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Birds as indicators of high biodiversity zones around the Middle Pleistocene Qesem Cave, Israel

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ABSTRACT

Israel is part of a corridor connecting Africa and Euro-Asia that has also been a major migratory route of birds throughout the Quaternary. Very few Middle Pleistocene sites have a large enough record of avian species to provide a taxonomic composition of ornithic paleocommunities to explain their geographic distribution and the human uses of birds in the Middle Pleistocene. The inspection of the fossil remains of birds from Qesem Cave has allowed the identification of fourteen taxa including residents and migratory birds that are typical dwellers of open country, cliffs and stony ground, woodland and bushland, bodies of water and corresponding vegetated fringes. Some of the migratory taxa identified are rare or accidental at present, and this may indicate different climatic conditions in the regions where these birds lived during the other seasons. The sample of avian taxa recorded at Qesem Cave is representative of several habitats and phenological statuses As all other finds at the cave were transported by humans as indicated by some taphonomic features, the sample of bird bones presented here is influenced by the humans as bioaccumulators, as expected in archaeological sites.

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1. Introduction

It is largely accepted that for many plants and animals, the Levant has been the main route of dispersal between Africa and the rest of the world (Tchernov et al., 1994). The many climate shifts that occurred throughout the Pleistocene played a major role in the reshaping of the regional biogeography. As a consequence, a trend toward increasing aridity during the Quaternary in this region has been suggested (Horowitz, 1992). These factors, together with the proximity of large deserts—the Eremian belt—influenced the extinction of Afro-Arabian and Eurasian faunal elements and conditioned the dispersion opportunities of hominins groups and other animal taxa out of Africa (Tchernov et al., 1994). A mixture of faunistic elements from both geographic areas has always been present in this region, despite phases of biogeographic isolation (Horowitz, 2002).

The number of species of the current ornithofauna in Israel is about 530 (Cohen et al., 2015; Lepage, 2015), although it would total almost 370 species after excluding rare and accidental occurrences. The living avian species in the Near East are a mixture of typical taxa in the Palearctic, Anatolia, northern Africa, and Arabian Peninsula. An estimated 500 million birds pass through this region every year in spring and autumn (Cohen et al., 2015). The Levantine corridor extends along the western margin of one major fly ways for migratory birds. One route connects eastern Africa to central and northern Europe and northern Asia, and the other two routes link Europe to Africa over the Strait of Gibraltar and Sicily, respectively. The timing of the appearance of long-distance migratory behavior in birds is under debate (Bell, 2000; Jahn et al., 2004; Salewski and Bruderer, 2007), but the current main routes were likely well established in the Pleistocene. The reason is that climates bearing marked seasonality have existed in the northern hemisphere since the late Cenozoic, irrespective of the long series of wet-dry and cool-warm fluctuations during the Pleistocene.

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Unfortunately, the available information about the birds that lived during the Pleistocene in the Near East is not very rich, although there is some data for the Pleistocene and the Holocene. For the early Pleistocene, the site of 'Ubeidiya offers an exceptionally rich and informative collection of birds (Tchernov 1968, 1979, 1980). Regarding the Middle Pleistocene, Simmons (2004) offered some notes on the avian record of the Acheulian Geser Benot Ya'aqov and reported the existence of 16 taxa, but the list of taxa is not provided. Umm Qatafa is the only Acheulian site that offers a relatively rich sample of birds (Vaufrey, 1931; Tchernov, 1962, 1979). The avian species identified in Zuttiyeh are scant (Tchernov, 1962). As in other regions, avian data from Late Pleistocene sites are more abundant (cf. Tyrberg, 1998, 2015). Most of these sites belong to the Natufian culture of the terminal Pleistocene. Only three Late Pleistocene localities have yielded large samples of the corresponding paleornithocenoses: the Levantine Mousterian layers of Kebara Cave in Mt. Carmel (Tchernov, 1962, 1979; Pichon and Tchernov, 1987); the Epipaleolithic, 23,000 year-old-site of Ohalo 2 (Simmons and Nadel, 1998); and the Natufian layers of Hayonim Cave (Bar-Yosef and Tchernov, 1966; Tchernov, 1979; Pichon, 1984) where the largest record of birds for this time period was found.

This paper presents the first results of the taxonomic study of the avian remains from Qesem Cave, a Middle Pleistocene site in Israel. A large collection of lithic artifacts unearthed during a series of field seasons, starting in 2001, has been assigned to the Acheulo-Yabrudian Cultural Complex (AYCC) of the late Lower Paleolithic (e.g., Gopher et al., 2005; Barkai and Gopher, 2013). Lithic artifacts and bones damaged by fire and tools are abundant in every layer, which indicates that humans visited the cave repeatedly (Stiner et al., 2009; Blasco et al., 2014, 2016). Some avian bones from the hearth unit (around 300 ka) and other contexts of the cave exhibit cut marks, supporting the incipient role of hominins in the accumulation of avian remains (Blasco et al., 2016). The taphonomic analysis of bird bones from other units of the sequence is currently underway. U–Th dates on speleothems indicate that the sediments range from 420 to ca 200 ka (Gopher et al., 2010), which agrees with the dating of the burnt flint and teeth through thermoluminescence and combined electro-spin resonance and U-series methods (Mercier et al., 2013; Falguères et al., 2016).

