The ornithological remains from Marathousa 1 (Middle Pleistocene; Megalopolis Basin, Greece)

Dimitrios Michailidis^{a*}, George E. Konidaris^b, Athanassios Athanassiou^c, Eleni Panagopoulou^c, Katerina Harvati^b

^aAmerican School of Classical Studies at Athens, The Malcolm H. Wiener Laboratory for Archaeological Science, Soudias 54, 10676 Athens, Greece

^bEberhard Karls University of Tübingen, Palaeoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, Rümelinstr. 23, 72070 Tübingen, Germany

^cEphorate of Palaeoanthropology-Speleology, Athens, Greece

*Corresponding author. E-mail address: dmichailidis@ascsa.edu.gr (D. Michailidis).

ABSTRACT

In the Middle Pleistocene open-air locality Marathousa 1 (Megalopolis Basin, Peloponnese, Greece), lithic artefacts are spatially and stratigraphically associated with faunal remains. Among the latter, birds are known by over 120 skeletal elements and represent an important part of the vertebrate fauna. The majority of them are identified as anseriform birds of various sizes, from swan size (*Cygnus olor*) to teal size (*Anas crecca*). The next largest group is gruiform birds, while, at least one small-sized passerine is also present (cf. *Cinclus cinclus*). A number of taxa are recorded for the first time in the Pleistocene of Greece. The taphonomic analysis of the deposit points to a minimal transfer of the avian skeletal

elements, accumulated possibly through the combined action of some raptors and natural transfer of unconsumed avian remains. The palaeoecological analysis reveals a rich lakeshore environment, under temperate climatic conditions, that would support large numbers of aquatic and terrestrial invertebrates and small vertebrates. The avifaunal composition and its richness demonstrate the importance of the palaeolake system, which would have contributed to the development of habitats capable of supporting a variety of species including hominins.

Keywords: avian fauna, Middle Pleistocene, palaeoecology, taphonomy, Palaeolithic

1. INTRODUCTION

The Megalopolis basin is located in the southwestern part of the Arcadia region of the Peloponnese, southern Greece (Fig. 1). Formed in a Mesozoic–Palaeogene basement, the basin was filled with Neogene and Pleistocene fluvial and lacustrine sediments, and during the Pliocene and the Pleistocene hosted periodically a large lake (Vinken, 1965). Today the area is characterized by the presence of economically important lignite deposits and is dominated by several active and inactive open-air lignite mines, some of which have been productive since 1969.

The area was investigated for palaeontological findings from the early 20th century with Professor Skouphos's excavations of 1902 (Skouphos, 1905), and since then several researchers have been excavating and describing fossils from localities both outside and within the lignite mines (Melentis, 1961; Mädler, 1971; Sickenberg, 1976; van Vugt, 2000; Theodorou, 2014; Athanassiou, this issue; Athanassiou et al., this issue). These studies resulted in the description of a rich flora (mainly fruits, seeds and wood) and fauna (micro-

and macro- mammals), including a human molar (Sickenberg, 1976; Harvati, 2016). Avian remains have not been reported from any past study. Here we report on the first avifauna from the basin, associated with other faunal and palaeolithic cultural remains, from the new open-air Middle Pleistocene site Marathousa 1.

The scope of this study is the taxonomic identification and the preliminary palaeoecological and taphonomic analysis of the avian remains from Marathousa 1. Birds are considered particularly useful for reconstructing terrestrial palaeoenvironments, (Mourer-Chauviré, 1993; Gal, 2004), for reasons that relate to their evolutionary stability, their often high degree of ecological specialization and the relative ease with which they can move from areas with suboptimal conditions. The taphonomic analysis of birds, in conjunction with that of other vertebrate remains and stratigraphic interpretations, can help reconstruct the depositional history of a site, and provide an insight on whether hominins contributed to the accumulation of fossil remains. The most numerous, in terms of taxonomic diversity, vertebrate group unearthed from Marathousa 1 is birds, therefore its study can make an important contribution to the study of the site.

2. LOCALITY, MATERIALS AND METHODS

Marathousa 1 (MAR-1) was discovered during systematic field surveys within the framework of the ERC project 'Paleoanthropology at the Gates of Europe' (PaGE; Harvati and Tourloukis, 2013; Tourloukis and Harvati, 2018), by a team of researchers from the Ephorate of Palaeoanthropology-Speleology of the Greek Ministry of Culture and the Palaeoanthropology department of the University of Tübingen, Germany (Panagopoulou et al., 2015; Panagopoulou et al., this issue; Harvati, 2016). In 2013, stratified macro-mammalian remains and lithic artefacts were identified in an exposed section of the

Marathousa Member (Choremi Formation), and since then, two excavation areas were delineated; Area A and Area B. Both areas yield lithics (see Panagopoulou et al., this issue and Tourloukis et al., this issue a), micro- and macro-fauna (fishes, amphibians, reptiles, birds, mammals; see also Doukas et al., this issue and Konidaris et al., this issue), as well as micro- and macro-flora (Field et al., this issue). In Area A, a partial skeleton of the elephant *Palaeoloxodon antiquus* was discovered in spatial and stratigraphic association with lithic artefacts and remains of several other vertebrate and botanical remains. In Area B, about 60 m south of Area A, a relatively rich assemblage of lithic artefacts was discovered, in association also with faunal remains.

Both areas exhibit very similar lithostratigraphic sequences (Fig. 1). Their stratigraphic columns are correlated with the sequence of deposits laid between the lignite seams II (lower) and III (upper) (the lignite seam characterization follows Löhnert and Nowak, 1965 and Vinken, 1965). These deposits are mostly silty sands rich in organic matter (Karkanas et al., this issue). They are divided into two parts by an erosional surface. The lower part (lithologic units UA4 to UA7 in Area A and UB6 to UB10 in Area B, Fig. 1) is variable in terms of layer thickness, grain size and organic content, comprising massive to thin-layered clayey to silty sands with variable organics. The lower part's uppermost unit (UA4, UB6) consists of bluish muddy sands exhibiting well-pronounced load deformation structures (Karkanas et al., this issue). The upper part comprises a series of graded units (coarser near their base, finer upwards) that start with silty sands rich in intraclasts and wood fragments with mudflow character (UA3, UB4), and continues with an alternation of silty sands rich in mollusk shells and massive silty sands (Karkanas et al., this issue).

The stratigraphic and sedimentological study of MAR-1 indicates that the main archaeological and fossiliferous layers in the two areas (contact of stratigraphic units UA3 and UA4 in Area A, and UB4 and UB5 in Area B) are correlated (Fig. 1), and that the faunal and anthropogenic material is found on remnants of an eroded and exposed surface, which

was part of an extensive mudflat surrounding the shores of the palaeolake (Karkanas et al., this issue). The finds were laying on the bluish muddy sands (UA4, UB6) and were subsequently covered by the mudflow sediments (UA3, UB4). Rapid burial in a fine-grained matrix ensured extraordinary conditions of preservation. The presence of cut marks in bones of the elephant skeleton, as well as in other elephant and mammal bones (Konidaris et al., this issue), along with the traits of the lithic assemblage (Tourloukis et al., this issue a) and the evidence from the geostatic spatial analyses (Giusti et al., this issue), altogether indicate that MAR-1 represents a butchering site. More information on the locality and the stratigraphy can be found in Panagopoulou et al. (this issue), Karkanas et al. (this issue) and Tourloukis et al. (this issue b). Preliminary dating of the locality, including post-infrared Infrared Stimulated Luminescence (post-IR IRSL), Electron Spin Resonance (ESR) and magnetostratigraphy, suggests an age at ca. 0.5–0.4 Ma (Blackwell et al, 2016; Jacobs et al., this issue; Tourloukis et al., this issue b).

