertebrate remains becomes more abundant and two whole *Ph. turbinatus* were detected (Fig. 14). These species live in a littoral environment, i.e. intertidal rocky shores. The malacological assemblage does not show pre-depositional alterations (Table 12) – generally connected to post-mortem damage caused by shore abrasion, bioerosion, carnivorous gastropods or other predators (such as birds or crabs) – ultimately suggesting that the shells were gathered alive and carried to the site. Nonetheless, we do not exclude the possibility at some of the damages might have been caused by post-depositional processes. Furthermore, 5% of the remains are characterized by cracks that are consistent with exposure to high temperatures, as also suggested by the decalcification index (total layers: 60%), since heat exposure (above 300 °C according to Milano *et al.*, 2016) modifies the shell structure and leads to dissolution and fragmentation. Thin sections of

**Figure 11.** Some determined mammal remains from SUs 15 and 17. (1) *Equus ferus.* $LM_3$. SU 15. (2) *Equus ferus.* $I_{lower}$. top SU 17. (3) *Sus scrofa.* Jugal tooth. SU 15 V tg. (4) *Sus scrofa.* $RI_{1-2}$. SU 17 I tg. (5) *Cervus elaphus.* $LI_1$ SU 17. (6) *Cervus elaphus.* $RM_1$ SU 17 I tg. (7) *Cervus elaphus.* First phalanx SU 17. (8) *Cervus elaphus.* $I_3$. SU 15. (9) *Capreolus capreolus.* $RP_2$. SU 17 I tg. (10) *Bos* sp. $I_{1-2}$. SU 17 I tg. (11) *Bos/Bison.* $LI_4$. SU 17. (12) *Rupicapra* sp. $RM_3$. SU 17. (13) *Lepus* sp. Left posterior proximal diaphysis of femur. SU 17 II tg. (14) *Vulpes vulpes.* $RP^4$. SU 17 II tg. (15) *Vulpes* sp. Proximal phalanx. SU 15. (16) *Meles meles.* Lower incisor. SU 17 I tg. (17) *Mustela nivalis.* $C^1$. SU 17. (18) *Martes* sp. $c_1$. SU 17 I tg. [Color figure can be viewed at wileyonlinelibrary.com].

small fragments of unidentified mollusc shells collected from most of the SUs of the deposit were observed (Spinapolice *et al.*, this special issue).

### *ZooMS*

Twelve bone fragments coming from SUs 15 and 17 were analysed to test the collagen preservation at Uluzzo C Rock Shelter. From this preliminary assessment, we observed that collagen is poorly preserved. Of the 12 samples here considered, only five provided taxonomic information, using standard peptide markers (Buckley *et al.*, 2009; Welker *et al.*, 2016). In all the samples, P1105 is highly deamidated, suggesting that these bones probably yielded antique endogenous collagen. We identified R116 as an Equidae, UC81 as a *Bos/Bison* and UC92 as a Cervidae. R35 and UC91 could belong either to Cervidae or Equidae, due to the lack of distinctive diagnostic peptides (Table 13).

All the other tested fragments did not yield sufficient collagen/peptides for ZooMS taxonomic identification.

### *Ancient DNA analysis*

Of the 14 sediment samples tested from SUs 3, 15 and 17, three contained traces of ancient mammalian mtDNA. All three positive samples were collected in SU 15. They contained ancient mtDNA fragments assigned to Equidae and/or Hyaenidae (Table 14). Given the low number of

**Figure 12.** Bone remains with anthropic marks from SUs 15 and 17. (1) *Bos/Bison* rib with defleshing cutmarks from SU 17 II tg: a–e, close up of traces. (2) Impact flakes from SUs 17 II tg. and 17. (3) Medium-sized to large ungulate rib with defleshing cutmarks from SU 17 II tg. Close up of single stria. (4) *Lepus* sp. proximal diaphysis of femur with scrape-marks from SU 17 II tg. a and a′, close up of traces. [Color figure can be viewed at wileyonlinelibrary.com].

mtDNA fragments representing these mammalian families, no attempts were made to identify the taxa at the genus or species levels. None of the tested samples contained evidence for the preservation of ancient hominin mtDNA (Table S3λ).

## Discussion

### Lithic behaviour

Despite the small number of available pieces, we can draw some general conclusions on the production and use of lithic resources at Uluzzo C, based on analysis of the lithic assemblage pertaining to both the old and new excavations. Layer C and SUs 3, 15 and 17 represent a palimpsest of different partial reduction sequences. Due to the presence of small fraction debris (DC 1–2), part of the knapping activities was apparently performed directly on site, whereas the initialization of the block possibly occurred outside the shelter (or in an area that has not yet been excavated). Blocks were introduced to the site at a medium stage of exploitation (as suggested by the low amount of attested cortical pieces). We highlight the presence of two main debitage objectives: bladelets (Fig. 7) and flakelets (Fig. 6). At the current state of research, these objectives seem to have been achieved by: (i) unidirectional debitage using the bipolar technique with no or little management of the convexities – which was observed on the basis of the four bipolar cores and the bipolar debitage products; and (ii) a unidirectional production characterized by the direct percussion technique with the lateral and distal

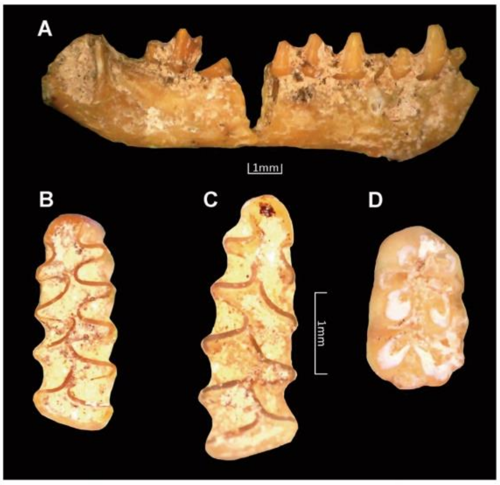


**Figure 13.** Some micromammal remains identified from Uluzzo C Rock Shelter. A (UC2018/sett. A/AA11/SU 17 tetto): right mandible of *Myotis myotis* in buccal view; B (UC2018/sett. A/A11/SU 15–17) and C (UC2018/sett. A/A11n/SU 17 II tg.): left and right first lower molars of *Microtus* (*Terricola*) *savii* in occlusal view; D (UC2018/sett. A/A11/SU 17 I tg.): right first lower molar of *Apodemus* (*Sylvaemus*) sp. Scale bars, 1 mm. [Color figure can be viewed at wileyonlinelibrary.com].

**Table 9.** Minimum number of individuals (MNI) and number of identified specimens (NISP) of the identified species by stratigraphic units of Uluzzo C Rock Shelter

| | SU 15 | SU 17 | Total |
|---|---|---|---|
| *Myotis myotis* | 0 | 1 | 1 |
| *Microtus* (*Terricola*) *savii* | 3 | 12 | 15 |
| *Apodemus* (*Sylvaemus*) sp. | 0 | 1 | 1 |
| MNI total | 3 | 14 | 17 |
| NISP total | 4 | 21 | 25 |

**Table 10.** Percentages of *Microtus* (*Terricola*) *savii* lower first molars from Uluzzo C Rock Shelter showing the different degrees of digestion. NR, number of remains used for the taphonomic analysis

| | NR | % |
|---|---|---|
| Light | 16 | 64 |
| Moderate | 3 | 12 |
| Heavy | 5 | 20 |
| Total | 25 | 100 |

**Table 11.** Mollusc taxa found at Uluzzo C with relative abundances (as NISP) and their habitat

| Taxon | Authority | Habitat | SU 15 | SU 17 | Total |
|---|---|---|---|---|---|
| Gasteropoda indet. | | | 5 | 2 | 7 |
| *Patella* sp. | Linnaeus 1758 | Interdital rocky shore | 1 | 5 | 6 |
| *Phorcus turbinatus* | (Born, 1778) | Interdital rocky shore | – | 7 | 7 |
| Total | | | 6 | 14 | 20 |

convexities being managed – based on the aligned negatives on the blanks. At this stage of the research, it is not possible to determine whether these two components are part of the same reduction sequence – which would imply the use of both direct and bipolar techniques in different moments of the reduction (e.g. such as at Roccia San Sebastiano – Collina *et al.*, 2020)- or if they are two different and independent reduction sequences. In both cases, the result is a low degree of standardization for both shape and edge delineation of the products, but a consistency in blank dimensions can be observed.

Among the retouched tools, two lunates were found in levels C and D of Borzatti's excavation. However, their use as projectiles – as has been attested to at Grotta del Cavallo (Sano *et al.*, 2019) – has not yet been tested.

Based on the technical evidence collected so far, we can consider the lithic assemblage of Uluzzo C as falling within the framework of the Uluzzian, since it presents several of the main characteristics of this techno-complex: principally local raw materials; additional concepts of debitage (unidirectional reduction sequence); use of the bipolar technique on an anvil; production of flakes and bladelets with several morphologies; low degree of standardization of the products; presence of lunates and end-scrapers and the absence of integrated concepts (i.e. Levallois) (Moroni *et al.*, 2018; Collina *et al.*, 2020; Marciani *et al.*, 2020a).

A point that deserves more attention is the production of blade-bladelets. These items are usually related to UP industries, even if their production has also been attested to in the Uluzzian (for a review see Marciani *et al.*, 2020a) and before, during the Mousterian (Ranaldo *et al.*, 2017; for a review see Carmignani, 2017). Even though the end-products are similar, the method of their production and the role that these objects may have played within these techno-complexes are different. Blade/bladelet reduction systems in the UP come from an integrated production where both the procedure and the traits of the obtained object are standardized (Marciani *et al.*, 2020a). For example, the Protoaurignacian is a bladelet-dominated industry with a significant technical investment in the production phase and standardized products that are obtained by a laminar–lamellar debitage on unidirectional and prismatic cores (e.g. Falcucci, 2018; Negrino and Riel-Salvatore, 2018). In contrast, the degree of standardization of the Uluzzian bladelets is undoubtedly lower. Furthermore, and perhaps of even greater importance, the conceptualization of the manufacture procedure is different, as the Uluzzian uses an additional unidirectional and orthogonal debitage. Moreover, the bipolar technique is used as a deliberate choice and is not dictated by the raw material (i.e. Moroni *et al.*, 2018; Collina *et al.*, 2020; Marciani *et al.*, 2020a). The presence of a possibly more standardized blade–bladelet production at Uluzzo C needs to be assessed in further detail, preferably with the addition of the materials from the other layers.

## *Hunting behaviour*

At Uluzzo C, the lithic industry is associated with bones from different taxa. Despite the fragmentary state of the macromammal remains, there is evidence for the defleshing of large ungulates, as in other areas of Italy in this period (for a complete review, see Romandini *et al.*, 2020). The analysis of the faunal assemblage from the more recent excavations agrees with the results obtained by Borzatti, both for the identified taxa (*Lepus* sp., *Vulpes vulpes*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Bos/Bison*) and the relatively large quantity of *Equus* remains that were recognized (Borzatti von Lowerstern,1965).

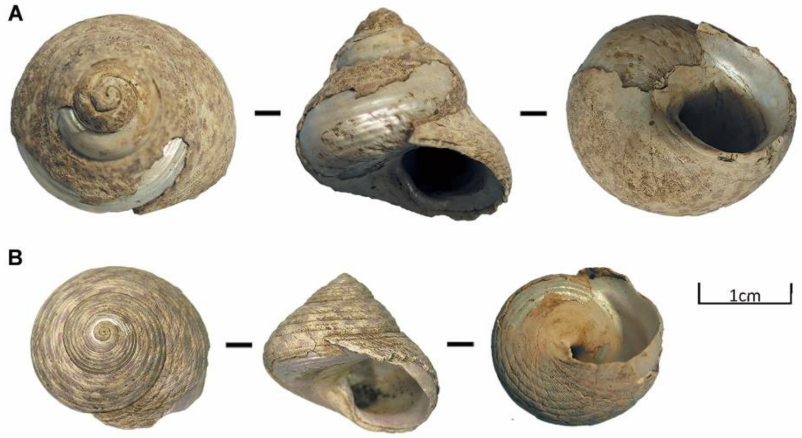


**Figure 14.** Two whole individuals of *Phorcus turbinatus* discovered in Uluzzo C site from SU 17 (A–B). [Color figure can be viewed at wileyonlinelibrary.com].

**Table 12.** List of taphonomic processes by identified marine taxa

| Layers | | SU 15 | SU 17 | Total | % |
|---|---|---|---|---|---|
| Nisp | | 6 | 14 | 20 | 100 |
| Pre-dep. Alt. | | – | – | – | – |
| Anthrop. Alt. | TAlt. | – | 1 | 1 | 5 |
| Post-dep. Alt. | Decal. | 1 | 11 | 12 | 60 |
| | Fragm. | 2 | 10 | 12 | 60 |
| | EscD. | – | 1 | 1 | 5 |

Abbreviations: pre-dep. Alt. – pre-depositional alterations; Antrop. Alt. – anthropogenic alterations; TAlt – thermo-alteration damage; Post-dep. Alt. – post-depositional alterations; Decal – decalcification; Fragm. – fragmentation; EscD. – excavation damage. Note: some specimens could have been exposed to more than one type of taphonomic alteration.

As for the Uluzzian levels of the nearby Grotta del Cavallo (i.e. EIII5), the most represented taxa in Uluzzo C correspond to *Equus* and *Cervus elaphus*. The taxonomic information obtained from the analysis of the faunal assemblage is coherent with the preliminary results of ZooMS and ancient DNA analyses.

Moreover, there are some common qualitative elements between these two sites: the predominant distribution of cutmarks on ungulate ribs and the presence of traces related to breakage of long bones, such as percussion cones or fractures and impact traces on diaphyseal long bones which are related to marrow extraction activities (Boscato and Crezzini, 2012; Romandini *et al.*, 2020). Unlike at Grotta del Cavallo, within Uluzzo C small to medium-sized mammals such as *Vulpes vulpes* and *Lepus* sp. are abundantly present.

Furthermore, this site is interesting for the exploitation of marine resources. Despite the limited amount of malacological remains, we can speculate on human consumption of this resource: collected gastropods are indeed commonly associated with dietary purposes during the MP and UP (Stiner, 1999, 2009; Colonese and Wilkens, 2005; Zilhão *et al.*, 2010; Colonese *et al.*, 2011; Hunt *et al.*, 2011; Bosch *et al.*, 2015; Hill *et al.*, 2015; Milano *et al.*, 2016; Ramos-Muñoz *et al.*, 2016). Today, the site of Uluzzo C is a few metres above the sea, but at the time it was a few kilometres beyond the emerged shelf, so it is unlikely that animals or other agents could have been responsible for the transportation of the molluscs. Additionally, a few fragments of *Ph. turbinatus* present evidence of thermal alterations that might be consistent with intentional heating for consumption purposes. From these preliminary findings, the presence of humans and rocky shore intertidal molluscs appears to be correlated, but more data are required to validate this hypothesis.

## Climatic and environmental reconstruction

Together, the information gathered through micromammals, macromammals and bird remains has disentangled the palaeoclimatic and palaeoenvironmental conditions related to the Uluzzian occupation. The micromammal assemblage of Uluzzo C is relatively dominated by the presence of *Microtus* (*Terricola*) *savii* (25 lower first molars), a Mediterranean species that inhabits open meadows and avoids dense forest areas (Amori, 2016). All the observed teeth presented some degree of digestion (Table 10), meaning that the micromammal accumulation must have been the result of predation (see

**Table 13.** Diagnostic peptides detected for the different samples and taxonomic identification based on CO1 peptide markers (see Welker *et al.*, 2016)

| | Peptide markers | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sample | P1 | A | A′ | B | C | P2 | D | E | F | F′ | G | G′ | Taxonomic identification |
| R35 | 1105.6 | | | 1427.7 | 1550.8 | | | | 2883.4 | | | | Cervidae/*Equus* |
| R116 | 1105.6 | | | 1427.7 | 1550.8 | | 2145.1 | | 2883.4 | | | | Equidae |
| UC81 | 1105.6 | | | 1427.7 | 1580.8 | 1648.8 | 2131.1 | | 2853.4 | | | | *Bos/Bison* |
| UC91 | 1105.6 | | | 1427.7 | 1550.8 | | | | 2883.4 | | | | Cervidae/*Equus* |
| UC92 | 1105.6 | | | 1427.7 | 1550.8 | 1648.8 | 2131.1 | | | | | | Cervidae |

**Table 14.** Ancient mammalian taxa identified in sediment samples using ancient DNA analyses. Only the three samples positive for the preservation of ancient DNA and only the taxa identified as ancient in each sample are shown. The number of mtDNA fragments assigned to each family is noted on the left column, and the percentage of fragments carrying a cytosine to thymine (C → T) substitution to the relevant reference genome at their 5′- and 3′-ends [with the lower bound of a one-sided 95% confidence interval (CI) in parentheses] are noted on the middle and right columns, respectively. Detailed results for all samples and negative controls are shown in Table S3

| | | Equidae | | | Hyaenidae | | |
|---|---|---|---|---|---|---|---|
| Sample | Provenance | No. of fragments | % 5 ′ C → T (low 95% CI) | % 3 ′ C → T (low 95% CI) | No. of fragments | % 5 ′ C → T (low 95% CI) | % 3 ′ C → T (low 95% CI) |
| C147 | SU 15; Square A11 | 21 | 50.0<br>(22.2) | 75.0<br>(24.9) | 68 | 50.0<br>(24.5) | 50.0<br>(27.9) |
| C170 | SU 15; Square A11 | 20 | 42.9<br>(12.9) | 75.0<br>(24.9) | – | – | – |
| C173 | SU 15; Square AA11 | – | – | – | 23 | 50.0<br>(15.3) | 75.0<br>(24.9) |

Andrews, 1990; Fernández-Jalvo *et al.*, 2016a). As pointed out by Berto *et al.* (2017), Savi's pine vole is a dominant species in both cold and warm phases during the late Pleistocene of southern Apulia in Grotta del Cavallo (Dalla Valle, 2008), Grotta dei Cervi di Porto Badisco (Cason, 2012) and Grotta delle Cipolliane (Bon and Menon, 2000). This means that it is not a good climatic indicator in this area. However, the relative predominance of *Microtus* (*Terricola*) *savii*, together with the presence of *Apodemus* (*Sylvaemus*) sp. and *Myotis myotis*, indicates a patchy landscape composed of open forest and grassland habitats, and compatible with the overall macrofaunal composition.

In accordance with other south-eastern Ionian sites, an increasing frequency of *Equus ferus* is registered in the Uluzzian sequence, suggesting the occurrence of sparse woodland and steppic environments, as is the presence of Cervidae, which are typical of Mediterranean evergreen forests (Romandini *et al.*, 2020). The presence of Equidae was attested to by both the DNA analysis of sediment samples and from palaeoproteomics. In this context, in accordance with the archaeozoological record, sample R116, identified by ZooMS as an Equidae, can be attributed to *Equus ferus*.

In addition, the ancient DNA data shows the presence of Hyaenidae at the site. However, the presence of hyena was not registered by morphological analysis on the osteological remains. This could be caused by the high degree of bone fragmentation of the faunal assemblage from Uluzzo C, which may have hampered the identification of this species. Notably, some bone fragments appear as corroded and rounded after being digested by carnivores.

Concerning avifaunal remains, two species provided precise palaeoenvironmental indications, coherent with the other investigated proxies. In particular, *Melanocorypha calandra* suggests the presence of grasslands and steppes, while *Pyrrhocorax pyrrhocorax* indicates the presence of rocky cliffs and crags with grassland areas (Cramp, 1998).

Faunal-based reconstruction of environmental settings at the time of the Uluzzian occupation of the Uluzzo C Rock Shelter fits well with the palaeoenvironmental reconstruction based on the study of sediments from the stratigraphic sequences reported in Spinapolice *et al.* (this special issue). The opening of the environment, the increase of aridity and the wind strength are registered in these units by an increase of the silt fraction, corresponding to loess. Dismantling of the roof and walls of the rock shelter and the accumulation of wind-blown sediments are two sedimentary processes compatible with the cold and arid environmental conditions that occurred during Marine Isotope Stages 4 to 2. Moreover, the occurrence of a frost-related breccia in layer C, probably formed under severe cold conditions, suggests decreased temperatures and cooler environmental conditions, probably during a stadial event (see Spinapolice *et al.* in this special issue).

## Conclusions

The reopening of the excavation at Uluzzo C Rock Shelter, the reviewing of old material and the study of the artefacts coming from the new excavations allowed us to better bring better into focus the evidence from this site in the context of the Bay of Uluzzo and, more generally, in the framework of the Uluzzian occupation in Italy. The Bay of Uluzzo is a crucial area for understanding of the Uluzzian – not only it is the place where the Uluzzian was first identified and described (Palma di Cesnola, 1964), but it is also where the entire development of the Uluzzian techno-complex was defined (Palma di Cesnola, 1993). Several sites with Uluzzian occupations are clustered in this area within a few kilometres from each other: Grotta del Cavallo, Grotta di Uluzzo, Uluzzo C Rock Shelter (in the Bay) and Grotta di Serra Cicora (a few kilometres in the hinterland). Palma di Cesnola described here the chrono-cultural development of this techno-complex based on typological traits, frequencies of retouched tools and the raw materials that were used. He defined the *archaic Uluzzian* based on layer EIII of Grotta del Cavallo; the *evolved Uluzzian* based on layers EII-I of Grotta del Cavallo; and the *late Uluzzian* based on layer D of Grotta del Cavallo, layer N of Uluzzo B, and layers D and C of Uluzzo C. The last phase of the Uluzzian *(final Uluzzian)* is absent at Grotta del Cavallo, and it has only been found at Serra Cicora in horizon D of layer B. The Uluzzian cycle is closed by a phase called the *Uluzzo-Aurignacian*, found at Serra Cicora in horizons A, B and C of layer B (Palma di Cesnola, 1993). Within the Bay of Uluzzo, the only other assemblage that was recently studied with a technological approach is the one from layer EIII at Grotta del Cavallo (Moroni *et al.*, 2018).