Compared with other localities of similar chronology, the faunal remains of Qesem Cave are abundant and well-preserved (Stiner et al., 2009, 2011; Blasco et al., 2014, 2016), and these rich and varied records have been the subject of a number of publications: on the dating (e.g., Barkai et al., 2003, 2010; Mercier et al., 2013; Falguères et al., 2016), lithic artifacts (e.g., Barkai et al., 2003, 2005, 2009, 2010, 2013; Gopher et al., 2005, 2010; Shimelmitz et al., 2011; Barkai and Gopher, 2013), stratigraphy and site-formation processes (Karkanas et al., 2007; Frumkin et al., 2009; Shahack-Gross et al., 2014), on taphonomy (Stiner et al., 2009, 2011; Blasco et al., 2014), hominin bones (Ben Dor et al., 2011; Hershkowitz et al., 2011), reptiles and micromammals (Maul et al., 2011; Smith et al., 2013), and on the chiropters (Horáček et al., 2013). The morphometric analysis of the hominine teeth unearthed from the cave concludes that they cannot be attributed to *Homo erectus*, but rather to modern human populations in the Levant, like the one represented at Skhul-Qafzeh, albeit with Neanderthal affinities (Hershkovitz et al., 2011).

1.1. Geological setting

Qesem Cave is located about 12 km east of the current Mediterranean shoreline, at an elevation of 90 m above present-day sea level (Fig. 1). The region of Samaria hills, where this cave is situated, is rich in karstic cavities formed through dissolution of the Cretaceous limestone of the Turonian B'ina Formation. In the Middle Pleistocene, the cavity was opened by erosion, which allowed the entry of humans and animals. A variety of sedimentological processes, such as subsidence, erosion, deposition, and cementation, affected the formation of the deposit during the Middle Pleistocene (Frumkin et al., 2009; Maul et al., 2011). The cave consists of a chamber with a plant size of 20 × 15 m and around 10 m high. The column of Qesem Cave is generally subdivided into two parts: the upper sequence (~4.5 m thick), which shows a strong cementation of the deposits by calcite precipitated from dripping waters and a recrystallization of the ash (Karkanas et al., 2007); and the lower sequence (>5 m thick), which shows a higher proportion of clastic sediments and gravel, indicating a more closed karst environment than in the top of the stratigraphy (Karkanas et al., 2007; Mercier et al., 2013). More refined stratigraphic subdivision is underway.

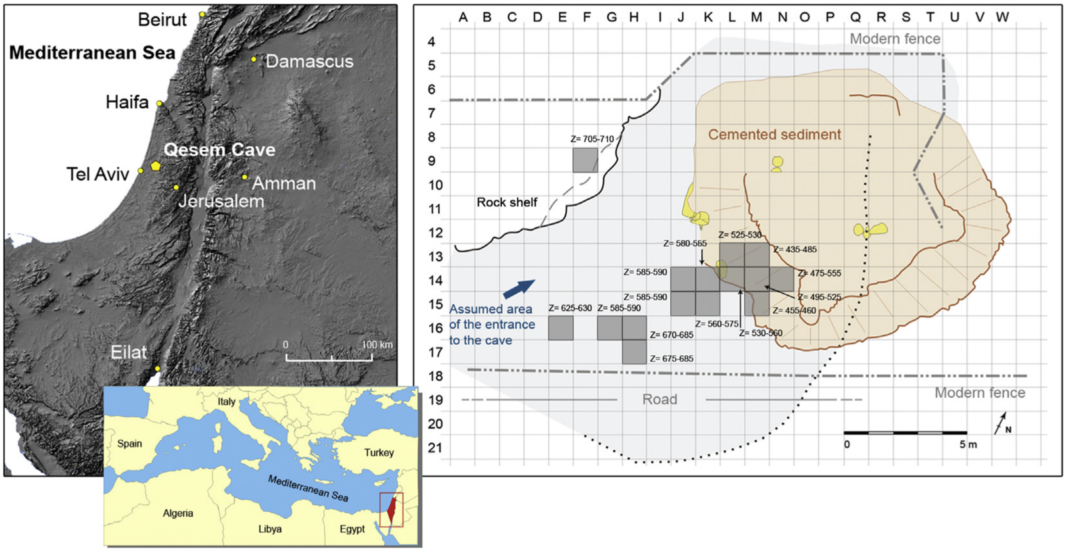

Fig. 1. Location of Qesem Cave in the Levant (left), position of the analysed sample –grey squares– in relation to the sequence and the grid system (right).

The whole sedimentary sequence, according to the dating methods performed (Gopher et al., 2010; Mercier et al., 2013), records a span of time of about 200 ka (420 ka to 200 ka, approximately). The cave was repeatedly frequented by hominins during a period of 200 ka and except for a rich microvertebrate assemblage deposited by raptors and birds that inhabited the cave, all of the finds were brought by humans (Blasco et al., 2016). After the chamber was filled with cultural deposits, it was sealed by the slope, to be discovered only in the year 2000 during the construction of a road. The cave has no intrusive deposits subsequent to the human occupation, and all bird remains presented in this paper were found within discrete occupational levels of the cave along with abundant lithic and faunal assemblages.