The material studied in this article includes all the avian specimens collected from MAR-1 during the field seasons 2013–2016. These were either collected from the excavation trenches as individual specimens or retrieved through water-sieving (1×1 mm mesh) of the sediment excavated from both areas. A total of 121 avian skeletal remains were recovered, 86 from Area A and 35 from Area B. All specimens are stored at the Ephorate of Palaeoanthropology–Speleology in Athens (Greece). For the identification of the specimens, we used the comparative osteological collection of the Malcolm H. Wiener Laboratory for Archaeological Science (American School of Classical Studies, Athens) and the avian reference collection housed at the Naturhistorisches Museum Wien, Austria. The anatomical terminology follows Baumel et al. (1993), systematics del Hoyo (1992), while the works of Cohen and Serjeantson (1996), Woolfenden (1961), Bacher (1967) and Woelfle (1967) were used for their identification keys. Mlíkovský (2002) and Tyberg (2007) were used for their record on avifaunas of similar age and geographical proximity to the Marathousa 1 avifauna.

For the taphonomic analysis, the protocol described in Lyman (1994) was used for calculating the values of units such as the NISP (number of identified specimens) and MNI (minimum number of individuals). These values can then be used in methods that attempt to determine possible agents of accumulation of the avian skeletal elements. NISP was calculated by counting all bones and bone fragments identified to a taxonomic level. MNI, was calculated by counting the most numerous skeletal element in each taxonomic group, taking into account both laterality and the preserved part of each skeletal element.

The surface of all avian skeletal elements was examined first by eye and then by stereomicroscope (Leica M10 Sterozoom microscope, M. H. Wiener Laboratory) and the location and degree of weathering were recorded, following the modification protocol described in Bochenski and Tomek, 1997.

In order to infer possible agents of accumulation and especially whether nocturnal or diurnal birds of prey were the main accumulators, three main methods have been proposed based on ratios of skeletal element representation: wing/leg, proximal/distal and core/limb. These are described and discussed below.

The first method, proposed by Ericson (1987), examines the percentage of representation of skeletal elements of the wing (humerus, ulna and carpometacarpus) to that of the leg (femur, tibiotarsus, tarsometatarsus) in order to reach conclusions relative to the agent of accumulation of avian remains. If leg elements predominate, humans are most likely responsible for the accumulation, as in these elements larger muscle tissue can be found. If the percentage of wing elements is higher, natural accumulation occurred. The same method can also be used to determine raptors as agents of accumulation, specifically by the result of the feeding habits of nocturnal and diurnal birds of prey (Bochenski, 2005). If the ratio is 1:1, or if the wing elements predominate by little, nocturnal birds of prey are important agents of accumulation. If the wing elements percentage greatly outnumbers the leg elements percentage, diurnal birds of prey played a decisive part in the accumulation.

The second method for the identification of avian predators, was proposed by Bochenski and Nekrasov (2001) and uses the ratio of the total number of proximal elements (scapula, coracoideum, humerus, femur and tibia), to distal elements (ulna, radius, carpometacarpus, tarsometatarsus). If the avian remains were deposited primarily from pellets of some diurnal birds of prey, the above ratio would be close to 1:1. If the remains were deposited because of the pellets produced by all nocturnal birds of prey and the uneaten remains of some diurnal birds of prey, proximal elements prevail by about 60%. Finally, if proximal elements dominate the assemblage, by 80% or more, golden eagles and their uneaten food remains are mostly significant in the accumulation of the avian remains.

The third method proposed by Bramwell et al. (1987) calculates the core (sternum, pelvis, scapula, coracoideum) versus limb elements (humerus, ulna radius, carpometacarpus, femur, tibiotarsus, tarsometatarsus) in order to distinguish between pellet materials and uneaten food remains (Bochenski, 2005).

The palaeoecological study of the Marathousa 1 avifauna is based on the analysis of habitat and climatic zone preferences of the taxa identified. Harrison (1982) was used for the codification of climatic zones and habitats, as well as the information provided in BirdLife International (<http://datazone.birdlife.org>), ARKive (<https://www.arkive.org/birds>) and the Handbook of the Birds of the World (del Hoyo et al., 1992).

3. SYSTEMATIC IDENTIFICATION

A total of 23 species have been identified from both Areas A and B (Table 1). Dabbling birds dominate the taxonomic list, whilst the presence of several taxa is recorded for the first time in Greece, including a taxon that is no longer recorded in Europe.

3.1 Area A

In Area A (Fig. 2) 7 orders and families of birds are represented and 18 taxa identified (Table 1 and Fig. 3) and out of the 86 skeletal elements recovered (in all three units: UA2–UA4), 66 were identified at species or at a minimum at genus level.

The family Anatidae dominates in the assemblage with 48 skeletal elements belonging to 10 species, ranging in size from the mute swan (*Cygnus olor*) to the teal (*Anas crecca*). There are representatives of the genera *Anas*, *Anser*, *Aythya*, *Cygnus*, *Mareca* and *Spatula*. *Anser* cf. *albifrons* is represented by a distal carpometacarpus (Fig. 2D). Regarding its dimensions, it is considerably smaller than *Anser anser* and larger than *Anser erythropus*. The partial preservation of the carpometacarpus and the lack of diagnostically secure features does not allow for a definite identification.

Rallidae is the next best represented family of birds, with three different species; the common coot (*Fulica atra*), common moorhen (*Gallinula chloropus*) and western water rail (*Rallus aquaticus*). Finally, there are remains of black-crowned night-heron (*Nycticorax nycticorax*), common redshank (*Tringa* cf. *totanus*), darter (*Anhinga* sp.) and a medium sized passeriform bird which, shows affinities to a dipper (cf. *Cinclus cinclus*).

The common redshank was identified based on the recovery of a complete coracoideum (Fig. 2O). The robusticity of some features of the reference material in comparison to the retrieved coracoideum does not allow a secure identification.

The presence of the darter is based on a partially preserved humerus (Fig. 2Q). Typically for Suliformes, the margo caudalis is very pronounced, contributing to the development of a triangularly shaped corpus in caudal view. The tuberculum dorsale is distally placed and the distal end of the caput humeri extends distally. In proximal view, the facies bicipitalis is relatively inconspicuous. The incisura capitis is not deeply excavated and is rounded in its distal border. In cranial aspect, the intumescentia humeri appears very elevated and the impressio musculo brachialis strongly excavated. The caput humeri extends considerably distally and the sulcus transversus is relatively shallow and short dorso-

ventrally. The preserved distal epiphysis appears flattened and squared-off, as is typically the case in Suliformes and the border of the fossa brachialis is relatively gracile. The above features can be observed in both *Anhinga rufa* and *A. melanogaster*. The lack of additional skeletal elements preserved does not allow a more precise identification and the remains are identified as *Anhinga* sp.