The acquired evidence suggests that modern human Uluzzian groups settled at Uluzzo C Rock Shelter between 42 and 40 ka (Spinapolice *et al.*, in this issue).

The lithic production of that layer is characterized by a significant component of mostly un-retouched small blades/ bladelets derived mainly from bipolar reduction. Among formal tools, end-scrapers and backed elements (mainly lunates) have a key role. The lithic assemblage from layer EIII consists of larger tools (e.g. end-scrapers and side-scrapers), and smaller tools (that include backed pieces that were presumably used in composite devices) (Moroni *et al*., 2018).

The lithic materials from Uluzzo C show: (i) the production of bladelets and flakelets; (ii) the presence of the bipolar technique on an anvil; and (iii) the presence of two lunates among the retouched tools. Recognizing the layer C/SUs 3, 15 and 17 as Uluzzian confirms and enriches with further information Borzatti's interpretation, which was mainly based on typological observations. Moreover, this recognition is in accordance with: (i) the reconstructed stratigraphy of the site, where the Uluzzian occupation follows the Mousterian occupation; (ii) the site's location, since the Bay of Uluzzo is the key area for the Uluzzian; and (iii) the chronology, since the grand weighted mean age for the Uluzzian occupations is 40.6 ± 1.4 ka, whereas for the end of the Mousterian it is 46 ± 4.0 ka (Spinapolice *et al*., in this issue). This chronology is in accordance with the Uluzzian occupation of Grotta del Cavallo dated between 45.5 ± 1.0 and 39.85 ± 0.14 ka (Zanchetta *et al*., 2018).

Data obtained from the macrofaunal composition of Uluzzo C are consistent with the Uluzzian levels of the nearby Grotta del Cavallo (i.e. EIII5), where Cervidae and Equidae were also identified as the most abundant taxa. The only difference is in the exploitation of small- to medium-sized mammals, such as *Vulpes vulpes* and *Lepus* sp., towards which Uluzzo C hunters seem to have been more inclined compared to those of Grotta del Cavallo. Except for the hyena, ZooMS, ancient DNA and archaeozoological analyses are consistent in identifying taxa within this context. Further analyses on the bone fragments recovered during the last excavation season in 2019 from the same levels are in progress. The aim is to improve our knowledge regarding the faunal composition through the application of palaeoproteomics.

In general, the analysis of macromammal, micromammal and bird remains agrees with the data obtained from sediments and from the stratigraphic sequence in indicating a patchy landscape composed of forests, grassland and rocky habitats in a cold and arid environment.

They butchered and consumed their food through the use of fire, hunted – probably near the site – medium-sized and large ungulates, as well as Leporidae, and collected marine gastropods (*Ph. turbinatus*) – probably for sustenance purposes – within a few kilometres from the rock shelter.

The application of a multidisciplinary methodological protocol – including lithic technology, use-wear, zooarchaeology, DNA from sediments and palaeoproteomics – shows the potential of integrated studies in understanding the technical and hunting behaviour of humans in relation to their environment. Finally, this study represents a new fundamental piece in the composition and understanding of the meaning of the complex Uluzzian cultural and ecological mosaic in Italy during the MP/UP transition.

***Author contribution***—ES, SB are the research and excavation coordinators and conceptualized the paper; SS, GM, MR wrote the first draft of the paper; SS, MR analysed the macrofaunal remains; GM, FR performed the lithic technological analysis; SA performed the use-wear analysis of the lithic items; LC carried out the analysis of the avifaunal remains; JMLG analysed the small mammal remains; FL, SS performed the ZooMS analysis; VS, MM analysed the DNA from sediments; LT analysed the malacofaunal remains; AF, EB made the topographic mapping; AC described the stratigraphic sequence; AZ was responsible for the geoarchaeological investigation on the stratigraphic sequence; MCM was responsible for the OSL dating campaign; OAH reviewed and edited the language and the manuscript; ES, SB, SS, MR, AF, EB, GO participated in the archaeological excavation of the site. All the authors collaborated in writing, reviewing and editing the final version of the paper.

## Supporting information

Additional supporting information can be found in the online version of this article.This article includes online-only Supplemental Data.

**Table S1**. Lithic items in each layer of Borzatti excavation, according to Borzatti (1965) and items currently stored at Museo della Preistoria di Nardò MPN.

**Table S2**. Lithic items in SUs 3, 15 and 17 (excavation 2016–2018).

**Table S3**. Sequencing results for all tested sediment samples and relevant negative controls. For the mammalian mitochondrial capture, results are only shown for Hominidae and for the two taxa identified as ancient in at least one of the samples. L – length; MQ – mapping quality; C – cytosine; T – thymine; CI – confidence interval.

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## *Data availability statement*

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

*Abbreviations*. DC, dimensional class; FA, formic acid; HPA, high-power approach; LP, Lower Palaeolithic; LPA, low-power approach; MH, Modern Human; MNI, minimum-number of individuals; MPN, Museo Della Preistoria di Nardò (Lecce, Apulia, Italy); NISP, number of identified specimens; SU, stratigraphic unit; UP, Upper Palaeolithic; WoRMS, World Register of Marine Species.

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# 6. Manuscript IV

## Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds

# Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds

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## Abstract

Investigation of ecological responses of species to past climate oscillations provides crucial information to understand the effects of global warming. In this work, we investigated how past climate changes affected the distribution of six bird species with different climatic requirements and migratory behaviours in the Western Palearctic and in Africa. Species Distribution Models and Marine Isotopic Stage (MIS) 2 fossil occurrences of selected species were employed to evaluate the relation between changes in range size and species climatic tolerances. The Last Glacial Maximum (LGM) range predictions, generally well supported by the MIS 2 fossil occurrences, suggest that cold-dwelling species considerably expanded their distribution in the LGM, experiencing more pronounced net changes in range size compared to temperate species. Overall, the thermal niche proves to be a key ecological trait for explaining the impact of climate change in species distributions. Thermal niche is linked to range size variations due to climatic oscillations, with cold-adapted species currently suffering a more striking range reduction compared to temperate species. This work also supports the persistence of Afro-Palearctic migrations during the LGM due to the presence of climatically suitable wintering areas in Africa even during glacial maxima.

## Introduction

The alternation of Pleistocene glacial and interglacial periods caused cyclic expansions, contractions and shifts of geographic ranges of species[1], including bird species, shaping their current genetic structure and diversity[2-7]. As for land-based ecosystems, these range shifts are linked to latitudinal and altitudinal shift of biomes and vegetation zones in response to climate oscillations[8-10]. For instance, during the Last Glacial Maximum (LGM: 19 - 26,500 years ago)[11], Mediterranean Europe was a climatic refugia for warm-adapted bird species, whereas the cold-adapted species were more widespread[12-14].

Investigation of adaptive responses and distributional shifts of bird species to past climate changes provide crucial information to understand present and future effects of global warming and to adopt suitable conservation strategies. Past geographic distributions can be reconstructed with the help of the fossil record. GIS paleoclimatic layers and mathematical tools, such as Species Distribution Models (SDM), allow to project the current climatic requirements of species onto different past climatic scenarios, generating predictions of past distribution of species that are basically envelopes of climatic suitability, assuming niche conservatism over time[15-19]. Climatic envelopes are increasingly used to explore the potential distribution of species in the past and test evolutionary and biogeographical hypotheses. They are often integrated with molecular data to reconstruct detailed phylogeography and past population history of species[7, 20-25.] Many works explore LGM species population dynamics[23, 26-31]; some of these are exclusively focused on bird taxa, aiming to clarify population dynamics in the refugia during climatic extremes, test niche stability, identify climate threats and effects to optimize current conservation efforts[20-22, 24, 32-42]. Among these, very few use the information provided by the fossil record to assess palaeobiogeographic hypotheses or to calibrate (or validate) the LGM predictive models[20, 22, 39, 41] and only two include the modelling of LGM wintering grounds of Afro-Palearctic migrants[20, 39].

The relationship between changes in range size (as effect of climate changes) and species thermal niche (climatic tolerance) has been theoretically investigated in mammalian species in the frame of past climatic oscillations, linking range shifts in Europe to niche optimum (cold-warm), and not to niche breadth[43]. In birds, this relationship has been investigated only for recent times' global warming, showing that cold-dwelling species have contracted more their range size than warm-dwelling species with current climate change[44]. The Species Thermal Index (STI), i.e., the average temperature experienced by a species across its distribution (see section *Present distribution of the selected species, fossil occurrences, climatic data and Species Thermal Indexes* in Methods summary*)*, and other thermal indexes are used as a proxy to estimate the thermal niche of species, to evaluate the effect of climate change and predict population dynamics[43, 45-53].

Here, we will investigate the effect of past climate oscillations, in the Western Palearctic and Africa, on six bird species that represent different categories of migratory behaviour and climatic requires. Three are sedentary species (*Pyrrhocorax graculus*, *Athene noctua*, *Perdix perdix*), one is a partially nomadic/irruptive species (*Bubo scandiacus*) and two are long-distance migrants that winter in sub-Saharan Africa (*Coturnix coturnix*, *Crex crex*) (an outline of the ecology of the six species is provided in the Supplementary Data S1). *Pyrrhocorax graculus* and *Bubo scandiacus* are restricted to cold climates whereas the other species are more climatic tolerant and adapted to a range of temperate climatic conditions[54-60] (Table 1). These species have been selected also due to their abundance and frequency in the fossil record[61, 62], thus, to provide an empirical support of the LGM prediction models. Here, we will map present-day and LGM European and African distributions of the six species using Species Distribution Models (SDMs), test the LGM predictions with the distribution of Marine Isotope Stage (MIS) 2 fossil records, discuss range shifts and potential implications for species migratory behaviour. Finally, we will address the following hypothesis: are the range size variations related to the thermal niches?

TABLE 1 SHOULD BE PLACED HERE

## Results

### *Present-day projections*

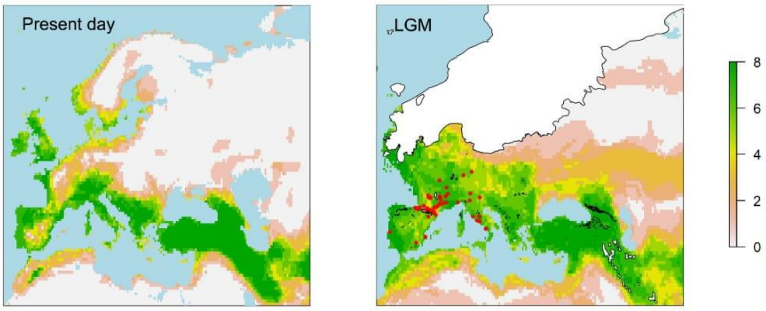
The model evaluation provided high AUC (Area Under the Curve) values for all the six species (see Supplementary Data S2). The projections of the models into the present-day climate are consistent with their present-day distributions (Figs. 1a, 2a, 3a).

### *LGM climatic ensembles*

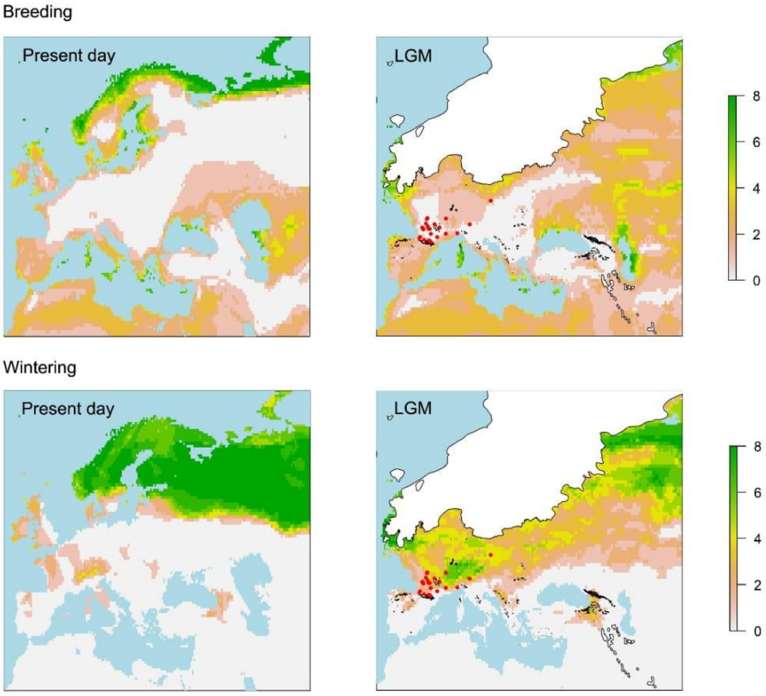
*Pyrrhocorax graculus*. The LGM ensemble strongly overlaps with the MIS 2 fossil occurrences of *P. graculus* (Fig. 1a). In the present day this sedentary species linked to cold climates survives with a relict distribution in the mountain areas of the mid-latitudes of the Palearctic, due to Holocene climate warming. In the LGM, as witnessed by models and MIS 2 fossil records, it experienced a considerable range expansion, spreading at lower altitudes due to the downward shifts of the mountain vegetation (Fig. 1a). The lowering of the upper limit of the tree-line favoured the expansion of the mountain pastures with rocky ravines and cliff faces that this species uses for feeding and nesting.

*Bubo scandiacus*. The MIS 2 fossil occurrences are not well predicted by the LGM wintering distribution ensemble neither by the breeding distribution ensemble; in any case, the LGM wintering projection predicts the fossil distribution better than the breeding projection (Fig. 1b). The models predict for the LGM a clear southward shift of both the breeding and the wintering distribution of this species, currently restricted to the arctic and boreal areas. In detail, the LGM breeding range is completely shifted towards central and southern Europe with no overlapping with the current breeding areas, probably due to the expansion of the ice cap (Fig. 1b). According to the LGM models, this species was considerably more widespread than the present day, as approximately the whole Europe satisfied the conditions of climatic suitability of this species, if we consider both the breeding and the wintering projections.

**a.** *Pyrrhocorax graculus*



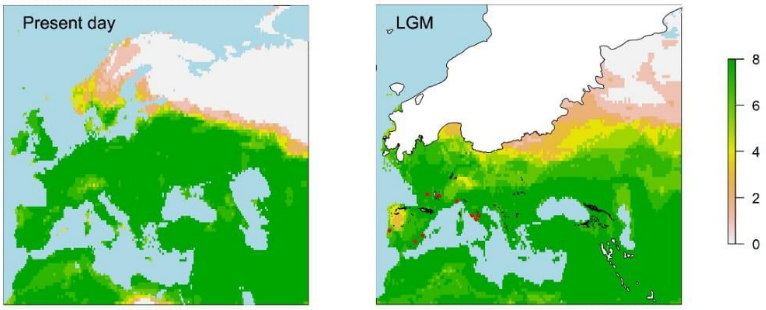
**b.** *Bubo scandiacus*



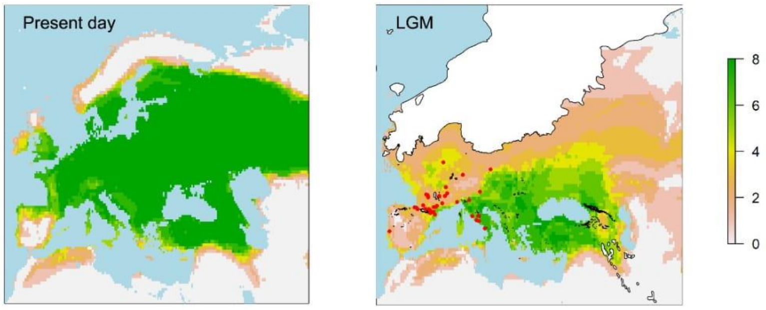
*Athene noctua*. The LGM predicted distribution of this species is well supported by the MIS 2 fossil occurrences, that are limited to Southern Europe (Italy, Spain, Portugal and Southern France) (Fig. 2a). A southward shift of the northern edges of the range due to the expansion of the ice cap is predicted by the LGM climatic envelopes, causing a reduction of the distribution area compared to the present distribution (Fig. 2a). The range reduction during LGM could have led to isolation of the different populations in the Mediterranean refugia (as during other glacial maxima[6]) as this species is best adapted to temperate and warm climates and has a limited dispersal capacity[60, 63, 64].

*Perdix perdix*. The MIS 2 fossil occurrences of this species are not very well predicted by the LGM ensemble (Fig. 2b). The models, together with the fossil occurrences, indicate that this sedentary species linked to open environments could have undergone a southward shift of the northern edges of its current distribution during the LGM, causing a slight range reduction compared to the present one (Fig. 2b). This is possibly due to the expansion of the ice cap and the consequent presence of unsuitable climatic and environmental conditions at the northern latitudes. This species proves to be tolerant to cold climatic conditions as, even during MIS 2, it seems to persist up to latitude 50° N.

**a.** *Athene noctua*



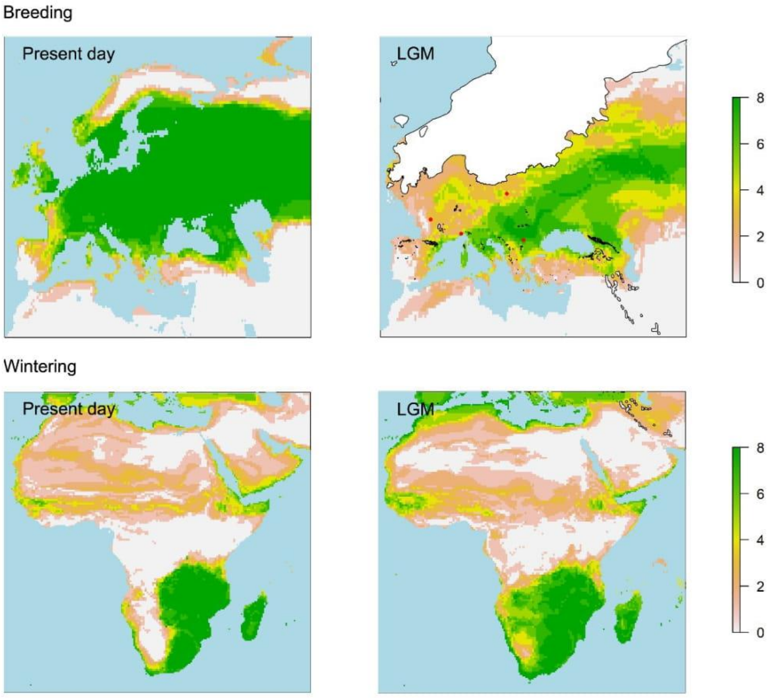
**b.** *Perdix perdix*



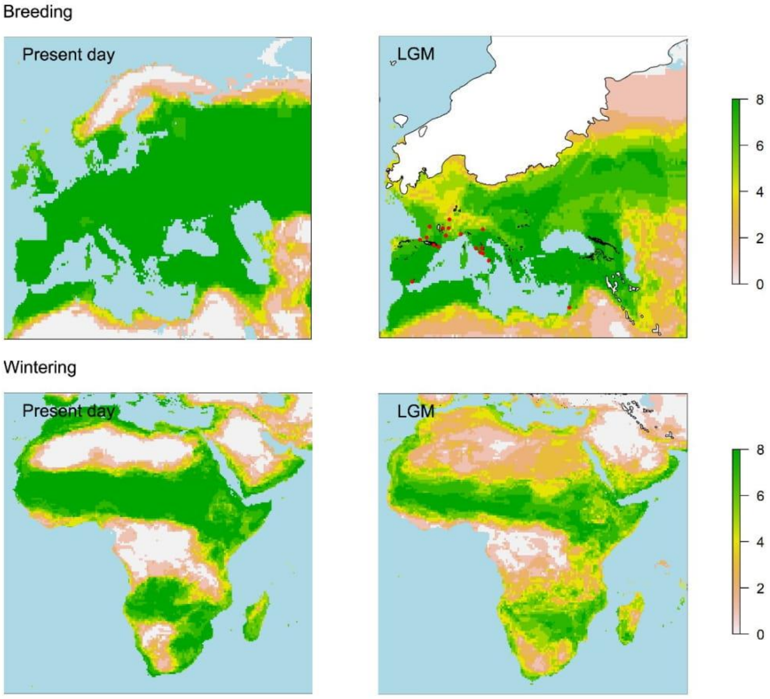
*Crex crex*. The LGM breeding ensemble is only partially supported by the MIS 2 fossil occurrences, that are very limited for this species (Fig. 3a). Based on the models, this species could have undergone a reduction of the northern edges of the breeding range due to the expansion of the ice cap, causing a range reduction compared to the present one (Fig. 3a). The Late Pleistocene fossil records of this species are very rare west to the Pyrenees[61, 62] and the species is still absent from Western Europe, being mostly spread in Eastern and Central Europe. The models predict an analogue distribution for the LGM. The LGM wintering African ensemble looks similar to the current range, or even somewhat larger, but always limited to South Africa (Fig. 3a).