1.2. *Faunal record*

The assemblage of large and medium-sized mammals consists of: *Dama* cf. *mesopotamica* (the predominant macrovertebrate); *Hystrix indica*, *Capreolus* sp., *Capra aegagrus*, *Sus scrofa*, *Equus* cf. *hydruntinus*, *Cervus elaphus*, *Equus caballus*, *Bos primigenius*, *Stephanorhinus hemitoechus*, and Hyaenidae indeterminate, all macromammals that belong to the palaearctic taxa (Stiner et al., 2009; Blasco et al., 2014). The group of reptiles is very rich. Maul et al. (2011) and Smith et al. (2013) found the following representatives of the herpetofauna: Testudines, *Chamaeleo* sp., *Stellagama* sp., *Pseudopus* sp., *Laudakia* sp., *Varanus* sp., Lacertidae, Gekkonidae, Scincidae, Colubroidea and Anura; the bone remains of *Chamaeleo* were the most abundant. There is also a large list of species of insectivores, rodents (Maul et al., 2011), and bats (Horáček et al., 2013): *Suncus etruscus*, *Crocidura* cf. *leucodon*, *Sciurus* cf. *anomalus*, *Cricetulus* cf. *migratorius*, *Microtus guentheri*, *Nannospalax ehrenbergi*, *Dipodillus* cf. *dasyurus*, *Meriones* cf. *tristrami*, Gerbillidae indet., *Mus* cf. *musculus*, *Apodemus* cf. *flavicollis*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Rhinolophus mehelyi*, *Miniopterus* cf. *schreibersii*, *Myotis blythii* and cf. *Rousettus* sp. The latter genus belongs to a group whose geographical distribution does not encompass the Middle East (Horáček et al., 2013).

2. Material and methods

We assume that annual migrating species between breeding and non-breeding areas remain mostly the same today as they were in the Pleistocene. That is, the migratory behavior (phenology) of a particular species remains unchanged, at least from the Pleistocene onward. We assume, as it is widely accepted for the environmental enquiries on the Pleistocene (Holm and Svenning, 2014), that the habitat preferences for each species were the same in the past as in the present.

A total of 54 skeletal elements have been studied, and 31 of them have been assigned to 14 species or genera. The remaining 23 specimens are fragments of bones that lack diagnostic characters and belong to small birds. The fossil material is stored at the Institute of Archaeology of the Tel Aviv University. The fossils were collected during fieldwork conducted between 2006 and 2012 from the grid squares: E/16, G/16, H/16 and 17, J/14 and 15, K/14 and 15, L/13 and 14, M/13, 14 and 15, N/13 and 14, and F/9, between elevation 455 and 710 cm below datum (see Fig. 1 for details). Thus, the avian assemblage presented here has been collected in the lower part of the upper sequence and in the upper part of the lower sequence of the stratigraphic column (e.g., Karkanas et al., 2007). In chronological terms, the contexts from which the avian assemblage presented here was retrieved are earlier than 280 ka. A more refined contextual study of the bird bones will be conducted in the future.

For the nomenclature of the skeletal anatomy, we have followed the work of Baumel and Witmer (1993). The phenology and current status of species are based on Cohen et al. (2015) and Lepage (2015).

3. Results

All of the bones identified up to the species level have been attributed to extant species. Several bone elements have been identified up to the genus level only because they lack diagnostic characters to reach the species level. This does not imply the existence of any undescribed species. Table 1 lists the taxa identified, together with the number of bones and the minimum number of individuals of each taxon.

Table 1
Avian taxa identified at Qesem Cave, indicating number of bones and MNI.

Families and species	Number of bones and MNI
Phasianidae	
Francolinus francolinus	2 (1)
Coturnix coturnix	4 (2)
Anatidae	
Cygnus sp.	1 (1)
Procellariidae	
Pterodroma sp.	1 (1)
Rallidae	
Crex crex	1 (1)
Strigidae	
Otus scops	1 (1)
Columbidae	
Columba sp.	5 (2)
Streptopelia sp.	1 (1)
Corvidae	
Corvus ruficollis	6 (2)
Alaudidae	
Galerida cristata	1 (1)
Lullula arborea	2 (2)
Hirundinidae	
Ptyonoprogne sp./*Hirundo rustica*	1 (1)
Sturnidae	
Sturnus sp.	4 (2)
Sylviidae	
Phylloscopus sp.	1 (1)

3.1. *Avian record*

Order Galliformes (Temminck, 1820)
Family Phasianidae (Vigors, 1825)
Subfamily Phasianinae Vigors, 1825
Genus *Francolinus* Stephens, 1819
Francolinus francolinus (Linnaeus, 1766)

Two fragments of bones belong to this species: the proximal end of one carpometacarpus (QC09, L13c, z: 525–530) (Fig. 2a) and one incomplete distal end of a tarsometatarsus (QC09, M13c, z: 482–485). In the carpometacarpus, the ventral and the dorsal edges of the trochlea carpalis protrude distally to the same extent. The processus extensorius is well developed and rounded. It is narrower in *Alectoris* Kaup, 1829, *Perdix* Brisson, 1760, and *Coturnix* Bonnaterre, 1791. In these phasianids, the cranial edge of the trochlea carpalis is pointed and protrudes distinctly proximally, contrary to what is seen in *Francolinus*. The ossa metacarpale majus and minus join each other very proximally, at the start of the trochlea carpalis. The carpometacarpus reaches the size of *Perdix perdix* (Linnaeus, 1758). The width of the proximal end of the carpometacarpus is 6.9 mm; the width of the metacarpale majus at midpoint is 2.2 mm; the width of the tarsometatarsus at midpoint is 2.9 mm.