The dipper was identified from a distal tarsometatarsus (Fig. 2P) and there are sufficient characters preserved to allow provisional assignment to *Cinclus*. However, the lack of a complete tarsometatarsus that would allow a verification based on measurements hinders its secure allocation to *Cinclus cinclus*.

3.2 Area B

In Area B, 4 orders and families are represented and 12 taxa of birds (Table 1, Figs 3, 4). Out of the 35 skeletal elements recovered, 27 were identified. The family Anatidae dominates also here the palaeoavifauna with representatives of the genera *Anas*, *Aythya*, *Branta*, *Mareca* and *Spatula*. In addition, remains of the common coot (*Fulica atra*), purple swamphen (*Porphyrio porphyrio*), glossy ibis (*Plegadis falcinellus*) and curlew sandpiper (*Calidris* cf. *ferruginea*), have been recovered.

Calidris cf. *ferruginea* was identified based on a small sized distal humerus (Fig. 4I). The humerus is morphologically and metrically closest to *Calidris ferruginea*; however, there are some morphological differences that do not allow a secure identification. Specifically, in the recovered humerus, the tuberculum supracondylare ventrale is placed more distally and it is smaller in size. The fossa brachialis is shorter proximo-distally, the epicondylus ventralis is smaller proximo-distally and so is the condylus dorsalis in dorsal aspect. For these reasons the remains are identified as *Calidris* cf. *ferruginea*.

3.3 Areas A and B

On tables 2 and 3, the values of NISP and MNI by taxon and unit for Areas A and B respectively, are provided. There are some taxonomic differences between the two Areas, but they are relatively slight and the most similar units in terms of species richness, as well as number of specimens are units UA3 and UB4. In general, there are fairly consistently low values of the NISP and MNI units in both areas. The most dominant species in Area A, both in terms of NISP and MNI is *Anas crecca* with an NISP of 10 and an MNI value of 4. In Area B, *Spatula clypeata* and *Anas platyrhynchos* are dominant, both with NISP values of 4 and MNI values of 2 each.

4. TAPHONOMIC REMARKS AND SKELETAL ELEMENT REPRESENTATION

The main fossiliferous and archaeological horizon in MAR-1 follows the contact between UA3 and UA4 in Area A, and UB4 and UB5 in Area B. This horizon belongs to the same depositional event and the two contacts are lithostratigraphically correlative (Fig. 1, Karkanas et al., this issue). For the taphonomic investigation of the avian remains we studied the specimens originating from UA3 and UA4 (bones from this unit originate close to contact UA3/UA4) of Area A, and UB4 and UB5 of Area B (bones from this unit originate close to contact UB4/UB5). We treated these units from each area as one assemblage, i.e., one assemblage includes specimens from Area A and the other from Area B.

The avian bone surfaces from both Area A and B do not show traces of rounding, and the majority of the bones present rather well-preserved surfaces with minor cracking and flaking: less than 10% of the retrieved skeletal elements show evidence of weathering [weathering stage 1, slightly weathered (Bochenski and Tomek, 1997)] due to surface exposure, or pitting caused by digestion. The low weathering stage observed is not surprising, as studies of modern avian bone assemblages reveal that weathering is biased

towards lower stages as avian skeletal elements wear quickly and complete destruction can be reached rapidly (Behrensmeyer et al., 2003; Cruz, 2008). About 20% of all skeletal elements are complete, while in the remaining 80%, often a significant part of the corpus is also surviving. All of the above suggest that the skeletal elements were not transported from great distances, and were deposited locally and relatively quickly. This is in agreement with the geological data, the spatial distribution of the lithics and the faunal remains, the taphonomic results of the large mammals, and the preservation condition of the lithic material, which indicate limited transport over a short distance and/or for a short time span, and a relatively quick burial (Giusti et al., this issue; Karkanas et al., this issue; Konidaris et al., this issue; Tourloukis et al., this issue a).

Carnivore mammals could potentially be one of the agents of accumulation of bird remains. *Canis* (wolf), *Vulpes* (fox), *Felis* (wildcat), *Lutra* (otter) and *Mustela* (polecat) are identified in the MAR-1 assemblage, and their diet might include among others also birds (MacDonald, 2009; Konidaris et al., this issue), which were possibly abundant close to the shores of the palaeolake. The presence of marks on bones, such as punctures, pits and grooves, related to mastication by mammalian predators would be a strong indication for mammals affecting the fossil assemblage. Studies on the characteristics of bone accumulations created by small carnivores report that almost 25% of bones of medium to large sized birds preserve such marks (Mallye et al., 2008). Bones of bird taxa that fell prey to foxes usually present a combination of characters, such as bite marks, no signs of digestion and a higher representation of wing skeletal elements (Monchot and Gendron, 2011). However, the majority of the MAR-1 avian bone: a) are not highly fragmented and are either complete or preserve most of the corpus, b) do not show traces of carnivore tooth marks, c) their broken ends are not rounded and smooth by digestion, and d) they are not perforated by the action of gastric acids (Stallibrass, 1990; Fernández-Jalvo and Andrews,

2016; Rufá et al., in press). Therefore, we can exclude that carnivores were at least the main agent of the birds' bone accumulation.

The results of Ericson's (1987) method of analysis, reveal that in both Areas A and B, and specifically in units UA3 and UA4, and UB4 and UB5 where avian remains were found along the cultural findings, the percentage of wing elements exceeds that of the leg elements (75% in Area A and 60% in Area B, Fig. 3). These percentages exclude hominins as significant agents of accumulation. This is in agreement with the so far absence of cut marks, "green" bone breakage, overextension damage, signified by breakage at the fossa olecrani and the proximal epiphyses of the radius and ulna (Laroulandie et al., 2008), and human toothmarks, such as tooth punctures and pits and crenulated edges (Landt, 2007) which if present would suggest human exploitation of the birds (Fiore et al., 2016). The percentages obtained, point for Area A to diurnal birds of prey as significant in the accumulation and for Area B to nocturnal birds of prey. The accuracy of this method however has been criticized (Livingston, 1989) and its accuracy also depends on the number of retrieved skeletal elements, which in the case of MAR-1 is relatively low.

In applying Bochenki and Nekrasov's (2001) method, in both Areas A and B, proximal elements are more abundant than distal elements (Fig. 3, 57% in Area A and 67% in Area B). According to the above method, the avian remains in both Areas were accumulated by the actions of mainly nocturnal birds of prey and some diurnal birds of prey.

When using Bramwell et al.'s (1987) method, limb elements predominate in Area A with 62% and in Area B with 59% (Fig. 3), indicating uneaten food remains of birds of prey as a source for the deposited avian material. Nevertheless, as remains of birds of prey have not been recovered so far from MAR-1, and as digestion traces are low and puncture marks absent, it is not possible to identify the taxon that might have produced the deposit, or even to uncontestably propose that birds of prey are the primary agents of accumulation of the avian remains.