*Coturnix coturnix*. The LGM breeding climatic envelopes support the MIS 2 fossil occurrences (Fig. 3b). The models suggest a reduction of the northern edges of the breeding ranges during the LGM compared to the present distribution, with a slight reduction of the distribution area. The LGM African wintering ensemble predicts a slight expansion of the conditions of climatic suitability in Africa during the LGM, compared to the present ones, except for the disappearing from the North African wintering areas (Fig. 3b). Nonetheless, we consider the predicted wintering presence of this species in the Sahara desert during the LGM as non-reliable, as during the LGM the Sahara was even larger than today in terms of latitudinal extent[65-68].

**a.** *Crex crex*



**b.** *Coturnix coturnix*



## Discussion

### *Consistency of LGM predictions and fossil occurrences*

Generally, our LGM range maps are consistent with the fossil occurrences of the six species investigated (Figs. 1, 2, 3). However, in the cases of *Bubo scandiacus* and *Perdix perdix*, the models only partially overlap with the fossil occurrences (Figs. 1b, 2b; Supplementary Data S3). In the case of *P. perdix*, we assume that this could be linked to the anthropic impacts that this species suffered historically. *P. perdix* has dramatically declined in numbers since the early part of the 20th century and the current populations, at least in Western Europe, is composed by a mixture of wild and farmed individuals that are released for conservation or hunting purposes. This aspect influenced both the distribution and the genetic diversity of the species, as the released individuals hybridize with the wild ones with a high risk of genetic introgressions[69, 70]. Therefore, we hypothesize that the current potential climatic niche and ecological requirements of *P. perdix*, modified by the anthropic impact and quantified using the present-day species distribution, might be different than the Pleistocene ones.

In the case of *B. scandiacus*, LGM map predictions do not overlap with the fossil occurrences especially in the case of the breeding areas. Here, our results indicate that the presence of this species in the European mid-latitudes, with a concentration in Southern France, might be explained by wintering individuals, providing interesting hints about *B. scandiacus* phenology during the LGM (Fig. 1b). However, this prediction does not agree with [71], where Southern France is included in the reconstructed LGM breeding range of this species. Furthermore, the species is reported to breed at the Middle Pleistocene fossil locality of l'Escal, in Southern France, based on the presence of sub-adult bones belonging to this species[61, 72, 73]. The wide distribution of this species during the LGM, evidenced by its fossil records, and more in general during the Late Pleistocene, contrasts with our narrow map predictions, and leads to hypothesize that the populations of this species had a wider climatic niche in the past. One of the possible reasons for this change, besides the climate warming, is the competition with the other Palearctic large owl, *Bubo bubo*. The distribution ranges of these two species widely overlapped during the Late Pleistocene, as witnessed by their fossil occurrences[61, 62]. [74] suggest that *B. scandiacus* may have arisen in the Early Middle Pleistocene from *Bubo ibericus* sp. nov. in Southern Europe, providing an explanation why *B. scandiacus* might not have always been tightly linked to glacial conditions. However, since the last late glacial, *B. bubo* might have increased its populations as a consequence of the climatic amelioration, forcing *B. scandiacus* to move to the high latitudes[71, 74]. After the LGM *B. scandiacus* possibly changed also some morphological and ecological traits to adapt to the environmental constraints of inhabiting high latitudes. In the present day, white plumage colour might be due to the persistent snow cover in the Arctic and the habit of day hunting during summer might be related to the hours of daylight at high latitudes. However, as suggested by some authors, during the late Pleistocene, when the species was spread at the mid-latitudes, it might have been a crepuscular/night hunter throughout the whole year, and its plumage might have been darker (brownish)[71].

The changes in the ecological requires of both *P. perdix* and *B. scandiacus* could explain the scarce consistency between the LGM envelopes and the fossil occurrences in the Western Palearctic (Figs. 1b, 2b).

### *Range shifts*

Based on the STI of the six species here investigated, *Pyrrhocorax graculus* and *Bubo scandiacus* can be defined cold-dwelling species, whereas the others are more tolerant with higher average annual mean temperatures across their distribution (Tab. 1). During the LGM, the expansion of the ice caps represented a major constraint for the distribution of living organisms at high latitudes. Our results show a clear latitudinal shift for *B. scandiacus* (Fig. 1b) and a reduction of the northern edges of the range for *Athene noctua*, *Perdix perdix*, *Crex crex* and *Coturnix coturnix* (Figs. 2, 3). In *P. graculus* there seems to be no latitude shift, but it is just because this species never reached the higher latitudes during postglacial expansions, that were instead reached by *B. scandiacus* during warm phases as the current one. An altitudinal movement is instead clear in *P. graculus*, with shifts towards high altitudes during the warm phases and downwards during cold phases, following the alpine meadows where this species feeds (Fig. 1a).

The models and the fossil occurrences together suggest that striking changes in range size between the present day and the LGM have occurred in the two cold-dwelling species *B. scandiacus* and *P. graculus* (Fig. 2). The former species expanded in the whole Europe during glacial times. It is reported as far south as Gibraltar (Gorham's Cave) in the Lateglacial[75] and in Southern Italy during the Lateglacial (Grotta Romanelli)[76], MIS 2 (Grotta di Cardamone)[62, 77] and MIS 3 (Ingarano)[78]. During the LGM, *P. graculus* followed the downward shift of the upper limit of the tree-line that, together with the retreat of the forest cover, led it to spread in a considerably larger area corresponding to approximately the whole non-glaciated Europe. The different ecological requirements of these two cold-adapted species led them to adopt different strategies to cope with warming climates such as during the Holocene: *P. graculus* moved towards higher elevations, whereas *B. scandiacus* moved towards higher latitudes, but both invariably reduced their range size, being considered "glacial relicts"[79]. These species were possibly also favored during glacial times by the expansion of open areas at the expense of forest cover, as they live in rocky areas (*P. graculus*) and open areas (*B. scandiacus*).

The models suggest, for the species adapted to temperate conditions (*A. noctua*, *P. perdix*, *C. crex* and *C. coturnix*), a slight reduction of the distribution during the LGM (compared to modern ranges), due to the southern retreat of the northern margins of their distribution owed to the expansion of the ice cap. The core of the mid-latitude distribution of these species remained unchanged throughout the last 20 ka (Figs. 2, 3). Despite a slight reduction in the size of their range due to major environmental constraints at the high latitudes, these species were possibly favored by the expansion of open areas typical of the cooler climatic phases, as they all exploit grasslands and/or steppe for their survival.

As the cold-dwelling species show clearly more pronounced net changes in range size between the LGM and the present day, we can infer that the thermal niche of Eurasian birds is highly predictive of range size variations due to climatic oscillations and represents a key ecological trait for explaining the impact of climate change in species distributions[43,44]. The net change in range size between the different climatic phases does not seem to be linked to the migratory behaviour, as birds with different migratory behaviours show similar variations in the range size whereas among the resident species we observed changes in range size of different magnitude. Likewise, the extent of range variations does not even seem to be related to the breadth of the thermal niche (see “Range” in Tab. 1). Evidence is here provided that cold adapted species are more threatened by the current climate warming and need more effective conservation measures, as their range is already considerably contracted and will suffer further reduction in the future. We expect the same difference, in reverse, for the species that are more adapted to warm climates (extreme range reductions during glacial periods and pronounced expansions during warm phases). These aspects should be investigated in further research.

As there is no standardized methodology to generate range map estimations, these are linked to the methodological choices of researchers. The LGM climatically suitable areas of *P. graculus*, *C. crex* and *A. noctua* modeled, respectively, by [41], [39] and [36], result smaller than those proposed in this work. All the three different approaches used algorithms that risk overfitting (e.g., GAMs) or Maxent with a hard threshold selection of 10th percentile of presences (forcing range maps to be small), resulting in maps that underestimate the real behaviour of these species. Our predictions have, in general, larger suitability values for Central and Northern Europe during the LGM. We believe that our maps are closer to reality, as these three species inhabit meadows and grasslands, which were widespread during the LGM. Furthermore, the northern distribution of these species during the LGM is documented by the fossil occurrences (see Figs. 1a, 2a, 3a and Supplementary Table S4).

### *LGM migrations*

The LGM projections of the distribution of the two long-distance Afro-Palearctic migrants *Coturnix coturnix* and *Crex crex* indicate that climatically suitable areas existed both in Africa in the wintering grounds and in the Western Palearctic in the breeding grounds, providing further evidence for the persistence of Afro-Palearctic migration during the LGM (Fig. 3). These data agree with the view that the migratory behaviour is linked to an increase in climate seasonality and deterioration of winter conditions[80-83]. Also, our results suggest that there is no evidence of the loss of the migratory behaviour in Afro-Palearctic migrants during the LGM[39] and that, as reported in a recent research[84], bird migration remained an important global phenomenon throughout the last 50,000 years. Our data therefore challenge the hypothesis that the migratory behaviour is mainly a phenomenon of interglacial periods (linked to the recolonization of northern de-glaciated areas in postglacial times) that considerably reduced during glacial phases[85-88].

The paucity of the sub-Saharan African fossil record hinders the reconstruction of the presence of the Western Palearctic breeders in Africa in the past. To date, fossil evidence of the presence of *C. coturnix* and *C. crex* in Africa during the LGM is lacking. Nevertheless, the presence of Eurasian long-distance migrants in the Pleistocene fossil record of sub-Saharan Africa, together with the absence of medullary bone in these fossils, supports the existence of the Afro-Palearctic migrations during Pleistocene[39, 89]. Among the LGM fossils of *C. coturnix*, two are located in Gorham's Cave (Gibraltar, Spain) and Ohalo II (Israel) (Fig. 3b), along two of the main Afro-Palearctic migration routes, possibly indicating that these routes were already used during the LGM.

## Methods summary

*Present distribution of the selected species, fossil occurrences, climatic data and Species Thermal Indexes*

The main ecological characteristics of the six species here investigated are reported in the Supplementary Data S1. The data polygons representing the current distribution of the six species have been downloaded from the IUCN database[54-59], with a single polygon for the sedentary species (*Pyrrhocorax graculus*, *Athene noctua*, *Perdix perdix*) and two polygons (one for the Palearctic breeding range and one for the wintering range) in the case of the migratory species[90] (*Bubo scandiacus*, *Coturnix coturnix*, *Crex crex*). Based on the IUCN data[54-59], the parts of the ranges where the species are introduced have not been considered, whereas the areas where the migratory species are resident have been merged with both wintering and breeding ranges using R, version 4.0.3 (2020-10-10). The resulting polygons are what we used as "presence" polygons (present-day distributions). As the BRT (Boosted Regression Trees) models also require "absences" polygons, the latter have been created ad-hoc for each species. "Absence" polygons were built manually using QGIS, so that they closely surround the "presence" polygons (without using any specific distance to make the polygons). In this way, the current distribution limits of the investigated species can be predicted more accurately and the potential variables limiting species ranges can be identified. So, we aimed to select a calibrating data set that was able to codify, besides presences, also the real limiting factors for these species. "Presence" and "absence" polygons used for this paper can be downloaded from https://www.dropbox.com/sh/twij289ss2gqmzk/AABOYP4Tl69x4fpJ4Zff4A8xa?dl=0.

An extensive bibliographic search allowed us to identify a total of 648 Western Palearctic sites dated to the Late Pleistocene (from 130 to 11.7 ka BP)[91, 92] that yielded fossil remains of at least one of the six species (identified with certainty to species level). We collected these fossil occurrences in a dataset. Multiple fossil occurrences of the same species from different stratigraphic units of the same deposit were counted separately due to their possible different age. Then, in order to identify those reliably dated to MIS 2 (29-14 ka BP), we thoroughly checked the age of each fossil occurrence, using the Radiocarbon Palaeolithic Europe database, v. 26[93], which reports radiocarbon conventional ages BP, or the PACEA geo-referenced radiocarbon database[94]. Each radiometric age has then been calibrated with OxCal 4.3 program[95], using the

IntCal13 calibration curve (95% CI) [96]. After this check, we found 48 fossil localities dating back to MIS 2, which are the ones that we used in this paper, and we georeferenced them. We report the list of the MIS 2 fossil occurrences of the six selected species in the Supplementary Table S4. It is worth mentioning that the relative abundance of fossil records in the western part of the Western Palearctic compared to the Eastern part is related to the higher number of fossil localities (mainly Palaeolithic sites) which have been investigated in the former area and shouldn't be regarded as an indication of the absence of the species from Eastern Europe. We also searched for African fossil records of the selected species dating back to MIS 2 in the literature, but none was found, due to the paucity of studies dealing with African fossil birds. Also, the Western Palearctic fossil occurrences of the migratory species do not necessarily indicate the breeding of those species in that specific locality, as they could also belong to individuals which were migrating. Only the finding of juvenile bones or medullary bone (calcium deposit in the bone cavity linked to egg-laying in female individuals) undoubtedly indicate the breeding of a species in a certain locality[97, 98].

We downloaded rasters of climate data for the present-day and the LGM (21 ka BP) from ecoClimate (https://www.ecoclimate.org)[99, 100]. In this dataset, eight different general circulation models (GCMs) were available (CCSM, CNRM, GISS, FGOALS, IPSL, MPI, MRI and MIROC, with a resolution of 0.5°) from the Couple Model Intercomparison Project (CMIP5) and Paleoclimate Modeling Intercomparison Project (PMIP3) working groups. We used all the eight simulations to model the present and LGM climatic envelopes of the six species.

To calculate the STI we coupled, using R (version 4.0.3), the IUCN polygons of the species' distribution with the CHELSA present-day climate raster and extracted the mean, median, minimum and maximum values of the Annual mean temperature experienced for each species across its distribution range, that is considered a valid estimate for the species' thermal niche[44]. For Afro-Palearctic migratory species (*C. coturnix* and *C. crex*), the STI has been calculated only for the Palearctic breeding ranges and using the Mean temperature of the warmest quarter instead that the Annual mean temperature.

The STIs of each species are provided in Table 1.

### *Species distribution models*

The present-day and the LGM climatic suitability of the six species have been modelled using BRT (Boosted Regression Trees). This is a flexible technique that allows to handle different types of predictor variables, express nonlinearities and interactions, and accommodate missing data. It consists in a boosting algorithm, that iteratively calls a regression-tree algorithm to construct a combination or ''ensemble'' of trees. Regression trees are good at selecting relevant variables and model interactions, whereas boosting combines large numbers of relatively simple tree models adaptively, overcoming the inaccuracies of single tree models and giving improved predictive performance[101-104]. All models were fitted in R, version 4.0.3 (2020-10-10), using packages Rpart (version 4.1 - 15)[105] and Caret (version 6.0 - 88)[106].

The models were calibrated using nowadays presence and absence polygons for each species, randomly sampling 300 species records from the presence polygons and 300 from the absence polygons. Absence polygons (generated in QGIS) were located surrounding the presence polygons, to avoid selectiong absence data far away from the observed distribution of the species. By doing this, we aim to detect the climatic variables that are actually limiting the current distribution range of the species. The selected data sets were successively randomly split in training data (80%) and testing data (20%). The selected model settings are *lr* (learning rate) of 0.1, *tc* (tree complexity) of 1 and bag fraction of 0.5. Evaluation of the model performance was calculated with the Area Under the Curve (AUC), ranging from 0.5 (random) to 1 (prefect prediction). All the values relative to evaluation and variable importance of each model are reported in the Supplementary Data S2. Models were then projected into the eight GCMs of the LGM cold climatic scenarios and the eight GCMs relative to the present-day climatic scenarios. The outputs are maps with each cell having an index of climatic suitability between 0 (no suitability) and 1 (suitability). Successively, in order to reduce the uncertainties related to individual model projections, we averaged the eight models related to the different GCMs in two ensemble forecasts for each species, one for the present-day and one for the LGM (Figs. 1, 2, 3). In the ensemble maps, the value of each cell in the grid indicates how many models (out of eight) predict the presence of the species in that given cell. The fossil occurrences were successively plotted in the LGM ensemble maps to test if the model outputs correctly predict the fossil distribution of the different species during the LGM. The values of the cells of the ensemble corresponding to each fossil occurrence have been reported in the Supplementary Data S3.

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## Author contributions statement

Authors' contributions: L.C. and S.V. planned the research and conducted the analyses; L.C., S.V. and M.P. analysed the results, wrote the paper and reviewed the manuscript.

## Additional information

The author(s) declare no competing interests.

## Table legend

**Table 1.** Species Thermal Indexes of the six bird species object of the work. The STI is identified with the average temperature experienced by a species across its distribution (i.e., mean temperature) and defines the climatic tolerance of species.

## Figure legends

**Figure 1.** Present-day and LGM ensemble forecasts of the two cold-dwelling species *Pyrrhocorax graculus* (a) and *Bubo scandiacus* (b). The ensembles represent an averaging of all the eight projections related to the different GCMs. The values of each cell in the map range from 0 (0 out of 8 models predict the occurrence of the species in that cell, colour light grey) to 8 (all 8 models predict the occurrence of the species in that cell, colour green). The maps were created with R, version 4.0.3 (https://www.R-project.org/).

**Figure 2.** Present-day and LGM ensemble forecasts of the two resident temperate species *Athene noctua* (a) and *Perdix perdix* (b). The ensembles represent an averaging of all the eight projections related to the different GCMs. The values of each cell in the map range from 0 (0 out of 8 models predict the occurrence of the species in that cell, colour light grey) to 8 (all 8 models predict the occurrence of the species in that cell, colour green). The maps were created with R, version 4.0.3 (https://www.R-project.org/).

**Figure 3.** Present-day and LGM ensemble forecasts of the two migratory temperate species *Crex crex* (a) and *Coturnix coturnix* (b). The ensembles represent an averaging of all the eight projections related to the different GCMs. For each species are shown the forecasts for the breeding grounds (above) and the African wintering grounds (below). The values of each cell in the map range from 0 (0 out of 8 models predict the occurrence of the species in that cell, colour light grey) to 8 (all 8 models predict the occurrence of the species in that cell, colour green). The maps were created with R, version 4.0.3 (https://www.R-project.org/).

## Tables

### Table 1

| **Species** | **Distribution** | **Chelsa variable** | **Min temp.** | **Max temp.** | **Range** | **Mean temp.** | **Standard dev.** | **Climatic tolerance** |
|---|---|---|---|---|---|---|---|---|
| *Pyrrhocorax graculus* | Annual | BIO1 (mean annual temperature) | -23.5 | 28.5 | 52 | **4.6** | 7.4 | **cold-dwelling** |
| *Bubo scandiacus* | Breeding+wintering | BIO1 (mean annual temperature) | -24.3 | 10.1 | 34.4 | **-5.2** | 6 | **cold-dwelling** |
| *Athene noctua* | Annual | BIO1 (mean annual temperature) | -23.5 | 31.5 | 55 | **9.5** | 8.6 | **temperate** |
| *Perdix perdix* | Annual | BIO1 (mean annual temperature) | -17.2 | 20.5 | 37.7 | **6.1** | 3.7 | **temperate** |
| *Crex crex* | Breeding | BIO 10 (mean temperature warmest quarter) | -12.7 | 28.4 | 41.1 | **18.2** | 3.2 | **temperate** |
| *Coturnix coturnix* | Breeding | BIO 10 (mean temperature warmest quarter) | -12.7 | 39.3 | 52 | **20.1** | 5.1 | **temperate** |

## SM Supplementary Material Carrera et al. (submitted) - *Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds.* Scientific Reports

### Data S1 - Outline of the ecology of the six species investigated

*P. graculus*, a polytypic species, is a sedentary gregarious corvid that lives in high-altitude mountain areas of the Palearctic mid-latitudes, from the Pyrenees to the Himalaya. It inhabits pastures with cliffs and rocky ravines, descending below the treeline only in winter. Nests on ledges or shelfs near the roof of a cave, in rock crevices or on cliff faces[1, 2]. This species is known in the Palearctic since the Early Pleistocene and becomes very common in the European Late Pleistocene localities[3,4]. *B. scandiacus* is a monotypic large owl that breeds in the Arctic regions of Eurasia and America, in the open tundra with sparse low vegetation, in coastal fields or open moorland. The nest is a shallow scrape on ground. The species is mostly migratory and nomadic, even if some individuals remain in the breeding areas all year round. In winter, birds move southwards in Northern Eurasia and North America, due to abundance of prey species (mainly lemmings and small voles), that causes the so called 'snowy owl irruptions'. The species is listed as vulnerable as it is undergoing rapid population decline[2, 5]. *B. scandiacus* is reported in the Palearctic fossil record since the Early Pleistocene[3,4]. *A. noctua* is a polytypic common small sedentary owl which is spread in a variety of semi-open habitats, from parklands to semi-desert regions, spanning from boreal to tropical areas of Eurasia and Northern Africa but preferring in general warm arid areas. It nests in cavities[2, 6]. This species is known in the fossil record since the Early Pleistocene[3,4]. *P. perdix* is a polytypic medium-sized sedentary Galliformes which occurs throughout much of the Western Palearctic. This species has suffered from massive declines during the XXth century owing to habitat loss and degradation caused by agricultural intensification. It is found in grasslands with some dense shrubby patches and nests in a shallow depression at the base of a hedge or other thick vegetation[2, 7]. *P. perdix* is reported in the Palearctic fossil record since the Early Pleistocene, being more abundant in the Late Pleistocene[3,4]. *C. crex*, a monotypic medium-sized rail, is a full long-distance migrant which breeds in Europe and central Asia, in open or semi-open environments, such as meadows with tall grass. The nest is on the ground, in dense vegetation. This species winters in eastern sub-Saharan Africa, where prefers dry grasslands and savannas[2, 8]. This species is known since the Early Pleistocene, becoming more abundant in the Late Pleistocene[3,4]. *C. coturnix* is a polytypic small Galliformes that breeds in the open grasslands of Eurasia. The nest is a scrape in herbaceous vegetation on the ground. It is a full long-distance migrant and spends the winters in sub-Saharan Africa, mainly in the Sahel zone[2, 9]. *C. coturnix* is known in the Palearctic fossil record since the Early Pleistocene and becomes more common in the Late Pleistocene[3,4].