Genus *Coturnix* Bonnaterre, 1791
Coturnix coturnix (Linnaeus, 1758)

Four skeletal elements have been assigned to the Common Quail: one cranial end of coracoides (QC12, K15b, z: 570–575), one

Fig. 2. *Francolinus francolinus*: (a) ventral aspect of the proximal end of one carpometacarpus. *Coturnix coturnix*: (b) dorsal aspect of one tarsometatarsus. *Cygnus* sp.: (c) dorsal aspect of the proximal part of the diaphysis of one carpometacarpus. *Pterodroma* sp.: (d) dorsal and (e) lateral aspects of the proximal end of a tarsometatarsus. *Crex crex*: (f) ventral aspect of the distal end of one ulna. *Otus scops*: (g) cranial aspect of the distal end of one tibiotarsus. *Columba* sp.: (h) dorsal aspect of one tarsometatarus. *Streptopelia* sp.: (i) dorsal aspect of the distal end of one tarsometatarsus. *Corvus ruficollis*: (j) ventral aspect of the distal end of one ulna. *Galerida cristata*: (k) caudal aspect of the proximal end of one humerus. *Lullula arborea*: (l) caudal aspect of the proximal end of one humerus. *Ptyonoprogne rupestris/Hirundo rustica*: (m) cranial aspect of the distal end of one humerus. *Sturnus* sp.: (n) caudal aspect of one humerus lacking its distal end. *Phylloscopus* sp.: (o) caudal aspect of one humerus with a partially broken crista bicipitalis. Bars to the right of the specimens equal 1 cm.

complete tarsometatarsus (QC09, M14c, z: 475–480) (Fig. 2b), one proximal end (QC09, M14a, z: 515–525) and one distal end (QC06, M14b, z: 520–525). This species is the smallest within the family. The facies articularis humeralis of the coracoid is proportionally shorter than in *Alectoris*, *Perdix*, and *Francolinus*. The processus acrocoracoideus is less developed than in the aforementioned taxa. The tarsometatarsus in quails is more slender than in partridges and francolins. The trochlea metatarsi II is less protruding internally than in the genera compared. The measurements of the metatarsi are in Table 2.

Table 2
Measurements (in millimeters) of some avian bones from Qesem Cave.

	Columba sp.	*C. coturnix*	*Sturnus* sp.
	Tarsometatarsus	Tarsometatarsus	Humerus
Maximum length	30.1	26.9	26.7–27.7 (n = 3)
Width of proximal end	7.4	4.8	8.5–8.8 (n = 4)
Width at midpoint	3.6	2.3	2.5–2.8 (n = 4)
Width of distal end	8.0	5.1–5.3 (n = 3)	6.3–6.8 (n = 3)

Order Anseriformes Wagler, 1831
Family Anatidae (Vigors, 1825)
Subfamily Anserinae Vigors, 1825
Genus *Cygnus* Bechstein, 1803
Cygnus sp.

A single partial bone is attributed to the genus *Cygnus*. It is the proximal part of the diaphysis of one carpometacarpus (QC13, F9c, z: 705–710) (Fig. 2c). The area of fusion of the ossa metacarpale majus and minus is preserved. The cross-section of the diaphysis is elliptical. The os metacarpale minus is considerably thinner than the os majus. The sulcus tendineus is shallow. In swans, the os metacarpale majus has the highest robustness in the family and shows light cranio-dorsal compression. The dimensions of the fragment found (dorso-ventral width of the shaft at midpoint: 8.6 mm; cranio-dorsal width at the same point: 6.5 mm) fall within the size range of current *Cygnus cygnus* (Linnaeus, 1758) and *Cygnus olor* (Gmelin, 1789), and the dimensions are larger than in *Cygnus columbianus* (Ord, 1815).

Order Procellariiformes Fürbringer, 1888
Family Procellariidae Vigors, 1825
Genus *Pterodroma* Bonaparte, 1856
Pterodroma sp.

This taxon is recorded by the proximal end of one tarsometatarsus (QC12, E16d, z: 625–630) (Fig. 2d,e). The genus is characterized by a broad and protruding hypotarsus, with a developed crista medialis hypotarsi. In lateral view, the crista medialis hypotarsi is triangular in shape, and its cranial edge is horizontal. Both cotylae are tilted dorsally and are situated at different levels. The eminentia intercotylaris stands out over both cotylae. The tuberositas musculi tibialis cranialis is absent. The maximum width of the proximal end is 6.7 mm.