Apart from role of avian predators, an alternative hypothesis that might account for the accumulation of the avian remains might be related to the varying density of skeletal elements of the different taxa represented in MAR-1. Livingston (1989) postulated, specifically for water birds, that bone density is related to their feeding and locomotive patterns (functional anatomy). Dabbling ducks and geese have strong and dense wing skeletal elements, as they often need to take flight quickly when threatened. On the contrary, diving birds (grebes, cormorants, pochards) rely more heavily on their legs for locomotion, take flight more slowly over deeper, open water and their leg skeletal elements are denser. Denser bones have a greater probability of survival and are therefore better represented in a deposit. Dabbling taxa (all *Anas* species identified, *Mareca strepera*, *Spatula clypeata*, *S. querquedula*) form the majority of the MAR-1 avifauna, which might explain the relative predominance of wing skeletal elements.

Taphonomic methods of analysis can suggest possible factors that affected the deposition of avian remains, but they occasionally falter on account of the complexity of the system that controls the character of the deposition. Post-depositional processes can affect the taphonomic signature and secure conclusions can only be reached with the analysis of a large number of remains. Based on the current data, it can be proposed that the avian remains were deposited through the combined action of some raptors and (more possibly) of locally deposited skeletal elements from the immediate vicinity of the palaeolake shore. However, as excavations at MAR-1 are still ongoing, and more avian skeletal elements are being retrieved, future analysis will allow a more refined taphonomic interpretation of the assemblage.

5. PALAEOECOLOGICAL REMARKS

The information retrieved through the study of the birds unearthed at an archaeological site contributes significantly to the reconstruction of the terrestrial palaeoenvironment (Sutherland, 1986; Mourer-Chauviré, 1993). The reasons that lead to the above conclusion relate to birds' evolutionary stability that allows for a direct comparison between ancient and modern taxa, the high niche specialization of many species, in terms of food and nesting requirements and temperature ranges and the relative ease with which they can abandon an area that does not provide favorable conditions.

A thorough palaeoecological analysis can focus on individual species identified, whereby emphasis is given on their stenotypic characteristics, or on the analysis of the identified avifauna as a whole. In the latter type of analysis, the ecological attributes of all species identified such as habitat and climatic zone, are codified and summed, allowing for the reconstruction of key palaeoecological features based on the most prevalent conditions.

5.1 Area A

An analysis of the habitat and climatic zone preferences of Area A avifauna can be seen on Table 4. Fresh-water habitats dominate the assemblage, followed by steppe-grassland and open woodland habitats; strictly forest taxa are so far absent. There is a fairly large range of climatic zone preferences for birds, from arctic to tropical, and most of the MAR-1 taxa identified have adaptations that allow them to habituate several climatic zones.

The common teal (*Anas crecca*), the most abundant taxon in Area A, prefers freshwater environments such as small lakes and marshes, with well vegetated margins and subsides on seeds of aquatic plants and grasses during the winter season and aquatic invertebrates in the spring and summer, which it feeds on by dabbling (Carboneras, 1992). The common coot (*Fulica atra*) is the second most abundant species in Area A and it prefers

slow moving bodies of water, like ponds and lakes, with muddy substrates. It has an omnivorous diet, but is primarily vegetarian consuming vegetative parts and seeds of aquatic and occasionally terrestrial plants and has also been observed consuming mollusks, insects and even small fish and amphibians (Taylor, 1996). The shoveler (*Spatula clypeata*) is the third most abundant taxon of Area A and prefers a range of freshwater wetlands, such as marshes and lakes with abundant vegetation and consumes, by dabbling, a variety of small sized invertebrates such as insects and mollusks and occasionally plants (Carboneras, 1992).

The presence of the darter (*Anhinga* sp.) is somewhat unexpected. Darters are presently found mostly around the tropical regions of the Old World. They live around freshwater lakes, swamps and slow moving rivers, require a scatter of trees, or islets of dense vegetation and feed mainly on fish, amphibians and aquatic invertebrates (Orta, 1992). They need trees for breeding and to perch in order to preen, digest their food and sun. As their plumage is not very insulating they require sunning to thermoregulate and for that reason they are found mostly in warmer areas than cormorants, although the two species are also frequently inhabiting the same areas. Darters do not live in Greece any more, but a subspecies of *Anhinga rufa* went extinct in Turkey in historical times (Orta, 1992). This species has also been identified from skeletal elements in Kyparissia quarry (Athanassiou et al., this issue), verifying its presence in the region during the Pleistocene. Pleistocene avifaunas are often not similar to modern ones as they include taxa whose natural range has shrunk and are often found in areas where species take refuge and only just manage to survive in suboptimal conditions. The darter from MAR-1 might represent such a taxon.

5.2 Area B

The analysis of habitat and climatic zone preferences of birds from Area B (table 5) reveals as in Area A, the domination of fresh water habitats, followed by steppe-grassland, while two

species show additionally a potential for coastal adaptations; there is a wide range of climatic zone preferences.

The shoveler (*Spatula clypeata*), one of the most abundant taxon in Area B, prefers shallow fresh water surrounded by rich vegetation, although it can be found on fens and marshes with plenty of open water; it consumes a variety of foods. The mallard (*Anas platyrhynchos*) is together with the shoveler the most abundant taxon from Area B. It inhabits rich wetlands that are relatively shallow with emergent vegetation and is omnivorous and highly opportunistic (Carboneras, 1992). It has been recorded consuming both aquatic and terrestrial plants, land and aquatic invertebrates and occasionally amphibians and fish, while when feeding it dabbles over water and grazes on land. The purple swamp hen (*Porphyrio porphyrio*) prefers still or slow-flowing bodies of water such as lakes and swamps with emergent vegetation and consumes primarily aquatic and terrestrial plants but has been observed to also consume aquatic and terrestrial invertebrates, and small vertebrates (Taylor, 1996). It is, like the darter, a warm adapted element of the MAR-1 avifauna, indicating refugium status for the site, in the same way as the darter does in Area A.

6. CONCLUDING REMARKS

In the present study, the preliminary results from the study of the avifauna of Marathousa 1 are presented. It is the first detailed report of avian remains from the Pleistocene of the Megalopolis basin and provides an insight on the accumulation processes and palaeoecology of the to-date oldest archaeological site unearthed in Greece.

Excavation Areas A and B are mostly similar in terms of species composition. On the whole, the MAR-1 avifauna is relatively rich, with 23 taxa identified, especially considering

the fairly modest number of avian skeletal elements recovered so far. There is a clear predominance of freshwater birds, with dabbling birds forming the majority of the taxonomic list. A review of the bibliography (Mlíkovský, 2002; Tyberg, 2007; Boev, 2010; Michailidis, 2013) reveals that MAR-1 is the first site in Greece to record the presence of several taxa, enriching thus our knowledge of the Pleistocene avifaunas of Europe. These include the following taxa: *Cygnus olor*, *Podiceps nigricollis*, *Porphyrio porphyrio*, *Nycticorax nycticorax*, *Plegadis falcinellus*, *Anhinga* sp., *Calidris* cf. *ferruginea* and *Tringa* cf. *totanus*.

The taphonomic character of the avifauna, specifically the presence of some complete skeletal elements and the lack of wear due to transfer, or exposure lead to the conclusion that there was minimal transfer of skeletal elements, which, were accumulated through the combined action of some raptors and the decomposition of unconsumed or partly consumed avian carcasses. The MAR-1 avifauna, when compared to a modern one, does not appear ecologically balanced. There is an absence of many passeriforms, woodland adapted species and raptors that would most likely occupy niches further away from the immediate vicinity of the palaeo-shore. Their absence might be because the MAR-1 deposit represents only the extremely local environment, a marshy, shallow freshwater environment. The recovery of additional avifaunal material from MAR-1 in the future will be essential for determining with more certainty the compositional traits of the assemblage, regarding taxonomic variety, and for refining the taphonomic and palaeoecological interpretations.