# Data S2 - Variable importance (relative influence of the five more important variables) and evaluation values of each model (CCSM, CNRM, FGOALS, GISS, IPSL, MIROC, MPI, MRI) for each species

## *Pyrrhocorax graculus* - CCSM

Var. importance: bio.8 18.3800831, bio.3 16.0713235, bio.2 8.3971183, bio.18 7.5067773, bio.9 7.1362126

Evaluation train
n presences : 237
n absences : 244
AUC : 1
cor : 0.9921315
max TPR+TNR at : 0.6151186

Evaluation test
n presences : 63
n absences : 56
AUC : 0.973356
cor : 0.8780461
max TPR+TNR at : 0.5027866

## *Pyrrhocorax graculus* - CNRM

Var. importance: bio.3 22.9945136, bio.2 16.0200376, bio.8 10.9674794, bio.19 7.9610327, bio.13 6.6381431

Evaluation train
n presences : 239
n absences : 242
AUC : 1
cor : 0.9960988
max TPR+TNR at : 0.7164497

Evaluation test
n presences : 61
n absences : 58
AUC : 0.9946297

```
cor            : 0.9425577
max TPR+TNR at : 0.6161275
```

***Pyrrhocorax graculus*** **- FGOALS**

Var. importance: bio.3 28.37778402, bio.8 15.79259811, bio.19 12.74193031, bio.11 8.84796531, bio.12 6.80968332

```
Evaluation train
n presences    : 240
n absences     : 240
AUC            : 1
cor            : 0.9934999
max TPR+TNR at : 0.7328617
```

```
Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9752778
cor            : 0.9166899
max TPR+TNR at : 0.6807326
```

***Pyrrhocorax graculus*** **- GISS**

Var. importance: bio.3 26.4024333, bio.8 11.4122872, bio.4 9.6939950, bio.19 8.9409073, bio.2 7.3981664

```
Evaluation train
n presences    : 246
n absences     : 236
AUC            : 0.9999139
cor            : 0.9845505
max TPR+TNR at : 0.6835134
```

```
Evaluation test
n presences    : 54
n absences     : 64
AUC            : 0.9748264
```

cor            : 0.8819202
max TPR+TNR at : 0.631979

***Pyrrhocorax graculus* - IPSL**

Var. importance: bio.3 27.3497044, bio.19 12.8601738, bio.5 10.7005723, bio.4 8.6736239, bio.14 8.0101202

Evaluation train
class          : ModelEvaluation
n presences    : 245
n absences     : 235
AUC            : 1
cor            : 0.9987745
max TPR+TNR at : 0.78706

Evaluation test
n presences    : 55
n absences     : 65
AUC            : 0.9876923
cor            : 0.9206223
max TPR+TNR at : 0.4379987

***Pyrrhocorax graculus* - MIROC**

Var. importance: bio.3 13.9051970, bio.8 11.4598980, bio.19  9.2772188, bio.13  9.0855225, bio.2 8.9160167

Evaluation train
n presences    : 244
n absences     : 236
AUC            : 1
cor            : 0.9916561
max TPR+TNR at : 0.686271

Evaluation test
n presences    : 56

```
n absences     : 64
AUC            : 0.9986049
cor            : 0.9600088
max TPR+TNR at : 0.6693516
```

***Pyrrhocorax graculus* - MPI**

Var. importance: bio.3 40.2250167, bio.8 12.0572192, bio.2  9.6545252, bio.6  6.1232959, bio.19 6.0636037

```
Evaluation train
n presences    : 240
n absences     : 240
AUC            : 0.9999826
cor            : 0.9877139
max TPR+TNR at : 0.4446355
```

```
Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9725
cor            : 0.8857112
max TPR+TNR at : 0.2923693
```

***Pyrrhocorax graculus* - MRI**

Var. importance: bio.4 17.0415457, bio.3 14.3266886, bio.13  9.4924036, bio.8  9.1918337, bio.15 6.8687489

```
Evaluation train
n presences    : 255
n absences     : 225
AUC            : 0.9932026
cor            : 0.9349929
max TPR+TNR at : 0.6041073
```

```
Evaluation test
```

```
n presences    : 45
n absences     : 75
AUC            : 0.938963
cor            : 0.7652218
max TPR+TNR at : 0.5930847
```

### ***Bubo scandiacus*, wintering range - CCSM**

```
Var. importance: bio.7 27.2239878, bio.1 15.5909058, bio.14  9.4530419, bio.15  7.3569528, bio.12
7.3277208

Evaluation train
n presences    : 240
n absences     : 240
AUC            : 1
cor            : 0.9991487
max TPR+TNR at : 0.8312412

Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9963889
cor            : 0.9521732
max TPR+TNR at : 0.8562762
```

### ***Bubo scandiacus*, wintering range - CNRM**

```
Var. importance: bio.3 16.7455687, bio.2 15.8073993, bio.8 14.4689629, bio.18 11.2705948, bio.4
7.4172494

Evaluation train
n presences    : 242
n absences     : 238
AUC            : 1
cor            : 0.9976284
max TPR+TNR at : 0.7211729
```

Evaluation test
n presences : 58
n absences : 62
AUC : 0.9799778
cor : 0.9063431
max TPR+TNR at : 0.5861419

**_Bubo scandiacus_, wintering range - FGOALS**

Var. importance: bio.1 21.07941739, bio.2 12.44932914, bio.5 11.57684057, bio.4 10.92289095, bio.10 9.78132705

Evaluation train
n presences : 237
n absences : 243
AUC : 1
cor : 0.9986841
max TPR+TNR at : 0.8216523

Evaluation test
n presences : 63
n absences : 57
AUC : 0.9885826
cor : 0.93763
max TPR+TNR at : 0.389507

**_Bubo scandiacus_, wintering range – GISS**

Var. importance: bio.4 39.0772485, bio.12 16.3543840, bio.3 8.5482351, bio.1 7.1132717, bio.13 4.8158901

Evaluation train
n presences : 230
n absences : 250
AUC : 1
cor : 0.9986837
max TPR+TNR at : 0.7920148

Evaluation test

n presences : 70

n absences : 50

AUC : 0.9945714

cor : 0.9445038

max TPR+TNR at : 0.468201

***Bubo scandiacus*, wintering range - IPSL**

Var. importance: bio.4 21.3357454, bio.3 14.5815777, bio.12 10.3697115, bio.8 9.9929003, bio.15 9.3718031

Evaluation train

n presences : 239

n absences : 241

AUC : 1

cor : 0.9988687

max TPR+TNR at : 0.8172766

Evaluation test

n presences : 61

n absences : 59

AUC : 0.9886079

cor : 0.9344117

max TPR+TNR at : 0.2361584

***Bubo scandiacus*, wintering range - MIROC**

Var. importance: bio.3 24.9953274, bio.1 18.2076517, bio.15 12.9824335, bio.4 6.0116626, bio.7 5.9562372

Evaluation train

n presences : 240

n absences : 240

AUC : 1

cor : 0.9985086

```
max TPR+TNR at : 0.7472241
```

```
Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9977778
cor            : 0.9587645
max TPR+TNR at : 0.3506854
```

### ***Bubo scandiacus*, wintering range – MPI**

Var. importance: bio.1 26.4607327, bio.18 12.4462073, bio.2 12.1054681, bio.4  7.5533832, bio.12 6.2563012

```
Evaluation train
n presences    : 240
n absences     : 240
AUC            : 1
cor            : 0.9982287
max TPR+TNR at : 0.7281611
```

```
Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9966667
cor            : 0.9590535
max TPR+TNR at : 0.3749381
```

### ***Bubo scandiacus*, wintering range – MRI**

Var. importance: bio.1 21.6283396, bio.4 18.9615116, bio.2  8.7262568, bio.12  8.4894958, bio.14 6.7380018

```
Evaluation train
n presences    : 245
n absences     : 235
AUC            : 1
```

cor : 0.997647
max TPR+TNR at : 0.7425055

Evaluation test
n presences : 55
n absences : 65
AUC : 0.9963636
cor : 0.9506461
max TPR+TNR at : 0.7300653

### *Bubo scandiacus*, breeding range - CCSM

Var. importance: bio.10 25.5475642, bio.5 21.6367823, bio.2 13.4077419, bio.3 11.5905906, bio.18 7.5116805

Evaluation train
n presences : 230
n absences : 250
AUC : 1
cor : 0.9957085
max TPR+TNR at : 0.5962335

Evaluation test
n presences : 70
n absences : 50
AUC : 0.9928571
cor : 0.9434722
max TPR+TNR at : 0.4396043

### *Bubo scandiacus*, breeding range - CNRM

Var. importance: bio.2 38.86506839, bio.10 12.13846465, bio.18 11.54050024, bio.3 10.50409802, bio.8 10.02260932

Evaluation train
n presences : 241
n absences : 239

AUC : 1
cor : 0.9962053
max TPR+TNR at : 0.7298184
Evaluation test
n presences : 59
n absences : 61
AUC : 0.9936093
cor : 0.9630463
max TPR+TNR at : 0.6134392

### ***Bubo scandiacus*, breeding range - FGOALS**

Var. importance: bio.2 63.023398182, bio.18 12.794795556, bio.3 5.772470297, bio.7 5.323328034, bio.5 3.428982334

Evaluation train
n presences : 242
n absences : 238
AUC : 1
cor : 0.9974436
max TPR+TNR at : 0.7373109

Evaluation test
n presences : 58
n absences : 62
AUC : 0.996941
cor : 0.9523647
max TPR+TNR at : 0.6373854

### ***Bubo scandiacus*, breeding range - GISS**

Var. importance: bio.8 35.13853357, bio.3 14.67880610, bio.10 14.28602553, bio.18 13.13751125, bio.9 5.57046846

Evaluation train
n presences : 242
n absences : 239

```
AUC            : 0.9999308
cor            : 0.9865104
max TPR+TNR at : 0.4385703
```

```
Evaluation test
n presences    : 58
n absences     : 61
AUC            : 1
cor            : 0.9753737
max TPR+TNR at : 0.4011146
```

***Bubo scandiacus*, breeding range - IPSL**

Var. importance: bio.18 41.52832071, bio.5 17.73191658, bio.10 16.49978445, bio.3  9.11739245, bio.16 3.17442494

```
Evaluation train
n presences    : 235
n absences     : 245
AUC            : 0.9999826
cor            : 0.9941468
max TPR+TNR at : 0.3883646
```

```
Evaluation test
n presences    : 65
n absences     : 55
AUC            : 0.9888112
cor            : 0.9730529
max TPR+TNR at : 0.4870946
```

***Bubo scandiacus*, breeding range - MIROC**

Var. importance: bio.2 32.4750836, bio.18 26.8869046, bio.5 13.0079504, bio.3  7.7053595, bio.4 4.3097379

```
Evaluation train
n presences    : 241
```

```
n absences     : 239
AUC            : 1
cor            : 0.9942988
max TPR+TNR at : 0.6493983

Evaluation test
n presences    : 59
n absences     : 61
AUC            : 0.9966657
cor            : 0.9415295
max TPR+TNR at : 0.3168652
```

### *Bubo scandiacus*, breeding range - MPI

Var. importance: bio.18 31.87432986, bio.10 19.40992072, bio.8 14.39910127, bio.3  7.68145144, bio.5 6.31720107

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 1
cor            : 0.9955193
max TPR+TNR at : 0.6977875

Evaluation test
n presences    : 58
n absences     : 62
AUC            : 0.9986096
cor            : 0.9691946
max TPR+TNR at : 0.5012148
```

### *Bubo scandiacus*, breeding range - MRI

Var. importance: bio.2 29.69420535, bio.18 19.04505073, bio.3 12.70456817, bio.10  8.98578139, bio.6 7.32160908

```
Evaluation train
```

```
n presences    : 241
n absences     : 239
AUC            : 1
cor            : 0.9930614
max TPR+TNR at : 0.4734608

Evaluation test
n presences    : 59
n absences     : 61
AUC            : 0.9944429
cor            : 0.944481
max TPR+TNR at : 0.8194517
```

### *Crex crex***, wintering range - CCSM**

Var. importance: bio.4 30.282804785, bio.2 17.200564045, bio.3 11.807693951, bio.12  9.216402669, bio.18  5.777278533

```
Evaluation train
n presences    : 238
n absences     : 243
AUC            : 1
cor            : 0.9940242
max TPR+TNR at : 0.3054828

Evaluation test
n presences    : 62
n absences     : 57
AUC            : 0.999717
cor            : 0.9740611
max TPR+TNR at : 0.699541
```

### *Crex crex***, wintering range - CNRM**

Var. importance: bio.4 46.100070457, bio.7 17.573725700, bio.13 14.510444670, bio.12  4.131934302, bio.1  3.413672391

```
Evaluation train
n presences    : 234
n absences     : 247
AUC            : 1
cor            : 0.9995034
max TPR+TNR at : 0.8145048
```

```
Evaluation test
n presences    : 66
n absences     : 53
AUC            : 0.9874214
cor            : 0.9336682
max TPR+TNR at : 0.6544742
```

### *Crex crex*, wintering range - FGOALS

Var. importance: bio.2 23.97015456, bio.3 19.32741040, bio.15 18.81200863, bio.19 10.27772809, bio.14 7.84980450

```
Evaluation train
n presences    : 235
n absences     : 246
AUC            : 1
cor            : 0.9983678
max TPR+TNR at : 0.6886163
```

```
Evaluation test
n presences    : 65
n absences     : 54
AUC            : 0.9985755
cor            : 0.9359414
max TPR+TNR at : 0.1149004
```

### *Crex crex*, wintering range – GISS

Var. importance: bio.4 17.25297635, bio.2 16.46719569, bio.9 14.59587665, bio.3 13.29858952, bio.18 7.62853476

```
Evaluation train
n presences    : 241
n absences     : 240
AUC            : 1
cor            : 0.9991592
max TPR+TNR at : 0.8454622

Evaluation test
n presences    : 59
n absences     : 60
AUC            : 0.9960452
cor            : 0.9693653
max TPR+TNR at : 0.6386525
```

***Crex crex*, wintering range - IPSL**

Var. importance: bio.3 20.46562367, bio.4 17.76917680, bio.14 15.34935657, bio.12 10.92635502, bio.15 7.43944547

```
Evaluation train
n presences    : 246
n absences     : 235
AUC            : 1
cor            : 0.9998264
max TPR+TNR at : 0.8678773

Evaluation test
n presences    : 54
n absences     : 65
AUC            : 1
cor            : 0.9850954
max TPR+TNR at : 0.09515892
```

***Crex crex*, wintering range – MIROC**

Var. importance: bio.4 55.26914083, bio.2 23.36702002, bio.3 10.06728435, bio.8  2.76942724, bio.15 2.58282018

```
Evaluation train
n presences    : 236
n absences     : 245
AUC            : 1
cor            : 0.9994265
max TPR+TNR at : 0.8540138
```

```
Evaluation test
n presences    : 64
n absences     : 55
AUC            : 0.9875
cor            : 0.9327763
max TPR+TNR at : 0.8809668
```

### ***Crex crex*, wintering range - MPI**

Var. importance: bio.4 45.943304712, bio.2 12.581368900, bio.6  7.533858253, bio.12  4.961918245, bio.7 4.766432485

```
Evaluation train
n presences    : 234
n absences     : 247
AUC            : 1
cor            : 0.9987048
max TPR+TNR at : 0.7589877
```

```
Evaluation test
n presences    : 66
n absences     : 53
AUC            : 1
cor            : 0.9771309
max TPR+TNR at : 0.3681444
```

### ***Crex crex*, wintering range - MRI**

Var. importance: bio.4 29.57187182, bio.2 27.35057617, bio.7  9.25284430, bio.5  6.21539381, bio.9 5.41813102

```
Evaluation train
n presences    : 237
n absences     : 243
AUC            : 1
cor            : 0.9991929
max TPR+TNR at : 0.846166
```

```
Evaluation test
n presences    : 63
n absences     : 57
AUC            : 0.9991646
cor            : 0.9742106
max TPR+TNR at : 0.5849
```

### ***Crex crex*, breeding range - CCSM**

Var. importance: bio.14 20.9035783, bio.17 18.6809529, bio.15 12.7963315, bio.10 12.0868336, bio.5 5.2841321

```
Evaluation train
n presences    : 243
n absences     : 238
AUC            : 0.9975101
cor            : 0.9705384
max TPR+TNR at : 0.4707432
```

```
Evaluation test
n presences    : 57
n absences     : 62
AUC            : 0.9949066
cor            : 0.9324419
max TPR+TNR at : 0.6328612
```

### *Crex crex*, breeding range - CNRM

Var. importance: bio.14 22.32631002, bio.3 21.98682569, bio.15 21.46837243, bio.5 13.38097802, bio.17 4.24931944

```
Evaluation train
n presences    : 238
n absences     : 242
AUC            : 0.9997569
cor            : 0.990436
max TPR+TNR at : 0.5261475

Evaluation test
n presences    : 62
n absences     : 58
AUC            : 0.9849833
cor            : 0.9171823
max TPR+TNR at : 0.5777403
```

### *Crex crex*, breeding range - FGOALS

Var. importance: bio.15 44.94148718, bio.3 16.28276996, bio.7  9.85999415, bio.5  6.16598337, bio.10 5.63304800

```
Evaluation train
n presences    : 240
n absences     : 240
AUC            : 1
cor            : 0.9963634
max TPR+TNR at : 0.5978673

Evaluation test
n presences    : 60
n absences     : 60
AUC            : 0.9961111
cor            : 0.9423702
max TPR+TNR at : 0.2245815
```

### *Crex crex*, breeding range - GISS

Var. importance: bio.14 30.5778367, bio.3 18.5401210, bio.15 12.1416935, bio.5 6.0467565, bio.2 5.2791969

```
Evaluation train
n presences    : 241
n absences     : 239
AUC            : 1
cor            : 0.998038
max TPR+TNR at : 0.7249346
```

```
Evaluation test
n presences    : 59
n absences     : 61
AUC            : 0.9872187
cor            : 0.8870871
max TPR+TNR at : 0.4323176
```

### *Crex crex*, breeding range - IPSL

Var. importance: bio.14 25.1566165, bio.15 13.5453563, bio.10 13.1348398, bio.3 11.3211041, bio.17 9.1949693

```
Evaluation train
n presences    : 234
n absences     : 246
AUC            : 0.9997915
cor            : 0.9858515
max TPR+TNR at : 0.4932286
```

```
Evaluation test
n presences    : 66
n absences     : 54
AUC            : 0.9963524
cor            : 0.952546
```

```
max TPR+TNR at : 0.7546186
```

***Crex crex*, breeding range - MIROC**

Var. importance: bio.14 31.5639239, bio.15 12.8959047, bio.10 12.2342087, bio.3 11.2694059, bio.2 11.0070826

```
Evaluation train
n presences    : 242
n absences     : 239
AUC            : 0.9999481
cor            : 0.9888414
max TPR+TNR at : 0.3116323

Evaluation test
n presences    : 58
n absences     : 61
AUC            : 0.9771057
cor            : 0.8814432
max TPR+TNR at : 0.7827192
```

***Crex crex*, breeding range - MPI**

Var. importance: bio.17 21.2818417, bio.15 21.2607932, bio.3 16.3947449, bio.5 12.1971519, bio.9 4.9545459

```
Evaluation train
n presences    : 245
n absences     : 235
AUC            : 0.9988363
cor            : 0.9767157
max TPR+TNR at : 0.4597665

Evaluation test
n presences    : 55
n absences     : 65
AUC            : 0.993007
```

```
cor            : 0.9463434
max TPR+TNR at : 0.3621413
```

**_Crex crex_, breeding range – MRI**

```
Var. importance: bio.14 36.7130578, bio.15 16.7919640, bio.10 16.1923290, bio.3  6.7294319, bio.17 4.3306131
```

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 1
cor            : 0.9932859
max TPR+TNR at : 0.2813261
```

```
Evaluation test
n presences    : 58
n absences     : 62
AUC            : 0.9655172
cor            : 0.8888126
max TPR+TNR at : 0.8022112
```