Order Ralliformes (Reichenbach, 1854)
Family Rallidae (Reichenbach, 1854)
Genus *Crex* Bechstein, 1803
Crex crex Linnaeus, 1758

One distal end of ulna (QC12, H16b, z: 695–700) is attributed to this species (Fig. 2f). The cross-section of the shaft is round. The condylus dorsalis is short. The tuberculum carpale is notably small and orientated distally—it does not protrude ventrally. The condylus ventralis is of reduced dimensions. In distal view, the outline of the bone is triangular. The incisura tendinosa of the condylus dorsalis is fairly marked. The tuberculum carpale is smaller in *Porphyrio* Brisson, 1760, *Fulica* Linnaeus, 1758, *Porzana* Vieillot, 1816, and *Gallinula* Brisson, 1760.

Order Strigiformes Wagler, 1830
Family Strigidae (Gray, 1840)
Genus *Otus* Pennant, 1769
Otus scops Linnaeus, 1758

This species has been identified through one distal end of a tibiotarsus (QC08, N14c, z: 495–510) (Fig. 2g). Both condyles, in caudal view, are more rounded in Strigidae than in Tytonidae. In this genus, the incisura intercondylaris is deep and the sulcus extensorius is shallow. *Bubo* Duméril, 1810, *Strix* Linnaeus, 1758, and *Asio* Brisson, 1760, are composed of species of lager sizes than *Otus*. The width of the distal end of the tibiotarsus is 5.3 mm. The fossil shows relatively small condyles, smaller than in *Glaucidium passerinum* (Linnaeus, 1758). In this species and in *Aegolius funereus* (Linnaeus, 1758), the region of the shaft close to the condyles is relatively large, as in *Bubo* and *Asio*, but not in *Otus* and *Athene*. In this genus the incisura intercondylaris is very deep, contrary to what is seen in *Otus scops*.

Order Columbiformes (Garrod, 1874)
Family Columbidae (Illiger, 1811)
Genus *Columba* Linnaeus, 1758
Columba sp.

Five bones have been assigned to this species: one complete tarsometatarsus (QC09, M14b, z: 505–510) (Fig. 2h), the distal end and shaft of one tarsometatarsus of a juvenile individual (QC08), one proximal end of carpometacarpus (QC09, M14b, z: 505) that was severely damaged, one small fragment of a distal end of a humerus (QC09, M14b, z: 510–515), and one proximal end with part of the corresponding shaft of a juvenile humerus (QC12, L14a-d, z: 530–560). The morphology of the bones of the columbiforms is fairly distinctive. The genus *Streptopelia* Bonaparte, 1855, encompasses forms of smaller sizes than *Columba*. The measurements of the complete tarsometatarsus (Table 2) correspond to a *Columba* species of the size of *C. livia* Gmelin, 1789, or *C. oenas* Linnaeus, 1758.

Genus *Streptopelia* Bonaparte, 1855
Streptopelia sp.

One distal end of a tarsometatarsus (QC11, N14c, z: 550–555) is assigned to this genus (Fig. 2i). MNI: 1. In *Streptopelia* and *Columba* the cross-section of the shaft is flattened dorso-ventrally and rounded in Pteroclidae (*Syrraptes* Illiger, 1811, *Pterocles* Temminck, 1815). This bone is more robust in Pteroclidae than in *Streptopelia*. In this genus, the trochlea digitis II protrudes more medially than in *Columba*. The width of the distal end of the fossil is 5.2 mm.

Order Passeriformes (Linnaeus, 1758)
Family Corvidae Vigors, 1825
Genus *Corvus* Linnaeus, 1758
Corvus ruficollis Lesson, 1830

Six skeletal elements have been ascribed to this species: one distal end of an ulna (QC12, K15a, z: 560–565) (Fig. 2j), two spoiled distal ends of two tarsometatarsi (QC12, K14d, z: 580–585; QC12, L14a-d, z: 530–560), the distal end of one falanx 1 digitis pedis I (QC12, k14d, z: 580–585), and two final pedal phalanges (QC09, M14a, z: 515–520; QC12, J15d, z: 585–590). MNI: 2. The bones of Corvidae are fairly distinguishable from those of other families because of their roundness and robust, inflated look. The genus *Corvus* includes the larger forms of the family. The maximum width of the distal end of the ulna is 10.8 mm; the width of the distal end of tarsometatarsus is approximately 8.3 mm; the maximum length of the distal pedal phalanx is 15.1 and approximately 16.0 mm. The value of the distal width of the ulna in the fossil matches *Corvus ruficollis*. It is lower than in *Corvus corax* Linnaeus, 1758, including *C. pliocaenus* (Portis, 1889) and *C. antecorax* Mourer-Chauviré, 1975, and higher than in *C. corone* Linnaeus, 1758 and *C. frugilegus* Linnaeus, 1758. The remaining bones have been ascribed to the same taxon.