The palaeoecological conclusions that can be reached through the study of the avifauna, point to an absolute predominance of water birds, a significant number of which are adapted to shallow waters, while most species are adapted to the temperate climatic zone, with few warm adapted species. The avifaunal composition reveals a rich lakeshore environment, with marshy areas, emergent vegetation, and some trees around the lake shore that would support large numbers of aquatic and terrestrial invertebrates and small

vertebrates. These results are in agreement with the palaeoecological conclusions for MAR-1 provided from the study of the palaeobotanical remains and the large mammals (Field et al., this issue; Konidaris et al., this issue). The richness of the area would also make it a particularly attractive region for a number of mammals, including hominins, whose presence is revealed through the cultural layers of Marathousa 1.

ACKNOWLEDGMENTS

This research was supported by the ERC StG no. 283503 PaGE and by the ERC CoG no. 724703 CROSSROADS awarded to K. Harvati, and the University of Tübingen (2016-17 field seasons). We are grateful to all the field team members for their contribution during the excavations, and to the Greek Ministry of Culture, the Municipality of Megalopolis, the authorities of the Peloponnese Prefecture and the Public Power Corporation S.A. for their support. We thank Dr. Anita Gamauf and all members of staff of the avian comparative collection of the Natural History Museum of Vienna for allowing use of their collections. We thank the editors and two anonymous reviewers for their constructive comments.

REFERENCES

Athanassiou, A., this issue. Pleistocene vertebrates from the Kyparíssia lignite mine, Megalopolis Basin, S. Greece: Rodentia, Carnivora, Proboscidea, Perissodactyla, Ruminantia. Quaternary International.

Athanassiou, A., Michailidis, D., Vlachos, E., Tourloukis, V., Thompson, N., Harvati, K., this issue. Pleistocene vertebrates from the Kyparissia lignite mine, Megalopolis Basin, S. Greece: Testudines, Aves, Suiformes. *Quaternary International*.

Bacher, A., 1967. Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Schwäne und Gänse. Ph.D. Thesis. Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München, Munich, Germany.

Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vaden Berge, J.C. (Eds.), 1993. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. Second Edition. Publications of the Nuttall Ornithological Club, No. 23. Harvard University, Cambridge, Massachusetts.

Behrensmeyer, A. K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology*, 4, 150–162.

Behrensmeyer, A. K., Stayton, C. T., Chapman, R. E., 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology* 29, 52–70.

Blackwell, B.A.B., Singh, I., Gopalkrishna, K., Chen, K.K., Sakhrani, N., Tourloukis, V., Karkanis, P., Florentin, J.I.B., Panagopoulou, E., Harvati, K., Skinner, A., 2016. ESR dating the fossil-bearing layers at the Marathousa 1 site, Megalopolis, Greece, *Paleoanthropological Society Meeting*, Atlanta, pp. A4–A5.

- Bochenski, Z., 2005. Owls, diurnal raptors and humans: signatures on avian bones. In: O'Connor, T., (Ed.) International Council of Archaeozoology; Biosphere to lithosphere new studies in vertebrate taphonomy, 31–45.
- Bochenski, Z.B., Nekrasov, A.E., 2001. The taphonomy of Sub-Atlantic bird remains from Bazhukovo III, Ural Mountains, Russia. *Acta zoologica Cracoviensia*, 44, 93–106.
- Bochenski, Z.B., Tomek, T., 1997. Preservation of Bird Bones: Erosion versus Digestion by Owls. *International Journal of Osteoarchaeology*, 7, 372–387.
- Boev, Z., 2010. Fossil avifauna of Greece and the Bulgarian contribution to its exploration. *Bulgarian Academy of Sciences News*, 10 (86).
- Bramwell, D., Yalden, D.W., Yalden, P. E., 1987. Black grouse as the prey of the golden eagle at an archaeological site. *Journal of Archaeological Science* 14, 195–200.
- Carboneras, C., 1992. Family Anatidae (ducks, geese and swans). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World*, vol. 1. Lynx Edicions, Barcelona, pp. 528–628.
- Cohen, A., Serjeantson, D., 1996. *A Manual for the Identification of Bird Bones from Archaeological Sites*. Archetype Publications.
- Cruz, I., 2008. Avian and mammalian bone taphonomy in southern continental Patagonia: A comparative approach. *Quaternary International* 180, 30–37.

del Hoyo, J., Elliott, A., Jordi Sargatal, J. (Eds.), 1992. Handbook of the Birds of the World. Lynx Edicions, Barcelona.

Doukas, C., van Kolfschoten, T., Papayianni, K., Panagopoulou, E., Harvati, K., this issue. The small mammal fauna from the Palaeolithic site Marathousa 1 (Greece). *Quaternary International*.

Ericson P.G.P., 1987. Interpretations of archaeological bird remains: a taphonomic approach. *Journal of Archaeological Science* 14, 65–75.

Fernández-Jalvo, J., Andrews, P., 2016. Atlas of taphonomic identifications. 1001+ images of fossil and recent mammal bone modification. Springer, Dordrecht.

Field, M.H., Ntinou, M., Tsartsidou, G., van Berge Henegouwen, D., Risberg, J., Tourloukis, V., Thompson, N., Karkanas P., Panagopoulou, E., Harvati, K., this issue. A detailed, local palaeoenvironmental reconstruction (based on palaeobotanical data) of the elephant site at Marathousa (site 1), Megalopolis, Greece. *Quaternary International*.

Fiore, I., Gala, M., Romandini, M., Cocca, E., Tagliacozzo, A., Peresani, M., 2016. From feathers to food: Reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane cave, unit A9. *Quaternary International* 421, 134–153.

Gal E., 2008. Faunal and taphonomic analyses of a Late Pleistocene bird-bone assemblage from a cave deposit in north-west Hungary. *Geobios*, 41, 79–90.

Giusti, D., Tourloukis, V., Konidaris, G.E., Thompson, N., Karkanas, P., Panagopoulou, E., Harvati, K., this issue. Beyond maps: Patterns of formation processes at the Middle Pleistocene open-air site of Marathousa 1, Megalopolis Basin, Greece. *Quaternary International*.

Harrison C. J. O., 1982. *An Atlas of the birds of the Western Palaearctic*. Collins. London

Harvati K. 2016. Paleoanthropology in Greece: recent findings and interpretations. In: K. Harvati K., Roksandic M., (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human Evolution and its Context*. *Vertebrate Paleobiology and Paleoanthropology Series*, 3–14. Springer: Dordrecht.

Harvati, K., Tourloukis, V., 2013. Human Evolution in the Southern Balkans. *Evolutionary Anthropology* 22, 43–45.

Jacobs, Z., Li, B., Karkanas, P., Tourloukis, V., Thompson, N., Panagopoulou, E., Harvati, K., this issue. Optical dating of K-feldspar grains from Middle Pleistocene lacustrine sediment at Marathousa 1 (Greece). *Quaternary International*, <https://doi.org/10.1016/j.quaint.2018.06.029>.