**_Coturnix coturnix_, wintering range - CCSM**

```
Var. importance: bio.4 17.9623448, bio.5 11.9151820, bio.8 10.4937027, bio.10  8.8285430, bio.6 7.2447972
```

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 0.9975693
cor            : 0.9657115
max TPR+TNR at : 0.4988285
```

```
Evaluation test
n presences    : 58
n absences     : 62
```

AUC : 0.9746941

cor : 0.8746813

max TPR+TNR at : 0.3329008

**Coturnix coturnix*, wintering range - CNRM***

Var. importance: bio.4 21.7372095, bio.7 9.9724024, bio.5 8.4476829, bio.16 7.3428954, bio.10 6.8990452

Evaluation train

n presences : 236

n absences : 244

AUC : 0.9976035

cor : 0.9556678

max TPR+TNR at : 0.419839

Evaluation test

n presences : 64

n absences : 56

AUC : 0.9933036

cor : 0.9206238

max TPR+TNR at : 0.6936789

***Coturnix coturnix*, wintering range - FGOALS**

Var. importance: bio.7 16.1020922, bio.1 10.5326047, bio.12 10.0178285, bio.18 8.5837885, bio.9 8.2434392

Evaluation train

n presences : 243

n absences : 237

AUC : 0.9998958

cor : 0.983663

max TPR+TNR at : 0.5491697

Evaluation test

n presences : 57

n absences : 63

AUC : 0.9922027

cor : 0.9242059

max TPR+TNR at : 0.5933

**_Coturnix coturnix_, wintering range - GISS**

Var. importance: bio.3 18.1918222, bio.1 11.9648465, bio.7  8.5846512, bio.4  6.8984376, bio.2  5.9054104

Evaluation train

n presences : 246

n absences : 234

AUC : 0.9999131

cor : 0.9819429

max TPR+TNR at : 0.4765673

Evaluation test

n presences : 54

n absences : 66

AUC : 0.9329405

cor : 0.7425909

max TPR+TNR at : 0.6442904

**_Coturnix coturnix_, wintering range - IPSL**

Var. importance: bio.7 29.245184, bio.12 12.148565, bio.17 10.662309, bio.6  7.989266, bio.5  6.187066

Evaluation train

n presences : 237

n absences : 243

AUC : 1

cor : 0.9936169

max TPR+TNR at : 0.650407

Evaluation test

n presences : 63

```
n absences     : 57
AUC            : 0.9944305
cor            : 0.9523136
max TPR+TNR at : 0.48306
```

### *Coturnix coturnix*, wintering range - MIROC

Var. importance: bio.6 14.1203613, bio.12 12.9834998, bio.4 11.8273751, bio.8 11.3047986, bio.5 8.9737631

```
Evaluation train
n presences    : 248
n absences     : 232
AUC            : 1
cor            : 0.9901551
max TPR+TNR at : 0.5562421
```

```
Evaluation test
n presences    : 52
n absences     : 68
AUC            : 0.9889706
cor            : 0.9044362
max TPR+TNR at : 0.4181047
```

### *Coturnix coturnix*, wintering range - MPI

Var. importance: bio.8 20.498409, bio.4 16.256101, bio.12 10.020766, bio.2  7.398379, bio.19  4.763113

```
Evaluation train
n presences    : 238
n absences     : 242
AUC            : 1
cor            : 0.9848642
max TPR+TNR at : 0.5068185
```

```
Evaluation test
n presences    : 62
```

```
n absences     : 58
AUC            : 0.9858176
cor            : 0.9163195
max TPR+TNR at : 0.4543837
```

### *Coturnix coturnix*, wintering range – MRI

Var. importance: bio.4 21.0393872, bio.1 16.8986830, bio.18  7.8305022, bio.7  7.8164008, bio.19 6.3770153

```
Evaluation train
n presences    : 237
n absences     : 243
AUC            : 0.9990624
cor            : 0.969939
max TPR+TNR at : 0.4817052
```

```
Evaluation test
n presences    : 63
n absences     : 57
AUC            : 0.9651908
cor            : 0.8370769
max TPR+TNR at : 0.6013944
```

### *Coturnix coturnix*, breeding range - CCSM

Var. importance: bio.19 29.2223697, bio.10 13.8134451, bio.1  8.9074008, bio.17  7.3405455, bio.8 6.6596123

```
Evaluation train
n presences    : 236
n absences     : 244
AUC            : 0.9997916
cor            : 0.9788055
max TPR+TNR at : 0.431902
```

```
Evaluation test
```

```
n presences    : 64
n absences     : 56
AUC            : 0.96875
cor            : 0.8673039
max TPR+TNR at : 0.8677223
```

### *Coturnix coturnix*, breeding range - CNRM

Var. importance: bio.17 17.9656688, bio.14 16.4324267, bio.15 14.6303822, bio.5  9.1382797, bio.2 6.7243966

```
Evaluation train
n presences    : 237
n absences     : 243
AUC            : 0.999236
cor            : 0.9698913
max TPR+TNR at : 0.4222124
```

```
Evaluation test
n presences    : 63
n absences     : 57
AUC            : 0.9908104
cor            : 0.9301162
max TPR+TNR at : 0.4307516
```

### *Coturnix coturnix*, breeding range - FGOALS

Var. importance: bio.15 27.4980444, bio.17 11.5847130, bio.10  8.7452647, bio.14  8.4438302, bio.5 7.6339922

```
Evaluation train
n presences    : 238
n absences     : 242
AUC            : 1
cor            : 0.9953713
max TPR+TNR at : 0.5848919
```

```
Evaluation test
n presences    : 62
n absences     : 58
AUC            : 0.9769188
cor            : 0.9233469
max TPR+TNR at : 0.8746123
```

### ***Coturnix coturnix*, breeding range - GISS**

Var. importance: bio.15 24.0487664, bio.17 12.8176999, bio.10 11.3415014, bio.5  9.7553471, bio.1 7.4547185

```
Evaluation train
 n presences    : 238
n absences     : 242
AUC            : 0.9995139
cor            : 0.9744827
max TPR+TNR at : 0.4289757
```

```
Evaluation test
n presences    : 62
n absences     : 58
AUC            : 0.958287
cor            : 0.8606796
max TPR+TNR at : 0.7558889
```

### ***Coturnix coturnix*, breeding range - IPSL**

Var. importance: bio.19 23.0988953, bio.17 14.5998462, bio.5 11.7479505, bio.10  9.2589389, bio.15 7.6796715

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 1
cor            : 0.989864
max TPR+TNR at : 0.421792
```

```
Evaluation test
n presences    : 58
n absences     : 62
AUC            : 0.9938821
cor            : 0.9319797
max TPR+TNR at : 0.1546534
```

### ***Coturnix coturnix*, breeding range - MIROC**

Var. importance: bio.19 19.5174500, bio.5 14.3639640, bio.17 12.1129567, bio.14  9.6495770, bio.3 7.0437288

```
Evaluation train
n presences    : 236
n absences     : 244
AUC            : 1
cor            : 0.9929026
max TPR+TNR at : 0.4988432
```

```
Evaluation test
n presences    : 64
n absences     : 56
AUC            : 0.9662388
cor            : 0.8421749
max TPR+TNR at : 0.5554222
```

### ***Coturnix coturnix*, breeding range - MPI**

Var. importance: bio.19 27.8303278, bio.15 16.0398969, bio.5 15.7456840, bio.8  6.3393267, bio.2 5.8255246

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 0.9999306
cor            : 0.9834607
```

```
max TPR+TNR at : 0.5833983
```

```
Evaluation test
n presences    : 58
n absences     : 62
AUC            : 0.987208
cor            : 0.9233983
max TPR+TNR at : 0.4652753
```

***Coturnix coturnix*, breeding range - MRI**

Var. importance: bio.17 44.0342040, bio.10 10.6438399, bio.19  9.0906091, bio.3  7.6872797, bio.5 4.5419607

```
Evaluation train
n presences    : 241
n absences     : 239
AUC            : 0.9993229
cor            : 0.9721603
max TPR+TNR at : 0.4684307
```

```
Evaluation test
n presences    : 59
n absences     : 61
AUC            : 0.9736038
cor            : 0.8742979
max TPR+TNR at : 0.2394595
```

***Athene noctua* - CCSM**

Var. importance: bio.11 18.6439081, bio.1 12.0165075,  bio.3 10.9995750, bio.18  8.3642021, bio.8 8.3135295

```
Evaluation train
n presences    : 241
n absences     : 239
AUC            : 1
```

cor : 0.9940568
max TPR+TNR at : 0.632494

Evaluation test
n presences : 59
n absences : 61
AUC : 0.9883301
cor : 0.9270336
max TPR+TNR at : 0.5241273

### ***Athene noctua*** **- CNRM**

Var. importance: bio.3 20.9184087, bio.11 15.6547577, bio.2 12.7514810, bio.1 10.9950320, bio.8 6.9049423

Evaluation train
n presences : 242
n absences : 238
AUC : 1
cor : 0.9969772
max TPR+TNR at : 0.7241992

Evaluation test
n presences : 58
n absences : 62
AUC : 0.987208
cor : 0.901498
max TPR+TNR at : 0.2855782

### ***Athene noctua*** **- FGOALS**

Var. importance: bio.11 24.514685, bio.1 12.708851, bio.3 9.306664, bio.13 8.081401, bio.8 5.454867

Evaluation train
n presences : 249
n absences : 231
AUC : 0.9967837

```
cor           : 0.9782365
max TPR+TNR at : 0.7078737
```

```
Evaluation test
n presences    : 51
n absences     : 69
AUC            : 0.9951691
cor           : 0.9405124
max TPR+TNR at : 0.6601653
```

### *Athene noctua* - GISS

Var. importance: bio.3 31.9721083, bio.11 17.0371972, bio.12  9.1929154, bio.8  8.0229132, bio.1 7.0424751

```
Evaluation train
n presences    : 251
n absences     : 229
AUC            : 0.9999478
cor           : 0.9872221
max TPR+TNR at : 0.5743415
```

```
Evaluation test
n presences    : 49
n absences     : 71
AUC            : 0.9945387
cor           : 0.9381722
max TPR+TNR at : 0.3389205
```

### *Athene noctua* - IPSL

Var. importance: bio.6 15.2132793, bio.1 13.5194233, bio.11 12.1745212, bio.3  9.5410608, bio.7 8.3599807

```
Evaluation train
n presences    : 235
n absences     : 245
```

```
AUC            : 1
cor            : 0.9938195
max TPR+TNR at : 0.6890475

Evaluation test
n presences    : 65
n absences     : 55
AUC            : 0.9946853
cor            : 0.923719
max TPR+TNR at : 0.3675275
```

***Athene noctua* - MIROC**

```
Var. importance: bio.3 31.0141007, bio.11 14.1930145, bio.1  9.6536193, bio.8  6.4603731, bio.15
5.3650119

Evaluation train
n presences    : 239
n absences     : 241
AUC            : 1
cor            : 0.9939859
max TPR+TNR at : 0.5315395

Evaluation test
n presences    : 61
n absences     : 59
AUC            : 0.9894415
cor            : 0.9131714
max TPR+TNR at : 0.6348607
```

***Athene noctua* - MPI**

```
Var. importance: bio.3 30.9601747, bio.11 19.5312486, bio.8  7.6808741, bio.2  5.4325166, bio.12
5.1016200

Evaluation train
n presences    : 247
```

```
n absences     : 233
AUC            : 1
cor            : 0.9962273
max TPR+TNR at : 0.7009319
```

```
Evaluation test
n presences    : 53
n absences     : 67
AUC            : 0.9811321
cor            : 0.8922638
max TPR+TNR at : 0.6930431
```

***Athene noctua*** **- MRI**

Var. importance: bio.1 23.1416300, bio.11 14.6345929, bio.14  7.3415449, bio.17  7.0933998, bio.12 6.9708652

```
Evaluation train
n presences    : 237
n absences     : 243
AUC            : 1
cor            : 0.9909717
max TPR+TNR at : 0.4629204
```

```
Evaluation test
n presences    : 63
n absences     : 57
AUC            : 0.9955444
cor            : 0.9368047
max TPR+TNR at : 0.623228
```

***Perdix perdix*** **- CCSM**

Var. importance: bio.1 16.322308, bio.10 15.862596, bio.19 14.951666, bio.15 11.302701, bio.17  9.556328

```
Evaluation train
n presences    : 245
```

```
n absences     : 237
AUC            : 1
cor            : 0.9988212
max TPR+TNR at : 0.7174145
```

```
Evaluation test
n presences    : 55
n absences     : 63
AUC            : 0.9939394
cor            : 0.9534171
max TPR+TNR at : 0.7064351
```

**_Perdix perdix_ – CNRM**

Var. importance: bio.15 39.7405088, bio.10  8.0932517, bio.5  7.8907712, bio.1  7.4604754, bio.3 6.5049240

```
Evaluation train
n presences    : 248
n absences     : 233
AUC            : 0.9997923
cor            : 0.9872866
max TPR+TNR at : 0.5755065
```

```
Evaluation test
n presences    : 52
n absences     : 67
AUC            : 0.999713
cor            : 0.9791666
max TPR+TNR at : 0.5144568
```

**_Perdix perdix_ - FGOALS**

Var. importance: bio.15 4.831420e+01, bio.17 1.464201e+01, bio.5 1.011540e+01, bio.8 8.076905e+00, bio.18 4.047200e+00

Evaluation train

```
n presences    : 236
n absences     : 244
AUC            : 1
cor            : 0.9997509
max TPR+TNR at : 0.9241894
```

```
Evaluation test
n presences    : 64
n absences     : 56
AUC            : 0.9866071
cor            : 0.9216309
max TPR+TNR at : 0.740028
```

***Perdix perdix* - GISS**

Var. importance: bio.17 19.058030107, bio.19 16.706378930, bio.10 16.270777901, bio.3  9.066544159, bio.5  7.027111292

```
Evaluation train
n presences    : 242
n absences     : 238
AUC            : 1
cor            : 0.9977341
max TPR+TNR at : 0.6105089
```

```
Evaluation test
n presences    : 58
n absences     : 62
AUC            : 0.9810901
cor            : 0.8995122
max TPR+TNR at : 0.2507997
```

***Perdix perdix* - IPSL**

Var. importance: bio.19 44.63000749, bio.10 17.12395841, bio.5  7.81144083, bio.15  6.23561744, bio.17 5.35595937

Evaluation train
n presences : 239
n absences : 241
AUC : 1
cor : 0.9955846
max TPR+TNR at : 0.6327539

Evaluation test
n presences : 61
n absences : 59
AUC : 0.9905529
cor : 0.9624265
max TPR+TNR at : 0.3374962

***Perdix perdix* - MIROC**

Var. importance: bio.19 38.5821392, bio.10 20.2412279, bio.17 14.7364038, bio.5 8.1896501, bio.1 3.7271071

Evaluation train
n presences : 243
n absences : 238
AUC : 1
cor : 0.9957908
max TPR+TNR at : 0.521158

Evaluation test
n presences : 57
n absences : 62
AUC : 0.9966044
cor : 0.9388863
max TPR+TNR at : 0.1468404

***Perdix perdix* - MPI**

Var. importance: bio.10 18.93415102, bio.19 16.32492366, bio.15 13.67923633, bio.8 10.38049365, bio.3 8.57528937

```
Evaluation train
n presences    : 236
n absences     : 245
AUC            : 0.9999654
cor            : 0.9928401
max TPR+TNR at : 0.3980764

Evaluation test
n presences    : 64
n absences     : 55
AUC            : 0.9928977
cor            : 0.9421292
max TPR+TNR at : 0.6264473
```

***Perdix perdix*** **- MRI**

Var. importance: bio.15 32.38157929, bio.1 11.83441988, bio.17  9.79539528, bio.5  9.70230038, bio.19 9.39490661

```
Evaluation train
n presences    : 237
n absences     : 243
AUC            : 0.999618
cor            : 0.9836852
max TPR+TNR at : 0.3259169