Family Alaudidae Vigors, 1825
Genus *Galerida* Boie, 1828
Galerida cristata (Linnaeus, 1758)

One proximal end (damaged) of a humerus (QC09, M14b, z: 505–510) is assigned to this species (Fig. 1). MNI: 1. The humerus in alaudids has a fossa pneumotricipitalis divided by the crus dorsale into a dorsal and a ventral part. The dorsal part is shallow and reduced. The crista deltopectoralis is long and has a straight contour. The tuberculum ventrale is underdeveloped. The ventral part of the fossa pneumotricipitalis is pneumatized in most of the specimens examined, although not in all. The crista bicipitalis is relatively small. In *Melanocorypha* Boie, 1828, the dorsal surface of the fossa pneumotricipitalis is deeper and the crista deltopectoralis is shorter than in the other species within the family. The latter feature is shared with *Eremophila* Brown, 1810. In a cranial view, the crista bicipitalis has a sharp appearance in *Alauda arvensis* Linnaeus, 1758. In *Lullula* Kaup, 1829, *Galerida*, *Melanocorypha,* and *Eremophila*, such a crista is more rounded. In *Calandrella* Kaup, 1829, the crista has an intermediate shape. *Galerida* reaches higher sizes than *Lullula*, *Calandrella,* and *Eremophila*. The maximum width of the proximal end is 7.4 mm.

Genus *Lullula* Kaup, 1829

Lullula arborea (Linnaeus, 1758)

Two proximal ends of right humeri (QC09, G16a, z: 585–590; QC09, H16c, z: 625–630) are attributed to this species (Fig. 2l). MNI: 2. See comments on morphology in the previous paragraph on *Galerida cristata*. The crista deltopectoralis is longer in *Lullula* than in *Calandrella*, and in this species the humerus is less robust. The maximum width of the proximal end is 6.6 and 6.9 mm.

Family Hirundinidae Vigors, 1825

Genus *Ptyonoprogne* (Reichenbach, 1850)

Genus *Hirundo* Linnaeus, 1758

Ptyonoprogne rupestris (Scopoli, 1769)/*Hirundo rustica* (Linnaeus, 1758)

One distal end of a humerus (QC12, J14d, z: 585–590) (Fig. 2m) is attributed with doubts to two hirundinids. MNI: 1. The processus flexorius is very robust and protrudes distally. The epicondylus ventralis is clearly distinguishable. The condylus dorsalis is far more developed than the condylus ventralis. The maximum width is 4.7 mm. The morphology of this fragment of humerus is common to all the members in the family. *Delichon urbica* (Linnaeus, 1758) and *Riparia riparia* (Linnaeus, 1758) are smaller, and *Hirundo daurica* (Linnaeus, 1771) has a more slender processus flexorius.

Family Sturnidae Rafinesque, 1815

Genus *Sturnus* Linnaeus, 1756

Sturnus sp.

There are three complete humeri (QC09, M14d, z: 495; QC12, M14/15, z: 455–460; QC09, M14b, z: 495–505) attributed to this genus and another lacking its distal end (QC09, M14b, z: 505–510) (Fig. 2n). Measurements are given in Table 2. The humerus has a crista deltopectoralis that is short, although well developed, and of curved contour. The tuberculum ventrale is broad. The fossa pneumotricipitalis is divided in two deep fossae. In *Turdus* Linnaeus, 1758, the crista deltopectoralis is longer—stretched out distally—than in *Sturnus*. In *Turdus*, the ventral part of the fossa pneumotricipitalis shows a deeper excavation than in *Sturnus*.

Family Sylviidae Vigors, 1825

Genus *Phylloscopus* Boie, 1826

Phylloscopus sp.

One complete humerus (QC08, M14b, z: 500–505) is ascribed to this species (Fig. 2o). Its distal end is partially eroded. The bone bears the triangle-shaped crista deltopectoralis and the flat caput humeri typical of the family. This species is the smallest in overall size. The maximum length of the bone is 15.4 mm; the maximum width of the proximal end is 5.4 mm.

Aves indet.

A total of twenty-three bone fragments of small birds have not been identified because of the absence of diagnostic features.

4. Discussion

The avian remains studied here have been collected in the lower part of the upper sequence and in the upper part of the lower sequence of the stratigraphic column of Qesem Cave. This avian assemblage can be viewed as a sample of the local ornithocenoses, corresponding to a relatively restricted span of time, around 300 ka. However, a specific characterization of the avian remains in a cultural context will be presented separately.

4.1. Paleoenvironmental traits

The set of taxa found at Qesem points to the existence of a wide range of habitats near the cave during the time humans were using it. Four out of the fourteen avian taxa identified are typical rocky dwellers (Table 3), which likely nested in cracks and hollows in the cave and its surroundings. The Common Quail and the two alaudids indicate the presence of open areas. The Brown-necked Raven also indicates the existence of open areas, as this bird nests on cliffs and, occasionally, in trees, although its habitat ranges from savanna to desert. The warblers and the Eurasian Scops-Owl are connected with forested areas, parkland, tree patches, or woodland. After evidence was found of *Dama*, *Cervus* and *Sus scrofa* (Stiner et al., 2009; Blasco et al., 2014), forested habitats with undergrowth have been considered a habitat. The warblers need a scrub layer or bushland. The occurrence of the Starling is compatible with a variety of landscapes, from rocky and open areas to parkland. The Black Francolin lives in the scrubland and in bushland, in the vicinity of bodies of water. The Corncrake also lives near water but avoids standing water; it spreads through meadows covered by lush vegetation. A dense plant cover, at least locally, was already suggested by Smith et al. (2013) owing to the abundance of chamäleons in the record of Qesem Cave. The unexpected coincidence of a swan and a petrel at an inland point in Israel may indicate the existence of a lake or a body of still water.