Karkanas, P., Tourloukis, V., Thompson, N., Giusti, D., Panagopoulou, E., Harvati, K., this issue. Sedimentology and micromorphology of the Lower Palaeolithic lakeshore site Marathousa 1, Megalopolis basin, Greece. *Quaternary International*, <https://doi.org/10.1016/j.quaint.2018.02.037>.

Konidaris, G., Athanassiou, A., Turloukis, V., Thompson, Giusti, D., Panagopoulou, E., Harvati, K., this issue. The skeleton of a straight-tusked elephant (*Palaeoloxodon antiquus*) and other large mammals from the Middle Pleistocene butchering locality Marathousa 1 (Megalopolis Basin, Greece): preliminary results. Quaternary International, <https://doi.org/10.1016/j.quaint.2017.12.001>.

Landt, M. J., 2007. Tooth marks and human consumption: ethnoarchaeological mastication research among foragers of the Central African Republic. *Journal of Archaeological Science* 34, 1629–1640.

Laroulandie, V., Costamagno, S., Cochard, D., Mallye, J.-B., Beauval, C., Castel, J. C., Ferrié, J. G., Gourichon, L., Rendu, W., 2008. Quand désarticuler laisse des traces: le cas de l'hyperextension du coude. *Annales de Paléontologie* 94, 287–302.

Livingston, S.D., 1989. The Taphonomic Interpretation of Avian Skeletal Part Frequencies. *Journal of Archaeological Science* 16, 537–547

Löhnert, E., Nowak, H., 1965. Die Braunkohlenlagerstätte von Khoremi im Becken von Megalopolis/Peloponnes. *Geol. Jb.* 82, 847–867.

Lyman R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge, UK.

Mädler, K., 1971. Die Früchte und Samen aus der frühpleistozänen Braunkohle von Megalopolis in Griechenland und ihre ökologische Bedeutung. *Beihefte zum Geologischen Jahrbuch* 110, 1–79.

MacDonald, D.W. (Ed.), 2009. The encyclopedia of mammals. Oxford University Press, Oxford.

Mallye, J. B., Cochard, D., Laroulandie, V., 2008. Accumulations osseuses en périphérie de terriers de petits carnivores: les stigmates de prédation et de fréquentation. *Annales de Paléontologie* 94, 187–208.

Melentis, J.K., 1961. Die Dentition der pleistozänen Proboscider des Beckens von Megalopolis im Peloponnes (Griechenland). *Annales Géologiques des Pays Helléniques* 12, 153–262.

Michailidis, D., 2013. Taxonomic and Palaeoecological study of the Pleistocene Avifauna of Greece. Implications to the Palaeoecology of *Homo*. Ph.D. Thesis, National and Kapodistrian University of Athens, Greece (in Greek with English summary).

Mlíkovský, J., 2002. Cenozoic Birds of the World. Part 1: Europe. Ninox Press, Praha.

Monchot, H., Gendron, D., 2011. Les restes d'une tanière de renard en milieu periglaciaire (Île Digges, rive sud du détroit d'Hudson, Canada. In: Laroulandie, V., Mallye, J.-B., Denys, C. (Eds.), *Taphonomie Des Petits Vertébrés: Référentiels et Transferts Aux Fossiles*. British Archaeological Reports, International series 2269, 65–76.

Mourer-Chauviré C., 1993. The Pleistocene avifaunas of Europe. In Morales Muniz, A., (Ed.) *Archaeofauna. Archaeornithology: Birds and the Archaeological record*. Proceedings of the first meeting of the ICAZ Bird working group. Universidad Autonoma de Madrid, 53–66.

Orta, J., 1992. Family Anhingidae (darters). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), Handbook of the Birds of the World, vol. 1. Lynx Edicions, Barcelona, pp. 354–361.

Panagopoulou, E., Turloukis, V., Thompson, N., Konidaris, G., Athanassiou, A., Giusti, D., Tsartsidou, G., Karkanas, P., Harvati, K., this issue. The Lower Palaeolithic site of Marathousa 1, Megalopolis Greece: Overview of the evidence. Quaternary International, <https://doi.org/10.1016/j.quaint.2018.06.031>

Panagopoulou, E., Turloukis, V., Thompson, N., Athanassiou, A., Tsartsidou, G., Konidaris, G.E., Giusti, D., Karkanas, P., Harvati, K., 2015. Marathousa 1: a new Middle Pleistocene archaeological site from Greece. Antiquity Project Gallery 89. <http://antiquity.ac.uk/projgall/panagopoulou343>

Rufà, A., Blasco, R., Roger, T., Rué, M., Camille Daujeard, D., in press. A rallying point for different predators: the avian record from a Late Pleistocene sequence of Grotte des Barasses II (Balazuc, Ardèche, France). Archaeological and Anthropological Sciences, <https://doi.org/10.1007/s12520-017-0469-6>.

Sickenberg, O., 1976. Eine Säugetierfauna des tieferen Bihariums aus dem Becken von Megalopolis (Peleponnes, Griechenland). Annales Géologiques des Pays Helléniques 27, 25–73.

Skouphos, T., 1905. Über die paläontologischen Ausgrabungen in Griechenland in Beziehung auf das Vorhandensein des Menschen, *Comptes rendus du Congrès International d'Archéologie*, 1re session, Athènes, 231–236.

Stallibrass, S., 1990. Canid damage to animal bones: two current lines of evidence. In: Robinson, D.E. (Ed.), *Experimentation and reconstruction in environmental archaeology*. Oxbow Books, Oxford, pp. 151–165.

Sutherland, S.A., 1986. The archaeological study of bird bones. Past and present, with particular reference to some Late Pleistocene Avifaunas in Britain. Ph.D. Thesis, University of Sheffield, U.K.

Taylor, P.B., 1996. Family Rallidae (rails, gallinules and coots). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World*, vol. 3. Lynx Edicions, Barcelona, pp. 108–209.

Theodorou, G., 2014. Megalopolis - 112 years after the first excavation by National and Kapodistrian University of Athens (NKUA) - and the Post Lignite era. In: Kostopoulos, D.S., Vlachos, E., Tsoukala, E. (Eds.), *Vlth International Conference on Mammoths and their Relatives*. Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Greece, Grevena-Siatista, pp. 195–196.

Tourloukis, V., Harvati, K., 2018. The Palaeolithic record of Greece: a synthesis of the evidence and a research agenda for the future. *Quaternary International* 466, 48–65.

Tourloukis, V., Thompson, N., Panagopoulou, E., Giusti, D., Konidaris, G.E., Karkanis,

P., Harvati, K., this issue a. Lithic artifacts and bone tools from the Lower Palaeolithic site Marathousa 1, Megalopolis, Greece: preliminary results. *Quaternary International*, <https://doi.org/10.1016/j.quaint.2018.05.043>.

Tourloukis, V., Muttoni, G., Karkanas, P., Monesi, E., Scardia, G., Panagopoulou, E., Harvati, K., this issue b. Magnetostratigraphic and chronostratigraphic constraints on the Marathousa-1 Lower Palaeolithic site and the Middle Pleistocene deposits of the Megalopolis basin, Greece. *Quaternary International*, <https://doi.org/10.1016/j.quaint.2018.03.043>.