Evaluation test
N presences    : 63
n absences     : 57
AUC            : 0.9966583
cor            : 0.9496465
max TPR+TNR at : 0.6055084
```

**Data S3 - Values of the cells of the LGM ensembles corresponding to fossil occurrences.** The values range from 0 (0 out of 8 models predict the occurrence of the species in that cell) to 8 (all 8 models predict the occurrence of the species in that cell).

*Pyrrhocorax graculus*: 6 6 5 7 5 7 6 5 6 6 6 7 7 4 6 6 5 7 5 6 6 6 7 6 8 7 4 4 7 7 6 6 4 6 6 7 7 5 6 8 6 7 8 8 4 6 8 8

*Bubo scandiacus* (breeding range): 0 0 0 0 0 0 1 1 0 1 1 0 0 0 1 0 1 0 0 0 1 1 0 0 0

*Bubo scandiacus* (wintering range): 0 2 2 3 0 2 1 6 0 2 4 2 1 1 5 3 2 4 2 4 1 1 3 2 1

*Athene noctua*: 7 8 8 8 8 8 8 7 8

*Perdix perdix*: 4 2 4 3 4 2 2 2 3 2 1 4 3 4 2 4 3 7 4 6 2 6 3 4 6 4 6 4 6 6 2 2 6 3 3

*Crex crex* (breeding range): 3 4 7 3

*Coturnix coturnix* (breeding range): 7 5 7 6 6 5 8 7 7 8 8 8 8 7 7 8 6 7

**Table S4 - List of the MIS 2 fossil occurrences of the six species in the Western Palearctic.** In the tables are reported the names of the fossil localities, the layers of provenance, the geographic coordinates and the main bibliographic references

*Pyrrhocorax graculus*

| Site name and layer | Latitude | Longitude | Bibliographic reference |
|---|---|---|---|
| Brillenhöhle (Baden-Württemberg) Layer V | 48.403935 | 9.780276 | 3 |
| Brillenhöhle (Baden-Württemberg) Layer VI | 48.403935 | 9.780276 | 3 |
| Sesselfelsgrotte (Bayern) Layer C | 48.935528 | 11.789297 | 4 |
| Sandalja II Layer E | 44.888780 | 13.883458 | 3 |
| Grotte de la Vache (Ariége) Layer IV | 42.821281 | 1.587741 | 3, 4, 10 |
| Grotte des Harpons (Haute-Garonne) Layer D | 43.234823 | 0.663978 | 3 |
| Abri de Campalou (Drôme) Layer 2 | 45.068396 | 5.254231 | 3 |
| Abri de Campalou (Drôme) Layer 3 | 45.068396 | 5.254231 | 3 |
| Grotte d'Embulla (Pyrénées-Orientale) Layer 1 | 42.581468 | 2.416360 | 3 |
| Isturitz (Pyrénées-Atlantiques) Layer Salle de St Martin | 43.352904 | -1.206127 | 3, 10 |
| Isturitz (Pyrénées-Atlantiques) Layer Salle de St Martin, La Grande Salle Niveau II | 43.352904 | -1.206127 | 3, 10 |
| La Madeleine (Dordogne) | 44.966876 | 1.036410 | 3 |
| La Madeleine (Dordogne) Layer 9 | 44.966876 | 1.036410 | 3 |
| La Madeleine (Dordogne) Layer 13 | 44.966876 | 1.036410 | 3 |
| Laugerie Haute Est (Dordogne) Layer 2-20 | 44.952249 | 1.001764 | 3 |
| Piage (Lot) Layer c-E | 44.8044 | 1.3897 | 3 |
| Rond-du Barry (Haute-Loire) Layer D | 45.071203 | 3.859404 | 3 |
| Rond-du Barry (Haute-Loire) Layer E | 45.071203 | 3.859404 | 3 |
| Rond-du Barry (Haute-Loire) Layer F | 45.071203 | 3.859404 | 3 |
| Salpêtriére à Remoulins (Gard) Layer C 4 | 43.938924 | 4.564192 | 3 |
| Salpêtriére à Remoulins (Gard) Layer C 5 | 43.938924 | 4.564192 | 3 |
| Salpêtriére à Remoulins (Gard) Layer D | 43.938924 | 4.564192 | 3 |
| Salpêtriére à Remoulins (Gard) Layer "ensemble i" | 43.938924 | 4.564192 | 3 |
| Salpêtriére à Remoulins (Gard) Layer 5 | 43.938924 | 4.564192 | 3 |

| | | | |
|---|---|---|---|
| Trois Frères (Ariège) | 43.032113 | 1.211584 | 3, 10 |
| Combe Sauniére 1 (Dordogne) Layer IV | 45.238806 | 0.873718 | 3 |
| Grotte du Bison (Yonne) Layer C | 47.601199 | 3.756028 | 3 |
| Grotte du Bison (Yonne) Layer C | 47.5911 | 3.7651 | 3 |
| Aurensan inférieure (Hautes-Pyrénées) | 43.617109 | -0.203386 | 3 |
| Baume de Gigny (Jura) Layer VI | 46.469155 | 5.475109 | 3 |
| Bois du Cantet (Hautes-Pyrénées) Layer Secteur 1 | 43.059066 | 0.295046 | 3 |
| Bois du Cantet (Hautes-Pyrénées)Layer Secteur 2 | 43.059066 | 0.295046 | 3 |
| Bois-de-Brousses (Hérault) Layer 1A | 43.553084 | 3.256859 | 3 |
| Bois-de-Brousses (Hérault) Layer 2B | 43.553084 | 3.256859 | 3 |
| Cauna de Belvis (Aude) Layer C6 | 42.849496 | 2.076573 | 3 |
| Grotte Gazel (Aude) Layer 7 | 43.323602 | 2.419950 | 3 |
| Grotte Gazel (Aude) Layer C.7 | 43.323602 | 2.419950 | 10 |
| Grotte Jean-Pierre No. 1 (Savoie) Layer 9 | 45.500497 | 5.843928 | 3, 4 |
| Grotta della Serratura (Salerno) Layer 9 | 39.998057 | 15.371955 | 4 |
| Arene Candide (Liguria) Layer P1 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P3 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P4 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P7 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P8 | 44.165450 | 8.330301 | 3 |
| Riparo Salvini (Lazio) | 41.287284 | 13.251601 | 3, 4 |
| Cueva de Abauntz (Navarra) Layer e | 43.013899 | -1.641201 | 4 |
| Aitzbitarte IV (Guipuzcoa) | 43.262471 | -1.895824 | 3 |
| Cova des Cendres (Alicante) Layer XI | 38.720295 | 0.182650 | 3, 4 |
| Cueva de Ambrosio (Almeria) Layer II (=Nivel 5) | 37.821993 | -2.099180 | 3, 4 |
| Ekain (Guipuzcoa) Layer IV | 43.236567 | -2.275960 | 3 |
| Ekain (Guipuzcoa) Layer Via | 43.236567 | -2.275960 | 3 |
| Ekain (Guipuzcoa) Layer VII | 43.236567 | -2.275960 | 3 |
| Ekain (Guipuzcoa) Layer VIII | 43.236567 | -2.275960 | 3 |
| Erralla Cave (Guipuzcoa) Layer Level IV (spit 11-12) | 43.2089 | -2.1819 | 3 |
| Arbreda (Gerona) Layer D | 42.161581 | 2.746261 | 3, 4; 11 |
| Arbreda (Gerona) Layer C | 42.161581 | 2.746261 | 3, 4, 11 |
| Arbreda (Gerona) Layer 13-16 (Probably Layers B, C) | 42.161581 | 2.746261 | 3, 4 |
| Urtiaga (Guipuzcoa) Layer F-G | 43.295176 | -2.353938 | 3 |
| Urtiaga (Guipuzcoa) Layer I | 43.295176 | -2.353938 | 3 |
| Combe-Cullier (Lot) Layer 5 | 44.8456 | 1.5664 | 3 |
| Grotte d'Ebbou (Ardèche) | 44.5100 | 4.0800 | 3 |
| Laroque II (Hérault) Layer b | 43.9167 | 3.7333 | 3 |
| Tournal (Aude) a | 43.3167 | 2.8833 | 3 |
| Tournal (Aude) b | 43.3167 | 2.8833 | 3 |
| Tournal (Aude) c | 43.3167 | 2.8833 | 3 |
| Tournal (Aude) Layer "Couche à sagaies" | 43.3167 | 2.8833 | 3 |
| Covolo di Trene (Vicenza) | 45.5214 | 11.4744 | 3 |
| Palidoro (Lazio) Layer 1 | 41.9333 | 12.1833 | 3 |
| Palidoro (Lazio) Layer 3 | 41.9333 | 12.1833 | 3 |
| Palidoro (Lazio) Layer 6 | 41.9333 | 12.1833 | 3 |
| Palidoro (Lazio) Layer 8 | 41.9333 | 12.1833 | 3 |
| Cueva de el Parco (Lérida) Layer N.IV Int. Cueva | 41.9086 | 0.9419 | 4 |
| Cueva de el Parco (Lérida) Layer N.VI Int. Cueva | 41.9086 | 0.9419 | 4 |

|  |  |  |  |
|---|---|---|---|
| Cueva de el Parco (Lérida) Layer N.X. Int. Cueva | 41.9086 | 0.9419 | 4 |
| Roccia San Sebastiano Layer c2 | 41.1357 | 13.8799 | 12, 13 |
| Roccia San Sebastiano Layer e | 41.1357 | 13.8799 | 12, 13 |
| Roccia San Sebastiano Layers cuts 1-6 | 41.1357 | 13.8799 | 12, 13 |
| Grotta del Pozzo | 41.9723 | 13.6717 | 12 |
| Coulet des Roches (Vaucluse) c | 44.0775 | 5.426308 | 14 |
| Aitzbitarte III Layer III | 43.2706 | -1.8905 | 15 |
| Cava a Filo | 44.44285 | 11.37982 | 16 |
| Lapa do Picareiro Layer T | 39.5305 | -8.6520 | 17, 18, 19, 20 |
| Grotta di Ortucchio | 41.9561 | 13.6467 | 21 |

## *Bubo scandiacus*

|  |  |  |  |
|---|---|---|---|
| Grotte de la Vache (Ariége) Layer IV | 42.821281 | 1.587741 | 3, 4 |
| Isturitz (Pyrénées-Atlantiques) Layer la Grand Salle Niveau I | 43.352904 | -1.206127 | 3 |
| Isturitz (Pyrénées-Atlantiques) Layer la Grand Salle Niveau II | 43.352904 | -1.206127 | 3 |
| La Madeleine (Dordogne) | 44.966876 | 1.036410 | 3 |
| Piage (Lot) Layer c-E | 44.8044 | 1.3897 | 3, 22 |
| Rond-du Barry (Haute-Loire) Layer E | 45.071203 | 3.859404 | 3 |
| Trois Frères (Ariège) | 43.032113 | 1.211584 | 3 |
| Combe Sauniére 1 (Dordogne) Layer IV | 45.238806 | 0.873718 | 3, 4 |
| Abri Dufaure (Landes) Layer 6 | 43.535847 | -1.072403 | 3, 4 |
| Baume de Gigny (Jura) Layer VI | 46.469155 | 5.475109 | 3 |
| Bois-Ragot, Gouex (Vienne) Layer BR5b | 46.365774 | 0.688330 | 3, 4 |
| Bois-Ragot, Gouex (Vienne) Layer BR4b | 46.365774 | 0.688330 | 3, 4 |
| Bois-de-Brousses (Hérault) Layer 1a | 43.553084 | 3.256859 | 3 |
| Arene Candide (Liguria) Layer P1 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P4 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P7 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P9 | 44.165450 | 8.330301 | 3 |
| Pekárna (Moravia) | 49.2628 | 16.7823 | 3, 23 |
| Flageolet II (Dordogne) Layer IX | 44.8500 | 1.0833 | 3 |
| Fontarnaud (Girondet) | 44.7500 | -0.1667 | 3 |
| Grotte du Placard (Charente) Layer "Brèche" | 45.6833 | 0.4167 | 3 |
| Grottes de Jaurias (Gironde) | 44.8261 | -0.2887 | 3, 22 |
| Covolo di Trene (Vicenza) | 45.5214 | 11.4744 | 3 |
| Coulet des Roches b | 44.0775 | 5.426308 | 14 |
| Grotte de Lourdes (Hautes-Garonne) coll. Harle (Middle and Upper Magd layer) | 43.091004 | -0.045874 | 22 |
| Plantade (Tarn-et-Garonne) corniche sup., excav. Brun, Middle and Upper Magdalenian layers | 45.5833 | 2.6000 | 22 |
| Gandil (Tarn-et-Garonne) c.20, c.25 et c.23, excav. Ladier | 44.0500 | 1.6667 | 22 |
| Saint-Germain-la-Riviere (Gironde) ens. sup., excav. Trecolle | 44.9500 | -0.3167 | 22 |
| Taillis des Coteaux (Vienne) Layer IIIa, excav. Primault | 46.53 | 0.85 | 22, 24 |
| Taillis des Coteaux (Vienne) Layer IIg, excav. Primault | 46.53 | 0.85 | 22 |
| Roc de Marcamps 2 (Gironde) excav. Lenoir | 45.0322 | -0.5020 | 22 |

## *Athene noctua*

|  |  |  |  |
|---|---|---|---|
| Rond-du Barry (Haute-Loire) Layer E | 45.071203 | 3.859404 | 3 |
| Combe Sauniére 1 (Dordogne) Layer IV | 45.238806 | 0.873718 | 3, 4 |
| Arene Candide (Liguria) Layer P7 | 44.165450 | 8.330301 | 3 |

| | | | |
|---|---|---|---|
| Arene Candide (Liguria) Layer P9 | 44.165450 | 8.330301 | [3] |
| Riparo Salvini (Lazio) | 41.287284 | 13.251601 | [3, 4] |
| Cueva de Ambrosio (Almeria) Layer I (=Nivel 6.1-6.3) | 37.821993 | -2.099180 | [3, 4] |
| Cueva de Ambrosio (Almeria) Layer II (=Nivel 5) | 37.821993 | -2.099180 | [3, 4] |
| Palidoro (Lazio) Layer 8 | 41.9333 | 12.1833 | [3] |
| Tossal de la Roca (Alicante) Layer III | 38.7902 | -0.2810 | [3] |
| Lapa do Picareiro Layer T | 39.5305 | -8.6520 | [17, 19, 20] |
| Grotta di Ortucchio | 41.9561 | 13.6467 | [21] |

## *Perdix perdix*

| | | | |
|---|---|---|---|
| Grotte du Bois Laiterie (Namur) Layer TT | 50.3500 | 4.8500 | [4] |
| Grotte du Bois Laiterie (Namur) Layer YSS | 50.3500 | 4.8500 | [4] |
| Grotte du Bois Laiterie (Namur) Layer BSC | 50.3500 | 4.8500 | [4] |
| Geissenklösterle (Baden-Württemberg) Layer AH Io | 48.398207 | 9.772127 | [3, 4] |
| Grotte de la Vache (Ariége) Layer IV | 42.821281 | 1.587741 | [3, 4] |
| Abri de Campalou (Drôme) Layer 2 | 45.068396 | 5.254231 | [3, 4] |
| Grotte d'Embulla (Pyrénées-Orientale) Layer 1 | 42.581468 | 2.416360 | [3] |
| La Madeleine (Dordogne) | 44.966876 | 1.036410 | [3] |
| Pont d'Ambon (Dordogne) Layer 4 | 45.3014 | 0.5382 | [3] |
| Rond-du Barry (Haute-Loire) Layer D | 45.071203 | 3.859404 | [3] |
| Rond-du Barry (Haute-Loire) Layer E | 45.071203 | 3.859404 | [3] |
| Rond-du Barry (Haute-Loire) Layer E 3 | 45.071203 | 3.859404 | [3] |
| Rond-du Barry (Haute-Loire) Layer F 2 | 45.071203 | 3.859404 | [3] |
| Salpêtriére à Remoulins (Gard) Layer D | 43.938924 | 4.564192 | [3] |
| Trois Frères (Ariège) | 43.032113 | 1.211584 | [3] |
| Combe Sauniére 1 (Dordogne) Layer IV | 45.238806 | 0.873718 | [3, 4] |
| Aurensan inférieure (Hautes-Pyrénées) | 43.617109 | -0.203386 | [3] |
| Baume de Gigny (Jura) Layer V | 46.469155 | 5.475109 | [3] |
| Bois du Cantet (Hautes-Pyrénées) Layer Secteur 1 | 43.059066 | 0.295046 | [3] |
| Bois-de-Brousses (Hérault) Layer 2B | 43.553084 | 3.256859 | [3] |
| Flageolet I (Dordogne) Layer V | 44.848653 | 1.068722 | [3] |
| Grotte Gazel (Aude) Layer 7 | 43.323602 | 2.419950 | [3] |
| Grotte Jean-Pierre No. 1 (Savoie) Layer 9 | 45.500497 | 5.843928 | [3, 4] |
| Grotta della Serratura (Salerno) Layer 9 | 39.998057 | 15.371955 | [4] |
| Arene Candide (Liguria) Layer P1 | 44.165450 | 8.330301 | [3] |
| Arene Candide (Liguria) Layer P3 | 44.165450 | 8.330301 | [3] |
| Arene Candide (Liguria) Layer P4 | 44.165450 | 8.330301 | [3] |
| Arene Candide (Liguria) Layer P7 | 44.165450 | 8.330301 | [3] |
| Arene Candide (Liguria) Layer P8 | 44.165450 | 8.330301 | [3] |
| Arene Candide (Liguria) Layer P9 | 44.165450 | 8.330301 | [3] |
| Riparo Salvini (Lazio) | 41.287284 | 13.251601 | [3, 4, 21] |
| Cueva de Abauntz (Navarra) Layer e | 43.013899 | -1.641201 | [4] |
| Arbreda (Gerona) Layer 13-16 (Probably Layers B, C) | 42.161581 | 2.746261 | [3, 4] |
| Arbreda (Gerona) 17 (Probably Layer D) | 42.161581 | 2.746261 | [3, 4] |
| Urtiaga (Guipuzcoa) Layer F-G | 43.295176 | -2.353938 | [3] |
| Tournal (Aude) a | 43.3167 | 2.8833 | [3] |
| Palidoro (Lazio) Layer 1 | 41.9333 | 12.1833 | [3] |
| Palidoro (Lazio) Layer 3 | 41.9333 | 12.1833 | [3] |
| Palidoro (Lazio) Layer 6 | 41.9333 | 12.1833 | [3] |

| | | | |
|---|---|---|---|
| Palidoro (Lazio) Layer 7 | 41.9333 | 12.1833 | 3 |
| Palidoro (Lazio) Layer 8 | 41.9333 | 12.1833 | 3 |
| Roc de la Melca (Gerona) | 42.4200 | 1.5500 | 3 |
| Grotta di Ortucchio (Aquila) | 41.9561 | 13.6467 | 4, 21 |
| Zupanov spodmol Layer C-D | 45.7450 | 14.1142 | 4 |
| Roccia San Sebastiano Layer c2 | 41.1357 | 13.8799 | 12, 13 |
| Roccia San Sebastiano Layer e | 41.1357 | 13.8799 | 12, 13 |
| Roccia San Sebastiano Layers cuts 1-6 | 41.1357 | 13.8799 | 12, 13 |
| Grotta del Pozzo | 41.9723 | 13.6717 | 12 |
| Aitzbitarte III Layers III | 43.2706 | -1.8905 | 15 |
| Pekárna Cave | 49.2628 | 16.7823 | 23 |
| Cava a Filo | 44.44285 | 11.37982 | 16 |
| Lapa do Picareiro Layer T | 39.5305 | -8.6520 | 17, 18, 19, 20 |
| Lapa do Picareiro Layer U | 39.5305 | -8.6520 | 17, 18, 19, 20 |

## *Crex crex*

| | | | |
|---|---|---|---|
| Bois-Ragot (Vienne) Layer BR5b | 46.365774 | 0.688330 | 3, 4 |
| Arene Candide (Liguria) Layer P1 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P9 | 44.165450 | 8.330301 | 3 |
| Temnata Cave Layer 3 c/d | 43.174288 | 24.072201 | 3, 4 |
| Biśnik Cave (Czestochowa uplands) Layer Complex II | 50.4264 | 19.8317 | 4, 25 |

## *Coturnix coturnix*

| | | | |
|---|---|---|---|
| Sandalja II Layer E | 44.888780 | 13.883458 | 3 |
| Abri de Campalou (Drôme) Layer 3 | 45.068396 | 5.254231 | 3 |
| Pont d'Ambon (Dordogne) Layer 4 | 45.3014 | 0.5382 | 3 |
| Rond-du Barry (Haute-Loire) Layer D | 45.071203 | 3.859404 | 3 |
| Rond-du Barry (Haute-Loire) Layer E | 45.071203 | 3.859404 | 3 |
| Rond-du Barry (Haute-Loire) Layer E 3 | 45.071203 | 3.859404 | 3 |
| Rond-du Barry (Haute-Loire) Layer F | 45.071203 | 3.859404 | 3 |
| Salpêtriére à Remoulins (Gard) Layer C3 | 43.938924 | 4.564192 | 3 |
| Salpêtriére à Remoulins (Gard) Layer "ensemble i" | 43.938924 | 4.564192 | 3 |
| Aurensan inférieure (Hautes-Pyrénées) | 43.617109 | -0.203386 | 3 |
| Baume de Gigny (Jura) Layer V | 46.469155 | 5.475109 | 3 |
| Grotta della Serratura (Salerno) Layer 9 | 39.998057 | 15.371955 | 4 |
| Arene Candide (Liguria) Layer P1 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P4 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P7 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P8 | 44.165450 | 8.330301 | 3 |
| Arene Candide (Liguria) Layer P9 | 44.165450 | 8.330301 | 3 |
| Riparo Salvini (Lazio) | 41.287284 | 13.251601 | 3, 4 |
| Cueva de Nerja (Malaga) Layer 13 | 36.761594 | -3.846283 | 3 |
| Arbreda (Gerona) Layer D | 42.161581 | 2.746261 | 3, 4, 11 |
| Arbreda (Gerona) Layer C | 42.161581 | 2.746261 | 3, 4, 11 |
| Palidoro (Lazio) Layer 8 | 41.9333 | 12.1833 | 3 |
| Roc de la Melca (Gerona) | 42.4200 | 1.5500 | 3 |
| Ohalo 2 (Galilee) | 32.722093 | 35.572143 | 4 |
| Roccia San Sebastiano Layer c2 | 41.1357 | 13.8799 | 12, 13 |
| Roccia San Sebastiano Layer e | 41.1357 | 13.8799 | 12, 13 |

| | | | |
|---|---|---|---|
| Roccia San Sebastiano Layers cuts 1-6 | 41.1357 | 13.8799 | 12, 13 |
| Aitzbitarte III Layers III | 43.2706 | -1.8905 | 15 |
| Grotta di Ortucchio | 41.9561 | 13.6467 | 21 |

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## 7. Manuscript V

### The presence of boreal bird species in the Mediterranean Basin during the Middle and the Late Pleistocene: a literature review

# The presence of boreal bird species in the Mediterranean Basin during the Middle and the Late Pleistocene: a literature review

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## Abstract

The fossil record attests the presence, during past cold climatic periods, of arctic and boreal bird species in Mediterranean Europe. The reports of the fossil occurrences of these species, which have important palaeobiogeographic and palaeoecologic value, are often old and not well documented. Here, we review the extant literature that concerns these fossil occurrences, in order to bring out the criticalities of the taxonomic attributions. We listed 109 Middle and Late Pleistocene fossil localities within the Mediterranean basin where the occurrence of 28 arctic and boreal species has been reported. 17 species' occurrences have been confirmed, as the identifications were supported by photos, drawings, measurements and descriptions. Most confirmed species are only recorded in few sites and with a small number of specimens. The 11 species that have not been confirmed lacked, in most cases, any kind of documentation in support of the identifications. These latter fossil remains need to be further analysed in order to clarify their taxonomic affinities. This work stresses the importance of yielding proper documentation along with systematic identifications, in order to provide reliable palaeobiogeographic data.

**Keywords:** Avifauna, fossils, range shifts, climatic oscillations, arctic species

## Introduction

Large-scale climate oscillations, such as those that characterized the Quaternary, triggered latitudinal and altitudinal shifts of the vegetational belts, that were followed by animal species (Hewitt 2000, 2004). The latter track their ecological niche modifying their distribution in response to climate-driven environmental changes, based on the species-specific climatic tolerances, dispersal capacity, genetic diversity, reproductive strategies, phenotypic plasticity, and population growth rates (Nogues-Bravo et al. 2018). For instance, the expansion of the ice cap during glacial phases forced plants and animals to move southwards, as the climatic conditions at the northern latitudes became unsuitable for their survival. The Last Glacial Maximum (LGM) was characterized by cool temperatures, reduced precipitations, and decreased $CO_2$ air concentration, that produced increased aridity conditions with the consequent expansion of desert/grassland/steppe areas and the retreat of forests in Southern Europe (Prentice et al. 2000; Harrison and Prentice 2003; Allen et al. 2010; Becker et al. 2015; Binney et al. 2017).

Several bird species which currently inhabit boreal and arctic areas, spread in Mediterranean Europe during glacial times, as witnessed by the fossil record (Tyrberg 1991, 1998, 2008; Sanchez Marco 2004; Smith et al. 2013; Holm and Svenning, 2014; Carrera et al. 2018b). The presence of these species in the mid-latitudes in the past carries several important palaeoecological and biogeographical implications. For instance, as these species are used as palaeoenvironmental indicators, their occurrence in Southern Europe indicates the presence of the habitats that the species currently inhabit at the high latitudes (tundra, steppe, or taiga). Likewise, it represents an evidence of past population dynamics of the species (such as contraction or expansion of the ranges, isolation in the climatic refugia, changes in the ecological niche), providing pivotal insights to reconstruct their genetic history (Avise and Walker 1998; Blondel and Mourer-Chauviré 1998; Newton 2003; Tietze 2018). Furthermore, it improves the knowledge of past adaptations to climate changes, that helps elucidate the current and future responses of birds to global warming and adopt more suitable conservation strategies. Given the multiple significance of these fossil occurrences, the reliability of the taxonomic identification of the fossil bones plays a key role.