Table 3
Avian taxa found in Qesem Cave, related preferential habitats and phenological status.

Taxa	Preferential habitats	Phenological status
Francolinus francolinus – Black Francolin	scrubs, bushland, scattered vegetation; not far from water.	Resident. Common.
Coturnix coturnix – Common Quail	Open country.	Summer and winter visitor. Rare.
Cygnus sp. – Swan	Lakes and ponds.	*C. olor* is a rare winter visitor. *C. cygnus* is accidental.
Pterodroma sp. – Petrel	Mostly, marine; inland bodies of water.	Accidental.
Crex crex – Corncrake	Meadows and lush vegetation.	Passage migrant on breeding season. Rare.
Otus scops – Eurasian Scops-Owl	Woodland or parkland.	Winter and summer visitor. Common in Spring and Summer.
Columba sp. – Pigeon	Rocky or wooded areas.	*C. livia* is resident and common. *C. oenas* is winter visitor and common.
Streptopelia sp. – Turtle-Dove, Laughing Dove or Collared-Dove	Rocky areas and scrubland.	Two species are resident, other one is a summer visitor. Common.
Corvus ruficollis – Brown-necked Raven	Rocky and arid areas.	Resident. Common.
Galerida cristata – Crested Lark	Open country and arid areas.	Resident. Common.
Lullula arborea – Woodlark	Woodland edges and open country.	Visitor. Common in winter. Rare in summer.
Ptyonoprogne sp./*Hirundo rustica* – Rock or Crag-Martin or Barn Swallow	Rocky areas and cliffs.	*Pt. rupestris* is a winter visitor and common. *Pt. fuligula* and *H. rustica* are resident and common.
Sturnus sp. – Starling	Parkland, open or rocky areas.	*St. vulgaris* is a winter visitor, common. *St. roseus* is a passage migrant, very rare.
Phylloscopus sp. – Warbler	Woodland, tree patches, bushland.	Species within this genus are recorded currently during passage on yearly migration. Relatively common.

Consequently, there must have been a complex pattern of habitats near Qesem Cave during the span of time recorded, which is also the result of a study of the microfaunal assemblage by Maul et al. (2011, 2016), since the authors find grassland, woodland, and rock dwellers. Both of the abovementioned studies and the present study agree that the vegetation cover was more extensive than at present.

The Early Pleistocene site of 'Ubeidiya constitutes by far the largest Quaternary record of avian remains in the Middle East, comprising about 50 taxa (Tchernov, 1968, 1979, 1980). A large number of them are aquatic and riparian birds, typical of lakes, swamps, and still water, with thick vegetation close to or in the water. The rest of the species can be assigned to grassland or open country, parkland, and rocky habitats. According to Simmons (2004) data –percentages on species by habitat-the Acheulean deposit of Gesher Benot Ya'aqov has a relatively high percentage of birds directly connected to bodies of water. Almost three quarters out of the 16 taxa are aquatic, the rest represents a group of grassland habitats. The Acheulean layers of Umm Qatafa contain over 35 avian taxa with different habitat requirements (Vaufrey, 1931; Tchernov, 1962, 1979). In addition to the rock species, there are representatives of more or less open and arid terrains and birds that live in parkland or tree patches with undergrowth. Only two species—*Gallinula chloropus* and *Crex crex*—are reliable indicators of nearby bodies of water. The small group of avian species found at the site of Zuttiyeh—rock dwellers or linked to a wide range of habitats—does not offer any valuable insight into the habitats occurring in this region during the Middle Pleistocene. Throughout the region, in localities with later lithic industries, the number of waterfowl is significant, with some exceptions. The rock shelter of Ksar 'Akil (Lebanon) has yielded a small collection of avian remains (Kersten, 1991), consisting of a handful of bones of cormorants and anatids. However, aquatic taxa are assigned to Epipaleolithic-bearing beds; the Mousterian layers have only provided diurnal raptors and passerines (Hooijer, 1961). The Mousterian-bearing sediments of Kebara Cave show nearly 50 taxa (Tchernov, 1962, 1979), although some degree of reworking cannot be dismissed (see Pichon and Tchernov, 1987). About 10 of these taxa are indicators of bodies of water and humid zones. Most of the birds recorded at this cave lived in open areas, and a few in the undergrowth. In the Early Epipaleolithic of Ohalo 2—dated to around 23 yBP and located close to the Galilee lake—Simmons and Nadel (1998) identified a wide assemblage of birds. Most are waterfowl and wandering species, which likely found suitable conditions in a lake or ponds nearby. The others are predominantly connected to open areas.

The presence of the group of avian taxa characteristic of water bodies and river banks is a constant in the archeological record of the Early and Middle Pleistocene in which a sufficient sample of the local paleornithocenoses has been recorded. Finlayson et al. (2011) already noted that wetlands, including marshes, lakes, and lagoons, are closely associated with human occupation sites in the Paleolithic of Eurasia. In the Late Pleistocene, however, the concurrence of hominins and aquatic birds that would indicate the existence of large bodies of water is not as clear.