Tyrberg, T., 2007. *Pleistocene Birds of the Palearctic: a Catalogue*. Publications of the Nuttall Ornithological Club No. 27, Cambridge Massachusetts.

van Vugt, N., 2000. *Orbital forcing in late Neogene lacustrine basins from the Mediterranean. A magnetostratigraphic and cyclostratigraphic study*. Ph.D. Thesis, Utrecht University, The Netherlands.

Vinken, R., 1965. Stratigraphie und Tektonik des Beckens von Megalopolis (Peloponnes, Griechenland). *Geologisches Jahrbuch* 83, 97–148.

Woelfle, E., 1967. *Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Enten, Halbgänse und Säuger*. Ph.D. Thesis, Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München, Munich, Germany.

Woolfenden, G.E., 1961. Postcranial osteology of the waterfowl. *Bulletin of the Florida state museum. Biological Sciences* 6 (1). University of Florida. Gainesville.

Figure 1. Geographic position of the Megalopolis Basin and the Marathousa 1 site (lignite mines expansion taken from www.openstreetmap.org in 2015), and simplified stratigraphic columns of Area A and Area B showing the stratigraphic units and correlation between the two areas [taken from Karkanas et al. (this issue)]; absolute elevation in m.a.s.l. (meters above sea level). The inset map of the eastern Mediterranean was adapted from d-maps.com.

Figure 2. Avian specimens from MAR-1, Area A. **A:** complete right coracoideum of *Anas acuta* (MAR-1-941/676-41), dorsal aspect; **B:** proximal left carpometacarpus of *Anas crecca* (MAR-1-941/674-13), ventral aspect; **C:** complete right coracoideum of *Anas platyrhynchos* (MAR-1-938/676-10), dorsal aspect; **D:** distal right carpometacarpus of *Anser* cf. *albifrons* (MAR-1-939/676-35), dorsal aspect; **E:** complete left tarsometatarsus of *Aythya fuligula* (MAR-1-940/674-45), dorsal aspect; **F:** proximal left radius of *Cygnus olor* (MAR-1-939/677-2), ventral aspect; **G:** proximal left coracoideum of *Mareca strepera* (MAR-1-939/673-3), dorsal aspect; **H:** distal left humerus of *Spatula clypeata* (MAR-1-938/676-21), cranial aspect; **I:** complete left coracoideum of *Spatula querquedula* (MAR-1-941/673-22), dorsal aspect; **J:** distal left femur of *Podiceps nigricollis* (MAR-1-937/672-6), caudal aspect; **K:** complete right coracoideum of *Fulica atra* (MAR-1-938/676-11), dorsal aspect; **L:** distal right humerus of *Gallinula chloropus* (MAR-1-941/676-47), cranial aspect; **M:** distal left humerus of *Rallus aquaticus* (MAR-1-939/674-39), cranial aspect; **N:** proximal right coracoideum of *Nycticorax nycticorax* (MAR-1-941/676-48), dorsal aspect; **O:** complete right coracoideum of *Tringa* cf. *totanus* (MAR-1-941/677-38), dorsal aspect; **P:** distal left tarsometatarsus of cf. *Cinclus cinclus* (MAR-1-939/675-47), dorsal aspect; **Q:** proximal right humerus of *Anhinga* sp. (MAR-1-938/677-7), caudal aspect. Scale bar equals 5 cm.

Figure 3. a, family composition of the Marathousa 1 avifauna in the stratigraphic units UA3+UA4 (Area A) and UB4+UB5 (Area B); birds' drawings (not to scale) were redrawn and modified from www.drawingtutorials101.com; **b**, percentages of survival for each skeletal element in Area A (A: UA3+UA4) and Area B (B: UB4+UB5). Numbers on the bars show the number for each skeletal element. The abundances of wing, leg, core, limb, proximal and distal bones follow Ericson (1987), Bramwell et al. (1987) and Bocheński and Nekrasov (2001). Schematic drawing of a dabbling duck (*Anas*) skeleton (by M. Coutureau and V. Laroulandie available at www.archeozoo.org) showing the identified Marathousa-1 avian bones and their anatomical part.

Figure 4. Avian specimens from MAR-1, Area B. **A:** distal left humerus of *Anas clypeata* (MAR-1-933/602-59), cranial aspect; **B:** complete right carpometacarpus of *Anas crecca* (MAR-1-932/596-38), ventral aspect; **C:** complete right coracoideum of *Anas platyrhynchos* (MAR-1-350/68-23), dorsal aspect; **D:** complete left coracoideum of *Mareca strepera* (MAR-1-933/602-32+33), dorsal aspect; **E:** distal right tibiotarsus of *Aythya ferina* (MAR-1-933/601-50), cranial aspect; **F:** complete left ulna of *Aythya fuligula* (MAR-1-934/602-69), ventral aspect; **G:** distal right ulna of *Aythya nyroca* (MAR-1-934/599-49), ventral aspect; **H:** distal left tibiotarsus of *Branta bernicla* (MAR-1-932/596-59), cranial aspect; **I:** distal left humerus of *Calidris cf. ferruginea* (MAR-1-934/601-24), cranial aspect; **J:** complete right tarsometatarsus of *Fulica atra* (MAR-1-933/601-57), dorsal aspect; **K:** distal left tarsometatarsus of *Porphyrio porphyrio* (MAR-1-934/603-18), dorsal aspect; **L:** distal right tarsometatarsus of *Plegadis falcinellus* (MAR-1-933/604-12), dorsal aspect. Scale bar equals 5 cm.

a

b

A

B

C

D

E

F

G

H

I

J

K

L

Order	Family	Genus	Species	Common name	Area A	Area B
Anseriformes	Anatidae	<i>Anas</i>	<i>acuta</i>	Northern Pintail	UA3, UA4	
Anseriformes	Anatidae	<i>Anas</i>	<i>crecca</i>	Common Teal	UA2, UA3	UB4, UB5
Anseriformes	Anatidae	<i>Anas</i>	<i>platyrhynchos</i>	Mallard	UA2, UA3, UA4	UB4, UB5
Anseriformes	Anatidae	<i>Anser</i>	<i>cf. albifrons</i>	Greater White-fronted Goose	UA3	
Anseriformes	Anatidae	<i>Aythya</i>	<i>ferina</i>	Common Pochard		UB4
Anseriformes	Anatidae	<i>Aythya</i>	<i>fuligula</i>	Tufted Duck	UA3	UB4
Anseriformes	Anatidae	<i>Aythya</i>	<i>nyroca</i>	Ferruginous Duck	UA3	UB4
Anseriformes	Anatidae	<i>Branta</i>	<i>bernicle</i>	Brent Goose		UB5
Anseriformes	Anatidae	<i>Cygnus</i>	<i>olor</i>	Mute Swan	UA3	
Anseriformes	Anatidae	<i>Mareca</i>	<i>strepera</i>	Gadwall	UA2, UA3, UA4	UB4, UB5
Anseriformes	Anatidae	<i>Spatula</i>	<i>clypeata</i>	Northern Shoveler	UA2, UA3, UA4	UB4
Anseriformes	Anatidae	<i>Spatula</i>	<i>querquedula</i>	Garganey	UA3	
Podicipediformes	Podicipedidae	<i>Podiceps</i>	<i>nigricollis</i>	Black-necked Grebe	UA3	
Gruiformes	Rallidae	<i>Fulica</i>	<i>atra</i>	Common Coot	UA3	UB4
Gruiformes	Rallidae	<i>Gallinula</i>	<i>chloropus</i>	Common Moorhen	UA4	
Gruiformes	Rallidae	<i>Rallus</i>	<i>aquaticus</i>	Western Water Rail	UA2, UA3	
Gruiformes	Rallidae	<i>Porphyrio</i>	<i>porphyrio</i>	Purple Swamphen		UB4
Pelecaniformes	Ardeidae	<i>Nycticorax</i>	<i>nycticorax</i>	Black-crowned Night-heron	UA4	
Pelecaniformes	Threskiornithidae	<i>Plegadis</i>	<i>falcinellus</i>	Glossy Ibis		UB4
Suliformes	Anhingidae	<i>Anhinga</i>	sp. *	Darter	UA3	
Charadriiformes	Scolopacidae	<i>Calidris</i>	<i>cf. ferruginea</i>	Curlew Sandpiper		UB4
Charadriiformes	Scolopacidae	<i>Tringa</i>	<i>cf. totanus</i>	Common Redshank	UA3	
Passeriformes	Cinclidae	<i>cf. Cinclus</i>	<i>cinclus</i>	White-throated Dipper	UA4	