The literature reports several fossil occurrences of boreal bird species in the Mediterranean basin during the Pleistocene. These reports often come from publications that are old and/or lack proper documentation in support of the taxonomic identifications, frequently just consisting in the mention of the species in a list of taxa without further detailing the identification in any way. With the expression “proper documentation” we mean whichever material that provides an evidence that the identification is correct and repeatable, such as photographs, drawings, measures, and accurate descriptions of the bones. The aim of this work is to check all the available existing literature concerning the presence of these species in the Mediterranean basin during the Middle and the Late Pleistocene, in order to bring out the criticalities of the taxonomic identifications and assess which species are supported by reliable documentation and which are not. The review of the literature available will also allow to chronologically detail the occurrences of the involved species.

## Material and methods

The species object of this research are those species that have been reported in the Middle and Late Pleistocene fossil record of the Mediterranean area, that have an extant arctic or boreal distribution, and that are currently irregularly, rarely or never observed in the Mediterranean countries, due to their climatic and ecological requirements (*Lagopus lagopus*, *Cygnus cygnus*, *Branta bernicla*, *Anser caerulescens*, *Anser brachyrhynchus*, *Histrionicus histrionicus*, *Leucogeranus leucogeranus*, *Fulmarus glacialis*, *Calidris maritima*, *Gallinago solitaria*, *Xema sabini*, *Larus hyperboreus*, *Sterna paradisaea*, *Catharacta skua*, *Pinguinus impennis*, *Alle alle*, *Uria aalge*, *Uria lomvia*, *Surnia ulula*, *Strix nebulosa*, *Bubo scandiacus*, *Falco rusticolus*, *Melanocorypha maxima*, *Eremophila alpestris*, *Bombycilla garrulus*, *Pinicola enucleator*, *Loxia pytyopsittacus*, *Loxia leucoptera*) (Tyrberg 1998, 2008; Cramp 1998; Baccetti et al. 2021; Rouco et al. 2019). Among these 28 species, we have included a few species, reported in the fossil record, that have never or very rarely been reported in the Western Palearctic (*Anser caerulescens*, *Leucogeranus leucogeranus*, *Gallinago solitaria*, *Melanocorypha maxima*) (Cramp 1998; Del Hoyo et al. 2014, 2016), and a species that went extinct in the XIX century (*Pinguinus impennis*). In the Western Palearctic fossil record are also reported several occurrences of large thrushes, such as *Zoothera dauma* and *Turdus migratorius*, that have never or very rarely been reported in the in this area in recent times (Cramp 1998; Del Hoyo et al. 2016), but we didn't include them in this work as they have already been object of revision by Louchart (2004). This author, after a thorough re-analysis of the above-mentioned remains, established that most of them should be rather attributed to cf. *Turdus viscivorus* (or cf. Turdidae) whereas others belong to the extinct species *Meridiocichla salotti* (Louchart 2004).

We didn't include the Early Pleistocene occurrences of the selected species in this work, as the current morphology of extant species is supposed to be more fixed and reliable from the Middle Pleistocene on, due to the younger age and to the greater abundance of fossil records (Mourer-Chauvire 1993; Tyrberg 1998, 2008; Finlayson 2011; Bedetti and Pavia 2013).

The Mediterranean watershed (Fig. 1) has been selected to represent the Mediterranean basin (Bouraoui et al. 2010; Malagò et al. 2019), as it is supposed to have strongly been influenced by the Mediterranean climate through time, maintaining relatively mild climatic conditions also during the cooler climatic peaks (Ray and Adams 2001; Becker et al. 2015; Binney et al. 2017).

We collected all the bibliographic references of Middle and Late Pleistocene fossil records (included "cf." or "aff." tentative attributions) of the selected species in the Mediterranean basin. Successively, we thoroughly checked in the literature the material provided in support of each taxonomic identifications. In detail, we distinguished several categories: name in a list (no documentation), photos of the bones, drawings of the bones, measures of the bones and description of the diagnostic osteological features of the bones. We assessed as reliable those fossil occurrences which were supported by at least one literature reference with proper documentation (photos, drawings, measures or descriptions or a combination of them), and as non-reliable the species for whom these supporting materials weren't available. In addition, we have been able to directly analyze a few of the fossil remains object of the present research.

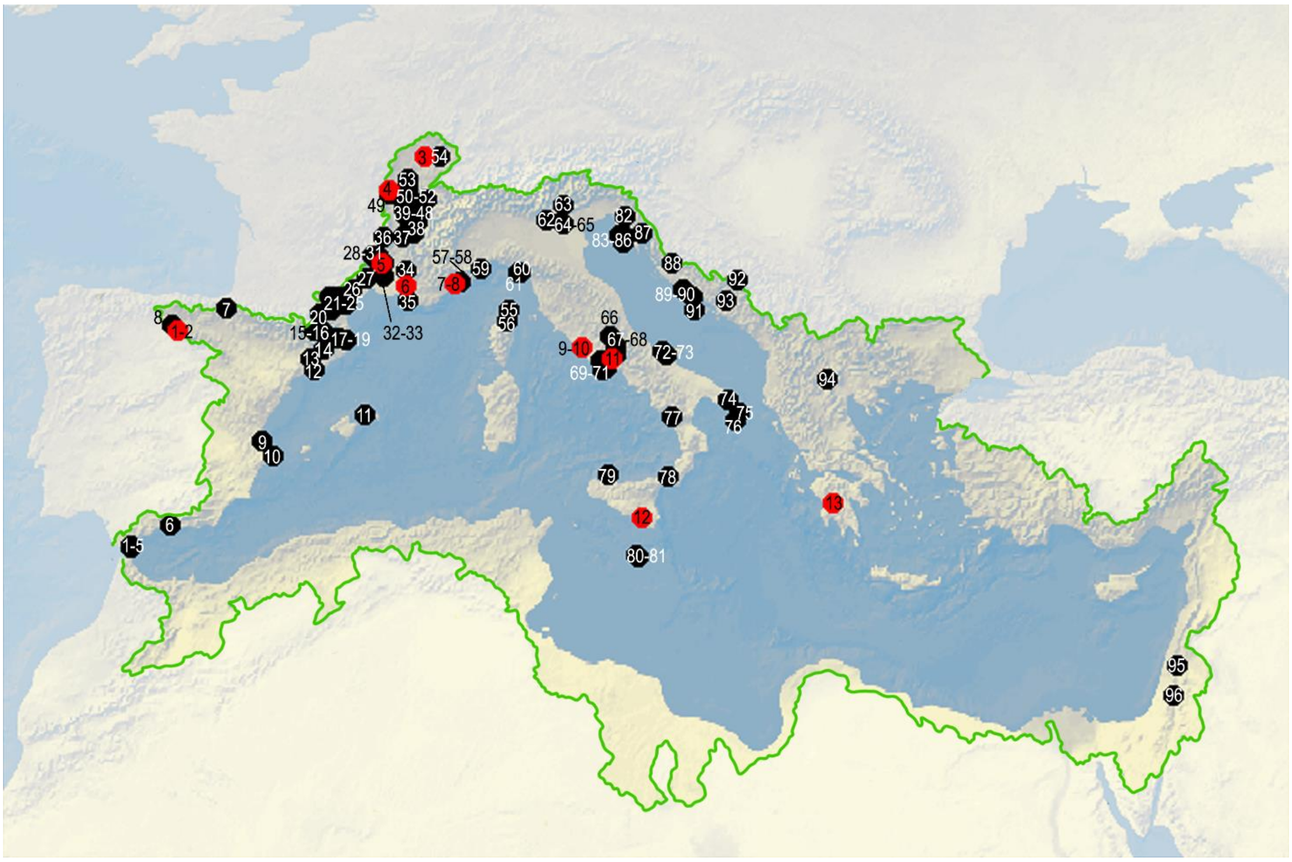

Fig. 1: Map of the Mediterranean area, with the Mediterranean watershed delimited by the green line. The red dots represent the Middle Pleistocene fossil localities with boreal species, based on the literature available: 1-Atapuerca-La Galeria (Tyrberg 2008); 2-Atapuerca-Boca Norte (Tyrberg 2008); 3-L'Aven de Romain-La-Roche (Tyrberg 2008); 4-Grotte de Rizerolles (Tyrberg 1998); 5-Orgnac 3 (Tyrberg 1998); 6-Grotte de l"Escale à Saint-Esteve-Janson (Tyrberg 1998); 7-Grotte du Lazaret (Tyrberg 1998); 8-Grotte du Lazaret Locus VIII (Tyrberg 1998); 9-Casal Selce (Pavia and Bedetti 2013; Pavia et al. 2019); 10-Malagrotta (Tyrberg 1998); 11-Colle Avarone (Tyrberg 1998); 12-Comiso (Pavia and Insacco 2013); 13-Marathousa 1 (Michailidis et al. 2018). The black dots represent the Late Pleistocene fossil occurrences of boreal species: 1-Gorham's Cave (Tyrberg 1998, 2008; Cooper 2005; Finlayson et al. 2015; Sanchez Marco 2018b); 2-Devil's Tower (Tyrberg 1998, 2008; Cooper 2005; Finlayson et al. 2015); 3-Ibex Cave (Cooper 2005; Tyrberg 2008; Finlayson et al. 2015); 4-Vanguard Cave (Cooper 2005; Tyrberg 2008; Finlayson et al. 2015); 5-Beefsteak Cave (Tyrberg 1998); 6-Cueva de Nerja (Tyrberg 1998); 7-Cueva de Abauntz (Tyrberg 2008); 8-Cueva de Valdegoba (Tyrberg 2008); 9-Cueva Volcan (Tyrberg 1998); 10-Cova des Cendres (Tyrberg 2008): 11-Punta des Sac des Blat (Tyrberg 2008); 12-Avenc del Gegant (Tyrberg 2008); 13-Abric Romani (Tyrberg 2008); 14-Cueva del Toll (Tyrberg 2008); 15-Cau de Olopte (Tyrberg 2008); 16-S'Espasa (Tyrberg 1998); 17-Arbreda (Tyrberg 2008); 18-Arbreda II (Tyrberg 1998); 19-Ramandils (Tyrberg 1998); 20-Cauna de Belvis (Tyrberg 1998); 21-Grotte de Laffray (Tyrberg 1998); 22-Canecaude I (Tyrberg 1998); 23-Tournal (Tyrberg 1998); 24-Grotte Gazel (Tyrberg 1998); 25-La Crouzade (Tyrberg 1998); 26-Bois-de-Brousses (Tyrberg 1998); 27-Salpetre a Pompignan (Tyrberg 1998); 28-Grotte d'Ebbou (Tyrberg 1998); 29-Grotte des Barasses II (Rufà et al. 2018); 30-Abri Superieur de Colombier (Tyrberg 1998); 31-Abri des Pêcheurs (Tyrberg 1998); 32-Balauzière (Tyrberg 1998); 33-Salpetriere à Remoulins (Tyrberg 1998); 34-Coulet des Roches (Crégut-Bonnoure et al. 2014); 35-Grotte Cosquer (Tyrberg 1998); 36-Grotte du Tai 2 (Tyrberg 2008); 37-Saint Romans (Tyrberg 1998); 38-Balme de Glos (Tyrberg 1998); 39-Abri de Campalou (Tyrberg 1998); 40-Grotte Jean-Pierre No. 1 (Tyrberg 1998, 2008); 41-Balme-les-Grottes (Tyrberg 1998); 42-Savigny (Tyrberg 1998); 43-Grotte des Romains (Tyrberg 1998); 44-Douattes (Tyrberg 1998); 45-La Colombiere (Tyrberg 1998); 46-Abri Gay (Tyrberg 1998); 47-Grotte des Hotetux (Tyrberg 1998); 48-La Grand Baille (Tyrberg 1998); 49-Solutré (Tyrberg 1998); 50-Grottes de Veyrier (Tyrberg 1998); 51-Baume de Gigny (Tyrberg 1998); 52-Caverne de Bèthenas Supérieure (Tyrberg 1998); 53-Grotte Grappin (Tyrberg 1998); 54-Abri de Rochedane (Tyrberg

1998); 55-Grotte Nord-Ouest de la Grotte de la Coscia (Tyrberg 2008); 56-Grotta di Funtanedu (Tyrberg 2008); 57-Grottes de Grimaldi (Tyrberg 1998); 58-Grotta del Principe (Tyrberg 1998); 59-Arene Candide (Tyrberg 1998); 60-Grotta dei Colombi (Tyrberg 1998); 61-Buca del Bersagliere (Tyrberg 1998); 62-Riparo di Fumane (Tyrberg 1998, 2008; Fiore et al. 2004; Peresani et al. 2011); 63-Riparo Dalmeri (Tyrberg 2008); 64-Covolo di Trene (Tyrberg 1998); 65-Grotta del Buso Doppio del Broion (Carrera et al. 2018b); 66-Grottoni (Tyrberg 1998); 67-Grotta di Ortucchio (Alhaique and Recchi 2001; Tyrberg 2008); 68-Carnello (Tyrberg 1998); 69-Riparo Salvini (Tyrberg 1998); 70-Grotta del Fossellone (Tyrberg 2008); 71-Cava di Sezze Romano (Tyrberg 1998); 72-Ingarano (Tyrberg 1998, Bedetti and Pavia 2007); 73-Grotta Paglicci (Tagliacozzo and Gala 2004); 74-Grotta di Cardamone (Tyrberg 1998, 2008); 75-Grotta Romanelli (Tyrberg 1998, 2008); 76-Grotta dei Giganti (Tyrberg 1998); 77-Grotta della Madonna (Tyrberg 1998); 78-Archi (Tyrberg 1998); 79-Grotta dell'Addaura (Tyrberg 1998); 80-Ghar Dalam (Tyrberg 2008); 81-Zebbug Cave (Tyrberg 2008); 82-Roska Spilja (Tyrberg 1998); 83-Romualdova pecina (Tyrberg 1998); 84-Sandalja I (Tyrberg 1998); 85-Sandalja II (Tyrberg 1998, Lenardić et al. 2018; Oros Sršen et al. 2014); 86-Ljubićeva pecina (Oros Sršen et al. 2014); 87-Vrtare male (Lenardic et al. 2018); 88-Pecina u Brini (Tyrberg 1998); 89-Mujina pecina (Lenardic et al. 2018); 90-Kopacina (Lenardic et al. 2018); 91-Vela spila (Lenardic et al. 2018); 92-Crvena Stijena (Tyrberg 1998); 93-Zelena Pecina (Tyrberg 1998); 94-Loutra Almopias (Boev and Tsoukala 2019); 95-Ohalo II (Tyrberg 2008); 96-Jericho (Tyrberg 1998).

| | **Middle Pleistocene** | **Late Pleistocene** |
|---|---|---|
| *Lagopus lagopus* | L'Aven de Romain-La-Roche | Cueva de Abauntz, Tournal, Grotte Gazel, La Crouzade, Bois-de-Brousses, Salpetre a Pompignan, Grotte d'Ebbou, Grotte des Barasses II, Abri Superieur de Colombier, Balauzière, Salpetriere à Remoulins, Grotte du Tai 2, Saint Romans, Balme de Glos, Abri de Campalou, Grotte Jean-Pierre No. 1, Balme-les-Grottes, Savigny, Grotte des Romains, Douattes, La Colombiere, Abri Gay, Grotte des Hotetux, La Grand Baille, Grottes de Veyrier, Baume de Gigny, Caverne de Bèthenas Supérieure, Grotte Grappin, Abri de Rochedane, Arene Candide, Riparo di Fumane, Riparo Dalmeri, Grotta di Ortucchio, Roska Spilja, Romualdova pecina, Sandalja I, Sandalja II, Ljubićeva pecina, Mujina pecina, Kopacina, Vela spila, Crvena Stijena, Zelena Pecina, Loutra almopias |
| *Cygnus cygnus* | Comiso | Ramandils, Balauzière, Grotte des Romains, Baume de Gigny, Grottes de Grimaldi, Arene Candide, Grottoni, Carnello, Cava di Sezze Romano, Grotta Romanelli, Grotta della Madonna, Grotta dell'Addaura, Sandalja II, Pecina u Brini, Crvena Stijena, Ohalo II, Jericho |
| *Branta bernicla* | Malagrotta, Marathousa 1 | Gorham's Cave, Ibex Cave, Vanguard Cave, Cueva de Nerja, Cova des Cendres, Arbreda, Arene Candide, Grotta di Ortucchio, Riparo Salvini, Grotta del Fossellone, Grotta di Cardamone, Grotta Romanelli, Grotta dei Giganti, Ghar Dalam, Zebbug Cave |
| *Anser caerulescens* | | Grotta Romanelli |
| *Anser brachyrhynchus* | Malagrotta, Colle Avarone | Grotte Gazel, Grotta Romanelli |
| *Histrionicus histrionicus* | Casal Selce | |
| *Leucogeranus leucogeranus* | | Grotta Romanelli |
| *Fulmarus glacialis* | | Gorham's Cave, Devil's Tower, Vanguard Cave |
| *Calidris maritima* | Atapuerca-La Galeria | Gorham's Cave |
| *Gallinago solitaria* | | Arene Candide |
| *Xema sabini* | | Ohalo II |
| *Larus hyperboreus* | | Arene Candide |
| *Sterna paradisaea* | | Abri Gay, Arene Candide, Buca del Bersagliere |
| *Catharacta skua* | | Gorham's Cave, Cueva de Nerja |
| *Pinguinus impennis* | | Gorham's Cave, Devil's Tower, Ibex Cave, Cueva de Nerja, Grotte Cosquer, Arene Candide, Grotta Romanelli, Archi |
| *Alle alle* | | Gorham's Cave, Devil's Tower, Baume de Gigny |
| *Uria aalge* | | Devil's Tower, Vanguard Cave, Beefsteak Cave, Cueva de Nerja, Cueva Volcan, Punta des Sac des Blat, Arene Candide |
| *Uria aalge/lomvia* | Grotte du Lazaret | |
| *Surnia ulula* | | Arene Candide, Grotta del Buso Doppio del Broion |
| *Strix nebulosa* | | Arene Candide |

| | | |
|---|---|---|
| *Bubo scandiacus* | Grotte de Rizerolles, Orgnac 3, Grotte de l"Escale à Saint-Esteve-Janson, Grotte du Lazaret, Grotte du Lazaret Locus VIII | Gorham's Cave, Cueva del Toll, S'Espasa, Cauna de Belvis, Grotte de Laffray, Canecaude I, La Crouzade, Bois-de-Brousses, Abri des Pêcheurs, Coulet des Roches, Saint Romans, Grotte des Romains, Abri Gay, Solutré, Baume de Gigny, Arene Candide, Grotta dei Colombi, Riparo di Fumane, Covolo di Trene, Grotta del Buso Doppio del Broion, Grotta del Fossellone, Ingarano, Grotta di Cardamone, Grotta Romanelli, Sandalja II, Vrtare male |
| *Falco rusticolus* | | Cueva Volcan, La Crouzade, Grotte des Romains, Arene Candide, Grotta di Cardamone |
| *Melanocorypha maxima* | | Arene Candide |
| *Eremophila alpestris* | Atapuerca-La Galeria, Grotte de l'Escale à Saint-Esteve-Janson | Grotte Nord-Ouest de la Grotte de la Coscia, Grotta di Funtanedu, Arene Candide, Riparo di Fumane, Grotta del Buso Doppio del Broion, Grotta Paglicci |
| *Bombycilla garrulus* | Orgnac 3 | Grotte Nord-Ouest de la Grotte de la Coscia, Grotta del Principe, Sandalja I, Sandalja II, Loutra Almopias Cave |
| *Pinicola enucleator* | Atapuerca-La Galeria, Atapuerca-Boca Norte, Grotte du Lazaret | Cueva de Valdegoba, Avenc del Gegant, Abric Romani, Cau de Olopte, Arbreda II, Abri des Pêcheurs, Arene Candide, Riparo di Fumane |
| *Loxia pytyopsittacus* | Grotte du Lazaret | Avenc del Gegant, Salpetrière à Remoulins, Arene Candide, Riparo di Fumane |
| *Loxia leucoptera* | | Arene Candide |

Tab. 1: List of the boreal bird species with Middle and Late Pleistocene fossil records in the Mediterranean basin. For each species are reported the Middle Pleistocene and the Late Pleistocene fossil localities where their occurrence has been reported in the literature. The literature for each locality is listed in Fig. 1.

## Results

After a thorough check of the literature available, we listed 109 Middle and Late Pleistocene fossil localities with reported occurrence of boreal species in the Mediterranean basin (Fig. 1, Tab. 1). Overall, high concentrations of sites with boreal species fossil occurrences are observed in the Mediterranean France. This is more likely due to the high number of French sites that have been studied, compared to other countries (Mourer-Chauviré 1975; Tyrberg 1998), rather than to real higher concentrations of the species. On the other hand, it is worth mentioning that the wide almost flat area of Central and Southern France facilitated the widespread of other boreal species such as *Rangifer tarandus* (Nadachowski et al. 2016).

We separated the fossil occurrences that are supported by proper documentations from those that are not, and we confirm the occurrence of several boreal species in the Mediterranean basin during the Middle and Late Pleistocene. Overall, we assessed as reliable the presence of 17 boreal species out of 28 reported in the literature (Tab. 2). The 11 species which resulted non-confirmed (*Anser caerulescens*, *Leucogeranus leucogeranus*, *Calidris maritima*, *Gallinago solitaria*, *Xema sabini*, *Larus hyperboreus*, *Catharacta skua*, *Strix nebulosa*, *Melanocorypha maxima*, *Pinicola enucleator*, *Loxia leucoptera*) include some species that have never or very rarely been reported in the Western Palearctic in recent times (*Anser caerulescens*, *Leucogeranus leucogeranus*, *Gallinago solitaria*, *Melanocorypha maxima*) (Cramp 1998; Del Hoyo et al. 2014, 2016). For a few of these species (*A. caerulescens*, *G. solitaria* and *M. maxima*), photos and measurements of the bones were reported in the relative bibliographic references (Cassoli 1980; Tagliacozzo and Gala 2002). The detailed analysis of the provided information revealed the absence of diagnostic characters or unique features that support the suggested identifications. In addition, if we take into account that, in the present day, the occurrence of these latter species in the Western Palearctic is considerably unlikely on a biogeographic basis, but also that the identifications are indicated as dubitative (cf.) in the case of *L. leucogeranus*, *G. solitaria* and *M. maxima*, we assessed their occurrence in the Mediterranean basin as non-reliable even if photographic documentation was available. The bones of *L. leucogeranus* have also been examined in person by one of the authors (M. P.), supporting the non-reliability of this occurrence. The specimens are highly fragmented, and the scarce preserved morphological characteristics do not allow to identify them as *L. leucogeranus* with certainty, or to refer them to other large crane species such as *Grus antigone* or *G. primigenia,* also following the opinion of Stewart (2007) about the uncertainty of the taxonomic attribution of the Pleistocene cranes. *Strix* cf. *nebulosa*, *Pinicola enucleator* and *Loxia leucoptera* represent a similar case, even if these are Western Palearctic species (Cramp 1998; Del Hoyo et al. 2016). Their presence is documented with photos and measures for the fossil locality of Arene Candide (Cassoli 1980). After the analysis of recent skeletons of *Strix nebulosa* and *S. uralensis* and their comparison with the original picture (Cassoli 1980, Tav. 6, 12), we think that the remains referred to *Strix* cf. *nebulosa* from the Arene Candide would be better referred to *Strix* sp. In fact, the two European larger species of *Strix* show very similar size and morphology in the distal tarsometatarsus which clearly differs only in proportions, being the one of *S. nebulosa* slender than *S. uralensis*. The picture of the fossil remain does not allow to appreciate the morphology in detail and the preserved shaft is too short to see if it is compatible with *S. nebulosa*. In addition, Cassoli (1980) only compared the fossils with *Strix nebulosa* and not with *S. uralensis*, which was not even mentioned as a possible species (Cassoli, 1980, pag. 189). Therefore, we consider the reported occurrence of this species as non-reliable. In the case of fossil *L. leucoptera,* the measures seem to rule out the species, based on its current size (Cramp 1998). Lastly, in the case of *P. enucleator*, we could assess the species as non-reliable as we analysed and measured the bones in person (M. P.), and the specimens might be referred to *Chloris chloris* on the basis of humerus length and bill morphology. In all the other cases of species whose presence in the Mediterranean basin is not confirmed, the reports of the fossil occurrences only consisted in a name in a list, with complete lack of proper documentation.