4.2. Phenology and geographical distribution

Currently, *Cygnus olor* (Mute Swan) is a rare winter visitor of irruptive character. An irruption of birds is a migration or movement of large numbers of individuals to areas further south than normal ranges. The primary cause of irruptions is unavailability of food in winter, or in usual winter quarters in the case of migratory species. It usually happens in harsh winters, and prompts the birds to move further south (Hochachka et al., 1999; Bonter and Harvey, 2008). *Cygnus cygnus* (Whopper Swan) is extremely rare in Israel today. *Coturnix coturnix* (Common Quail) is observed infrequently during its summer and winter movements and has the current status of rare visitor (Table 3). Occurrences of petrels (*Pterodroma* sp.) are currently very scarce. These birds are mostly circumscribed to the southern hemisphere and have a marine lifestyle. The record of such birds at Qesem Cave can be indicative of harsh climatic conditions in marine environments. *Crex crex* (Corncrake) is likewise a rare bird in this region, seen on passage while migration. *Otus scops* (Eurasian Scops-Owl) is a visitor species during winter and summer that is common in breeding season. The four bones assigned to *Columba* sp. can correspond to *C. livia*, *C. oenas*, or to both. *Columba livia* (Rock Dove) has the status of resident and is very common. *Columba oenas* (Stock Dove) is also common, although as a winter visitor. Three species within the genus *Streptopelia* are part of the current ornithofauna of Israel. The Eurasian Collared and the Laughing Doves are resident; the European Turtle Dove occurs in the breeding season. All three are common. Among the passeriforms identified, *Corvus ruficollis* (Brown-necked Raven) and *Galerida cristata* (Crested Lark) are both common and residents in Israel today. The other alaudid recorded, *Lullula arborea* (Woodlark), is a common winter visitor, albeit rare in summer. As for the three hirundinids that could be alternatively recorded in Qesem Cave, *Ptyonoprogne rupestris* (Crag Martin) is a common winter visitor, and *Pt. fuligula* (African Rock Martin) and *Hirundo rustica* (Swallow) are residents and likewise common (Table 3). Both starlings have different statuses. *Sturnus roseus* (Rose-colored Starling) is very rare and seen on passage during its migration. *Sturnus vulgaris* (Common Starling) is a common wintering species. The warblers (*Phylloscopus* spp.) are relatively common during their migration. The array of resident birds found at Qesem Cave refers to the current population today, which may be understood as a consequence of prevailing Mediterranean climactic conditions. However, there are some differences with regard to the group of migrant and visitor species.

Within the avian assemblage of Qesem Cave, there are four taxa that would be considered today as rare or accidental (*Coturnix coturnix*, *Cygnus* sp., *Pterodroma* sp., and *Crex crex*), representing one third of the total. Taking into account the low probability of a single individual becoming part of the fossil record, it seems unlikely that these taxa had been that uncommon in the past. It is worth noting that all of the mentioned taxa correspond to migrant birds, none of them having the status of resident in the extant regional fauna. Assuming that these taxa exhibited migratory behavior in the past, their presence in the Middle East would imply different climatic or environmental conditions in their respective areas of origin. The appearance of breeding (*Crex crex*) and wintering (*Cygnus* sp.) migrants would entail the nearby existence of permanent water bodies throughout the year.

The resident species—non-migratory in this case—are a key to reconstructing the climate and local environmental framework in the past as they fit in the biotic and abiotic conditions throughout the year and are an expression of the biogeographic interactions. The resident taxa recovered in the deposit still live in Israel and they can be considered as a consistent sample of the eastern Mediterranean avian fauna of the Quaternary.

During the Pleistocene, the presence of several non-migratory birds, whose geographical distributions were confined to northern Europe, has been recorded in fossil localities from the south of the continent. This fact has been explained as northern avian irruptions during the Quaternary cold phases. This kind of species has not appeared so far either in Israel or in northern Africa, in agreement with the notion of the steady Mediterranean refugia (Sánchez Marco, 2004).

5. Conclusions

The Qesem Cave assemblage of bird bones has not revealed any extinct avian species. The non-migratory birds found there belong to the eastern Mediterranean avian fauna. The avian assemblage of Qesem Cave did not include any non-migratory birds that presently live in more northern or southern latitudes. Thus, during the time recorded at the cave, the climatic regime in this region was not much different from that of the present. On the other hand, the migratory taxa found in the cave are considered rare or accidental at present, and this may indicate a different climatic regime or different environmental conditions than currently exist in the territories where these birds spend the rest of the year. In this sense, the find of *Cygnus* and the record of *Pterodroma* in inland water bodies could be connected to harsh and chilly winters at latitudes farther south and north.

Close to Qesem Cave, there would have been bodies of still water, possibly around the large springs to the southwest. Another biotope would be a system of lagoons along the coast to the west of the site, consistent with a series of consolidated sand (*kurkar*) ridges and swampy trough basins between the ridges to the west of the cave (present along the coast up to the late 19th and early 20th century) that provided rich riparian vegetation throughout the year. Other biotopes included woodland or tree patches, bushland or undergrowth, and open lands, apparently with more extensive wooded coverage than at present. The Qesem Cave finds seem to correspond with the tendency of humans in the Early and Middle Pleistocene to occupy and use rich habitats near large bodies of water, as indicated by the presence of some waterfowl linked to this kind of aquatic environment.

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