Table 1. Avifaunal list from Marathousa 1 and species distribution at the different units of Areas A and B.

* *Anhinga* is the only species identified that is not presently found in Greece.

AREA A	NISP	MNI	UNIT
<i>Anas crecca</i>	1	1	UA2
<i>Anas platyrhynchos</i>	1	1	UA2
<i>Mareca strepera</i>	1	1	UA2
<i>Spatula clypeata</i>	1	1	UA2
<i>Rallus aquaticus</i>	1	1	UA2
<i>Anas acuta</i>	4	1	UA3
<i>Anas crecca</i>	10	4	UA3
<i>Anas platyrhynchos</i>	4	2	UA3
<i>Anser cf. albifrons</i>	1	1	UA3
<i>Aythya fuligula</i>	3	2	UA3
<i>Aythya nyroca</i>	1	1	UA3
<i>Cygnus olor</i>	1	1	UA3
<i>Spatula clypeata</i>	7	2	UA3
<i>Spatula querquedula</i>	2	1	UA3
<i>Mareca strepera</i>	4	2	UA3
<i>Anhinga sp.</i>	1	1	UA3
<i>Fulica atra</i>	9	2	UA3
<i>Podiceps nigricollis</i>	1	1	UA3
<i>Rallus aquaticus</i>	1	1	UA3
<i>Tringa cf. totanus</i>	1	1	UA3
<i>Anas acuta</i>	1	1	UA4
<i>Anas cf. platyrhynchos</i>	1	1	UA4
<i>Mareca strepera</i>	2	1	UA4
<i>Spatula clypeata</i>	3	2	UA4
<i>Gallinula chloropus</i>	2	1	UA4
<i>Nycticorax nycticorax</i>	1	1	UA4
<i>cf. Cinclus cinclus</i>	1	1	UA4
TOTAL	66	36	

Table 2. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) for the taxa identified from Area A, by stratigraphic unit.

AREA B	NISP	MNI	UNIT
<i>Anas crecca</i>	1	1	UB4
<i>Anas platyrhynchos</i>	4	2	UB4
<i>Aythya ferina</i>	2	1	UB4
<i>Aythya fuligula</i>	2	1	UB4
<i>Aythya nyroca</i>	1	1	UB4
<i>Mareca strepera</i>	2	1	UB4
<i>Spatula clypeata</i>	4	2	UB4
<i>Calidris cf. ferruginea</i>	1	1	UB4
<i>Fulica atra</i>	2	1	UB4
<i>Plegadis falcinellus</i>	1	1	UB4
<i>Porphyrio porphyrio</i>	1	1	UB4
<i>Anas crecca</i>	2	1	UB5
<i>Anas platyrhynchos</i>	2	1	UB5
<i>Branta bernicla</i>	1	1	UB5
<i>Mareca strepera</i>	1	1	UB5
TOTAL	27	17	

Table 3. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) values for the taxa identified from Area B, by stratigraphic unit.

Species \ Habitat	Climatic Zones	Arid- Rocks	Steppe- Grassland	Wide range	Open Woodland	Forest	Fresh water	Mountains	Coast
<i>Anas acuta</i>	Subarctic- Subtropical		S				FW		
<i>Anas crecca</i>	Subarctic- Subtropical						FW		
<i>Anas platyrhynchos</i>	Subarctic- Subtropical						FW		
<i>Anser cf. albifrons</i>	Arctic- Temperate		S				FW		
<i>Aythya fuligula</i>	Subarctic- Subtropical						FW		
<i>Aythya nyroca</i>	Temperate- Subtropical						FW		
<i>Cygnus olor</i>	Boreal- Subtropical						FW		
<i>Mareca strepera</i>	Boreal- Subtropical		S				FW		
<i>Spatula clypeata</i>	Subarctic- Subtropical						FW		
<i>Spatula querquedula</i>	Arctic- Subtropical						FW		
<i>Podiceps nigricollis</i>	Subarctic- Subtropical						FW		
<i>Fulica atra</i>	Boreal- Subtropical						FW		
<i>Gallinula chloropus</i>	Boreal- Subtropical						FW		
<i>Rallus aquaticus</i>	Subarctic- Subtropical						FW		
<i>Tringa cf. totanus</i>	Arctic- Tropical		S				FW		
<i>Anhinga sp.</i>	Tropical- Subtropical				OW		FW		
<i>Nycticorax nycticorax</i>	Temperate- Subtropical				OW		FW		
<i>cf. Cinclus cinclus</i>	Arctic- Temperate						FW		
HABITAT PREFERENCE SCORE			4		2		18		

Table 4. Habitat and climatic zone preferences of the taxa identified from Area A.

Habitat Species	Climatic Zones	Arid- Rocks	Steppe- Grassland	Wide range	Open Woodland	Forest	Fresh water	Mountains	Coast
<i>Anas crecca</i>	Subarctic- Subtropical						FW		
<i>Anas platyrhynchos</i>	Subarctic- Subtropical						FW		
<i>Aythya ferina</i>	Subarctic- Subtropical						FW		
<i>Aythya fuligula</i>	Subarctic- Subtropical						FW		
<i>Aythya nyroca</i>	Temperate- Subtropical						FW		
<i>Branta bernicla</i>	Arctic- Temperate						FW		C
<i>Mareca strepera</i>	Boreal- Subtropical		S				FW		
<i>Spatula clypeata</i>	Subarctic- Subtropical						FW		
<i>Fulica atra</i>	Boreal- Subtropical		S				FW		
<i>Porphyrio porphyrio</i>	Subtropical- Tropical		S				FW		
<i>Calidris cf. ferruginea</i>	Arctic- Subtropical		S				FW		C
<i>Plegadis falcinellus</i>	Temperate-Tropical				OW		FW		
HABITAT PREFERENCE SCORE			4		1		12		2

Table 5. Habitat and climatic zone preferences of the taxa identified from Area B.