Most of the species are reported to have occurred in France and Spain’s Mediterranean coastal areas but not in the Balkans (*Branta bernicla*, *Anser brachyrhynchus*, *Fulmarus glacialis*, *Sterna paradisaea*, *Pinguinus impennis*, *Alle alle*, *Uria aalge*, *Surnia ulula*, *Bubo scandiacus*, *Falco rusticolus*, *Eremophila alpestris*, *Loxia pytyopsittacus*), but this is likely due to the scarcity of Balkan fossil localities that have been studied. Some species aren’t reported in the Iberian Peninsula (*Lagopus lagopus, Cygnus cygnus, Anser brachyrhynchus, Sterna paradisaea, Surnia ulula, Eremophila alpestris, Bombycilla garrulus, Loxia pytyopsittacus*) and others seem to haven’t spread in Southern Italy (*Fulmarus glacialis*, *Sterna paradisaea*, *Alle alle*, *Uria aalge, Surnia ulula*, *Bombycilla garrulus, Loxia pytyopsittacus*). Very few species haven’t been reported nor in the Balkans and neither in Southern Italy nor Iberian Peninsula (*Sterna paradisaea*, *Surnia ulula*, *Loxia pytyopsittacus*). Some species seem to be mostly (*Cygnus cygnus*, *Branta bernicla*, *Sterna paradisaea*, *Alle alle, Falco rusticolus*,) or exclusively (*Fulmarus glacialis, Pinguinus impennis, Uria aalge*) linked to coastal areas, which is not surprising following the ecological characteristics of those taxa.

As for the chronological distribution of the fossil occurrences here analyzed, most of them date to the MIS1/MIS2 boundary and to the MIS 2 (see Tab. 3). This frame perfectly agrees with the climatic features of these phases, characterized by cold conditions that favoured the spread of arctic and boreal species southwards.

| | **Verified Middle Pleistocene occurrence in the Mediterranean basin** | **Verified Late Pleistocene occurrence in the Mediterranean basin** |
|---|---|---|
| *Lagopus lagopus* | V | V |
| *Cygnus cygnus* | V | V |
| *Branta bernicla* | V | V |
| *Anser caerulescens* | | \ |
| *Anser brachyrhynchus* | \ | V |
| *Histrionicus histrionicus* | V | |
| *Leucogeranus leucogeranus* | | \ |
| *Fulmarus glacialis* | | V |
| *Calidris maritima* | \ | \ |
| *Gallinago solitaria* | | \ |
| *Xema sabini* | | \ |
| *Larus hyperboreus* | | \ |
| *Sterna paradisaea* | | V |
| *Catharacta skua* | | \ |
| *Pinguinus impennis* | | V |
| *Alle alle* | | V |
| *Uria aalge* | | V |
| *Uria aalge/lomvia* | V | |
| *Surnia ulula* | | V |
| *Strix nebulosa* | | \ |
| *Bubo scandiacus* | V | V |
| *Falco rusticolus* | | V |
| *Melanocorypha maxima* | | \ |
| *Eremophila alpestris* | \ | V |
| *Bombycilla garrulus* | V | V |
| *Pinicola enucleator* | \ | \ |
| *Loxia pytyopsittacus* | V | V |
| *Loxia leucoptera* | | \ |

Tab. 2: Results of the re-assessment of the known fossil occurrences of boreal species in the Mediterranean basin, based on the bibliographic check. "V" indicates that the presence of the species in the Middle or in the Late Pleistocene is confirmed, whereas "\" indicates that the species was reported in the literature, but its presence is not confirmed after the literature check.

| | **MIS 1/2** | **MIS 2** | **MIS 3** | **MIS 4** | **MIS 5** | **LP** | **MP** | **Unknown age** |
|---|---|---|---|---|---|---|---|---|
| *Lagopus lagopus* | 23 | 10 | 4 | | 2 | 5 | 1 | |
| *Cygnus cygnus* | 6 | 1 | 1 | 2 | | 7 | 1 | |
| *Branta bernicla* | 3 | 3 | 1 | | | 5 | 2 | 3 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| *Anser brachyrhynchus* | 1 | 1 |  |  |  |  | 2 |  |
| *Histrionicus histrionicus* |  |  |  |  |  |  | 1 |  |
| *Fulmarus glacialis* |  |  |  |  |  | 2 |  | 1 |
| *Sterna paradisaea* | 2 | 1 |  |  |  |  |  |  |
| *Pinguinus impennis* | 2 | 2 | 1 |  |  | 3 |  |  |
| *Alle alle* |  |  | 2 |  |  | 1 |  |  |
| *Uria aalge* | 1 | 3 |  |  |  | 3 |  |  |
| *Uria aalge/lomvia* |  |  |  |  |  |  | 1 |  |
| *Surnia ulula* |  | 1 | 1 |  |  |  |  |  |
| *Bubo scandiacus* | 5 | 8 | 8 |  |  | 4 | 5 | 1 |
| *Falco rusticolus* | 2 | 3 |  |  |  |  |  |  |
| *Eremophila alpestris* |  | 1 | 3 |  |  | 2 | 2 |  |
| *Bombycilla garrulus* | 2 | 1 |  |  |  | 2 | 1 |  |
| *Loxia pytyopsittacus* |  | 2 | 1 |  |  | 1 | 1 |  |
| **Total** | **47** | **37** | **22** | **2** |  | **35** | **17** | **5** |

Tab. 3: Chronological distribution of the fossil occurrences of the boreal and arctic species whose presence in the Mediterranean basin has been confirmed by this work. The numbers indicate the number of fossil localities where each species has been reported. The age of each fossil occurrence has been taken from Tyrberg 1988, 2007 and from the Radiocarbon Palaeolithic Europe database, v. 26 (Vermeersch 2019). The radiometric ages have been calibrated with OxCal 4.3 program (Bronk Ramsey 2009), using the IntCal13 calibration curve (95% CI) (Reimer et al. 2013). Boundaries of the Marine Isotopic Stages have been taken by Lisiecki and Raymo, 2005.

## Discussion

Overall, the results confirm that large-magnitude range shifts of the boreal species towards southern latitudes have taken place during the Middle and the Late Pleistocene. Nevertheless, this phenomenon results less common than previously thought, as we confirmed the occurrence of 17 species out of 28 reported in the literature (Tab. 2). This has several biogeographic and palaeoecological implications. Firstly, we should consider that the majority of the fossil occurrences here analysed belong to two species, i.e., *Lagopus lagopus* (with 46 fossil localities) and *Bubo scandiacus* (with 26 fossil localities) (Tab. 1). These two cold-adapted boreal species were clearly widespread during cool climatic phases, with high densities in France (see Results and Fig. 1). The marked spreading of these two species in the Pleistocene could be linked to several factors, besides climate cooling. In the case of *L. lagopus*, its huge range expansion might be due to its adaptability to different kinds of vegetation cover, from treeless tundra to deciduous woodlands (Cramp, 1998) and to the low competition with other galliform species driven southward by the cooler climatic conditions. In the case of *B. scandiacus*, this species might not have always been tightly linked to glacial conditions as it currently is. In the Pleistocene, this species likely had wider ecological requirements than the present day, that would have favoured its spread in Europe, as it may have arisen in Southern Europe during the Early Middle Pleistocene from the extinct *Bubo ibericus* (Meijer et al. 2017). Successively, since approximately the Holocene, this species possibly narrowed its ecological niche (Carrera et al. in press) and shifted its main distribution range north of the Polar Circle, mostly because of the competition with the other Palearctic large owl, *Bubo bubo*. The latter might have increased its populations after the late glacial as a consequence of the climatic amelioration, forcing *B. scandiacus* to move to the high latitudes (Potapova 2001; Meijer et al. 2017). Two other species, *Cygnus cygnus* and *Branta bernicla*, show a quite abundant number of records, whereas the remaining species confirmed occur at no more than 8 fossil localities each. Therefore, the palaeoclimatic and palaeoenvironmental inferences traditionally derived from the presence of these boreal species in the Mediterranean area, such as the extensive presence of tundra and other arctic habitats in Central and Southern Europe, result weakened. Furthermore, this suggests that the species that haven't been considered as reliable possibly never reached Southern Europe during the Middle and Late Pleistocene, providing hints on their biogeographic and genetic history, on their dispersal capacity, climatic tolerances, and population dynamics. Among the arctic and boreal species with reliable fossil records in the Mediterranean basin, the water and sea birds are well represented. In general, the presence of arctic seabirds in the Mediterranean is due to their habit to exploit coastal environments and to their progressive southward colonization of the Atlantic coasts during glacials. The spread of boreal and arctic seabirds along the Spanish Atlantic coasts is confirmed by the avian fossil assemblages from Santa Catalina (Elorza 2005, 2014) and El Castillo (Sanchez Marco 2018a), and by the assemblages coming from the fossil localities of the Strait of Gibraltar (Gorham's Cave, Devil's Tower, Ibex Cave, Vanguard Cave and Beefsteak Cave). This area is included in the present study as falls within the Mediterranean basin watershed, but it is strongly affected, from a climatic perspective, by the Atlantic Ocean influence. The arctic seabirds which are reported (and confirmed by this study) in the sites of the Strait of Gibraltar are *F. glacialis*, *P. impennis*, *A. alle and U. aalge*. Among these, *F. glacialis* and *A. alle* have never been reported on the Mediterranean coasts except Gibraltar (see Tab. 1 and Tab. 2).

Considering the current distribution and phenology of the involved species (Cramp 1998), the presence in the Mediterranean area of boreal migratory species (*C. cygnus*, *B. bernicla*, *A. brachyrhynchus*, *B. scandiacus*, *E. alpestris*) is probably related to wintering (or migratory) individuals, as well as the presence of seabirds *F. glacialis*, *S. paradisaea*, *A. alle*, *U. aalge* and *Uria aalge/lomvia*. An exception among the seabirds is *P. impennis*, an extinct non-flying Alcidae, whose occurrence in the Mediterranean coasts was likely due to sedentary populations, if we consider it a species with scarce mobility (Mourer-Chauviré and Antunes 1991), or to non-breeding individuals wintering southwards from the breeding colonies of the North Atlantic Ocean (Montevecchi and Kirk 2020) or a combination of origins also related to the various Pleistocene climatic oscillations. The presence of resident species (*L. lagopus*, *S. ulula, S. nebulosa, F. rusticolus*, *B. garrulus* and *L. pytyopsittacus*), could be linked to a southward shift of the breeding/all-year range, but in the case of *B. garrulus* and *L. pytyopsittacus,* also to seasonal winter southwards irruptions (Cramp 1998). The single coracoid of *Histrionicus histrionicus* found in the Middle Pleistocene of Central Italy likely belonged to a vagrant individual (Pavia and Bedetti 2013).

At this point it is worth to discuss about the meaning of the widely used concept of "Mediterranean refugia". Climate refugia are intended as locations that enabled species survival in an otherwise inhospitable region, during unfavourable climatic phases (Bennett and Provan 2008; Keppel et al. 2012; Gavin et al. 2014). Mediterranean refugia are climate refugia located in the southern offshoots of the European continent, i.e., the Iberian Peninsula, Italy and the Balkans, where species retreated during cold climatic phases (Sanchez Marco 2004; Svenning et al. 2008; Hewitt 2011; Linares 2011; Salvi et al. 2013; Pellegrino et al. 2014; Horníková et al. 2021). In general, considering the different ecological requirements of the species, if one species is adapted to warm climates, it will retreat in southern refugia during cold climatic phases, whereas if the species is adapted to cold climates, it will retreat in the high latitudes and in the high altitudes during warm phases. Conversely, during favourable climatic periods, species will expand their ranges, with expansions southwards for cold-dwellers in cold climatic phases and expansions northwards and towards higher altitudes for warm-dwellers during warm climatic phases. In synthesis, these dynamics and the locations of the refugial areas strictly depend on the ecological requirements of the species and differ between cold- and warm-adapted species. Considering the arctic and boreal species object of the present paper, their expansion in the Mediterranean area isn't linked to a southern "retreat" during non-favourable climatic phase, but rather to a range expansion due to the spread of favourable climatic phases (Tyrberg 1991; Carrera et al. in press). For this reason, the use of the term "Mediterranean refugia" in the case of boreal and arctic cold-dwelling species is conceptually wrong; it should be used only when dealing with temperate or warm species whose distribution retreats in the Iberian Peninsula, Italy and the Balkans during cold climatic phases.

This work stresses the importance of providing proper documentation along with taxonomic identifications, and especially for those rare taxa with high palaeobiogeographic significance such as boreal, arctic or vagrant species or species with peculiar palaeoecological importance. Most of the taxonomic attribution we found only consisted in a name in a list and only very few of them were supported by photos, drawings, measures or descriptions. All the former fossil remains need to be further analysed and re-evaluated in order to clarify their identification and provide reliable palaeobiogeographic information. Even photos or drawings are sometimes not enough to guarantee a correct identification. For instance, those species that belong to taxonomic groups represented by a lot of similar species (and with bones with very few diagnostic traits), such as Anatidae and Passeriformes, would need more detailed descriptions and measures (Pavia & Bedetti, 2013; Elorza, 2005). On the other hand, for those species that have peculiar bone characteristics, a photo or a drawing of a bone would be enough in most cases, such as *Alle alle* (Mourer-Chauviré, 1975) assuring the repeatability of the identification.

We thus recommend that the analysis on new avian fossil assemblages or further studies of already published material should consider these aspects and include a taxonomic treatment of the analysed taxa with description, measurements and photos, in order to provide reliable data for the scientific community and a more solid base to palaeobiogeographic research, even when the main goal of the study is not the bird taxonomy (Louchart 2011; Carrera et al. 2018a, 2018b, 2021; Pavia 2020; Núñez-Lahuerta et al. 2021; Pavia et al. 2022).

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## 8. Concluding remarks

This work provides new knowledge about birds' responses to glacial-interglacial transitions in the Western Palearctic. I used several approaches at different geographic and temporal scales, emphasizing the importance of the bird fossil record for paleoecological and conservation biology studies. The taxonomic and taphonomic analyses of the avian fossil assemblages from four Italian Mid-Upper Pleistocene sedimentary successions (Manuscripts I, II and III), spanning the last two glacial-interglacial cycles, allowed to recognize the local-scale patterns in the bird species responses to climatic oscillations. Considering all the fossil localities analyzed, the bird assemblages related to different climatic phases are characterized by presence of temperate species, even during cold phases and by the occasional presence of cold-dwelling species (or an increase of them) only during glacial maxima. The presence of cold-adapted species in the Western Palearctic mid-latitudes is related to shifts in their distribution towards lower altitudes or southwards, in the case of boreal species. These local patterns of turnover in bird communities are widely supported by the patterns identified at the continental scale. Indeed, the modeling of the present-day and LGM climatic envelopes of species with different climatic requirements and migratory behaviors (Manuscript IV), shows a substantial stability in the temperate species' distribution and large-magnitude range changes in cold-dwelling species, supported by their fossil records. Manuscript IV also shows that the responses to climate shifts are species-specific and related to the thermal niche of the single species, which represents a key ecological trait explaining the impact of climate change in species distributions.

The identification of the patterns in the turnover of bird species in response to climate changes improves the interpretation of fossil assemblages in terms of paleoenvironmental and paleoclimatic implications. Considering Manuscripts I, II, and III, which analyze the avian fossil assemblages from Grotta del Cavallo (Apulia), Grotta di Fumane (Veneto), Grotta di Castelcivita (Campania), and Grotta di Uluzzo C (Apulia), it is clear how avian fossil assemblages can provide unprecedented detailed frameworks of the evolution of the landscapes during glacial-interglacial cycles, sometimes better than those provided by other proxies (see Manuscript I), enhancing the importance of fossil birds for paleoenvironmental and paleoclimatic reconstructions. Manuscripts II and III also show how the paleoecological inferences derived from birds, if coupled with those derived from other proxies (for instance micro- and macro-mammals), can provide extremely detailed paleoecological frames.

Cold adapted species represent a more effective paleoecological tool than the temperate species and act as an important proxy of cold climatic conditions, as they are the most impacted by climatic changes (as highlighted in Manuscript IV). As for a correct interpretation of the fossil record, I can conclude that the fossil evidence of the presence of cold-dwelling species outside the limits of their current distribution (due to large-magnitude latitudinal or altitudinal changes in response to cold climatic phases) should be considered a a proxy of a climate colder than the present one.

Furthermore, in Manuscript I, due to the richness of the avian fossil assemblages from Grotta del Cavallo, I could explore the potential of new multidisciplinary exchanges and applications in the analyses of fossil communities. Indeed, the ordination analysis applied on the taphonomic dataset delineated the main drivers of taphonomic damages, whereas the rarefaction analyses on the bird assemblages coming from the different sedimentary units highlighted the dynamics of species diversity in relation to climate-driven paleoenvironmental changes.

Manuscript V clarified the dynamics of another large-scale phenomenon in bird distributions, the presence of boreal and arctic bird species in Mediterranean Europe during the Middle and the Late Pleistocene due to southern range shifts. After a reassessment of the reliability of the existing fossil evidence, I show that this phenomenon is not as common as previously thought. This suggests the need for a revision of the paleoecology and the paleoclimatic significance of the species involved, further improving the interpretation of bird fossil assemblages from a paleoecological point of view. Moreover, I point out how the concept of "Mediterranean refugia" shouldn't be used to explain boreal species' presence in Mediterranean Europe, as it represents evidence of a range expansion during favourable climatic phases rather than a reduction of the range during unfavourable climatic phases. Manuscript V also emphasizes the relevance of providing exhaustive documentation in support of the taxonomic identifications, with photos, detailed descriptions, and measures (as in Manuscript I). The use of high-quality reference material for the taxonomic analyses of the fossil bird assemblages provides the identification of a high number of different bird species and, consequently, very detailed paleoecological reconstructions. In the case of Grotta del Cavallo (Manuscript I), the use of a wide taxonomic collection allowed us to identify the first fossil occurrences ever of *Larus genei*, a gull species, and the first occurrence in Italy of *Emberiza calandra*, a small Passeriformes.

The documentation of birds' past responses to climatic changes reported in this PhD thesis provides a baseline to help the future conservation of the cold-dwelling species, that turn out to be the most impacted by global warming. This integrated approach at different scales will also provide new data to disentangle natural climate effects from more direct anthropic impacts on targeted avian species.

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